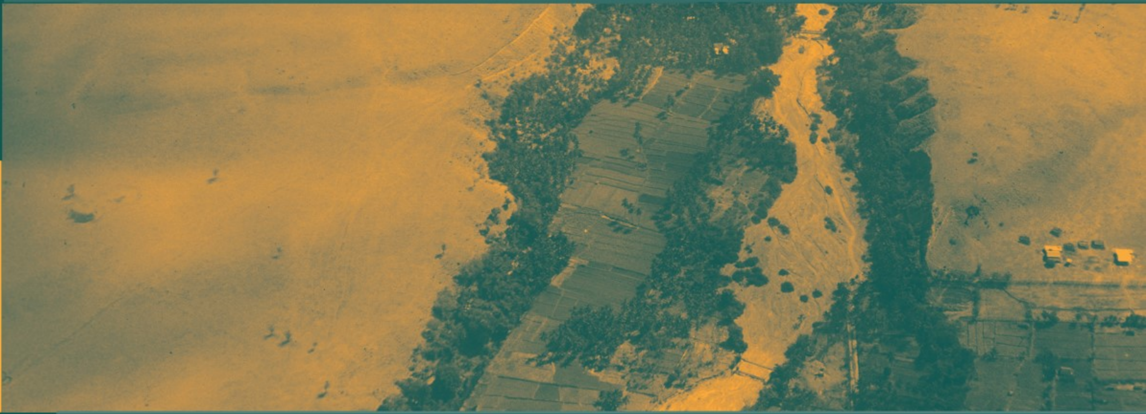
David L. Hawksworth
Alan T. Bull
Editors

TOPICS IN BIODIVERSITY AND CONSERVATION



Human Exploitation and Biodiversity Conservation

Springer

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TOPICS IN BIODIVERSITY AND CONSERVATION

Volume 3

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Edited by

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and

Alan T. Bull

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Cover Photo: Palu Valley in Sulawesi, Indonesia, showing the contrast between arid and over-grazed land and rich river valley agriculture.
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Introduction

Human exploitation of biodiversity and conservation: a question of balance?

The sustainable use of the components of biodiversity is one of the three key objectives of the 1992 Convention on Biological Diversity[1]. But this far from a new idea. The need to strike a balance between human utilization and conservation is at the heart of the UNESCO Man and the Biosphere (MAB) Programme launched in 1971; there are now 482 Biosphere Reserves in 102 countries,"living laboratories for people and nature". Is not *the* key to conserving biodiversity long-term securing the commitment of those who use it? Local peoples are the front-line of the exploitation *vs.* conservation conflict, whether in Amazonas, Kalimantan, the Pacific North-West, or the Camarge. Sound conservation practice has to be recognized as beneficial and implemented by the people who use it from subsistence farmers to skiers and pharmaceutical bioprospectors. Fortunately, there is now a hightened concern over biodiversity conservation and the state of the environment than ever before. Voluntary groups undertake work to protect endangered species, create and maintain new biodiversity reserves, and prevent the destruction of natural habitats. But, more critically, the numbers of conservation- and environmentally-aware has passed a"tipping point" and is influencing policy from the global to the local level.

At the same time, indigenous peoples utilize enormous numbers of plants, fungi, and fish particularly for foods and medicines. This has to be allowed for in conservation planning, and is a source of potentially new food sources. The world's staple foods, of which potatoes and rice are prime examples, were first exploited by indigenous groups. Yet over-exploitation can drive species towards extinction, from tigers in south-east Asia to North Sea Cod, the South Indian Lady's Slipper orchid and Giant Pitcher plants, and even perhaps to Matsutake mushrooms. Use of particular species has to be monitored and controlled, and fortunately such cases are increasingly the subject of international agreements, for example under the Convention on Trade in Endangered Species of Wild Fauna and Flora (CITES).

The range of issues of concern on this theme is enormous, and this issue gathers together a wide range of papers submitted to *Biodiversity and*

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[1] The other two are the conservation of biological diversity, and the equitable sharing of benefits

Conservation, contributions addressing diverse aspects of front-line human involvement in biodiversity exploitation and conservation. Collectively, they provide a snap-shot of on-going action and state-of-the-art research, and as such it is envisaged that having these together in one number of the journal will be particularly convenient to those running courses including biodiversity and/or conservation issues, and to advanced students and researchers working in related fields. The scope of the included papers embraces cases involving, birds, crop plants, invertebrates, land use changes, livestock, mammals, marine organisms, and medicinal plants. Issues related to the importance of gardens, hedges and green lanes, housing developments, hunting, invasive species, local community involvement, sacred groves, socioeconomic factors, and trade. Examples presented here come from studies in 17 countries including ones in Africa, Asia, Europe, and North and South America.

In my experience, specialists on one group of organisms can find solutions or approaches to problems they are addressing by looking at the methods used in other groups of organisms. This compilation provides an opportunity to see a wide range of original papers in which methodologies that may be pertinent to, or have analogues with, research in another, and hopefully stimulate research in this critical aspect of the conservation of biodiversity. Advances in science paradigms in a particular field are commonly a result of knowledge transfer from one area to another, and I learnt long ago that this is especially relevant in issues related to biodiversity and conservation studies where so many papers are embedded in organismal focussed journals. Indeed, this is why I have found *Biodiversity and Conservation* of such value to me personally in my own work on fungi since it was launched in 1992.

The papers included here on topical cases will I hope stimulate your thoughts and future work programmes. Collectively such work is critical to attainting a sustainable balance between the conservation and sustainable exploitation of biodiversity, and ultimately a positive prognosis for the long-term prospects for human societies on planet Earth.

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Impacts of demographic and socioeconomic factors on spatio-temporal dynamics of panda habitat

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Abstract Demographic and socioeconomic factors of individual people and households may have significant impacts on their environment, which in turn may affect the spatio-temporal dynamics of wildlife habitat and local biodiversity. In the Wolong Nature Reserve (China) for giant panda conservation, local households live a rural lifestyle that has caused forest degradation by activities such as cutting fuelwood. Based on field data and a spatial agent-based model that integrates cross-scale data and cross-discipline models, we examine how panda habitat would respond to changes in a set of socioeconomic and demographic factors individually, and under a conservation scenario and a development scenario (setting factors to values that would benefit or degrade habitat, respectively). The model simulates each family member's life history (including needs, attitudes, and activities) and the household agents' interactions with each other and with the environment through their activities over 30 years. Our simulations show that among all the factors under consideration, providing cheaper electricity and changing the age structure through increasing marriage age or prolonging the interval between consecutive births could change habitat quantity significantly (at $\alpha = 0.05$ level); and the differences in panda habitat between the two scenarios escalate over time. In addition to benefiting local policy-making, this study provides a new approach to studying human–environment interactions from the perspectives of individual needs and decisions.

Introduction

Human activities have radically altered the earth's surface, oceans, and atmosphere, especially over the past 200 years (Turner 1990), which reminds the current generation of the warning by Malthus that unrestrained population growth would eventually be limited by fixed natural resources (Malthus 1798). To address this serious situation, many researchers have called for efforts to study effects of human activities upon the environment. In particular, changes in human demographic and socioeconomic factors (e.g., public policy) have exerted great impacts on the environment and need to be paid more attention (e.g., Pebley 1998; Liu et al. 1999a; Liu 2001; Lambin 2003). Pebley (1998) suggested that environmental issues (such as effects of demographic variables on environmental outcomes) become one of the mainstream topics in demography rather than peripheral topics as in the past.

An increasing number of researchers, including ecologists, geographers, sociologists, and demographers, have conducted studies to understand human–environment interactions (e.g., Liu et al. 1999a; Perz 2001; Axinn and Barber 2003). However, there are few studies of the impacts of socioeconomic and demographic factors on the environment at an individual or household level in a spatially explicit manner, partially due to the complexities of many social or individual choices in the coupled society-biodiversity systems (United States National Research Council 1999). Such systems usually have variant socioeconomic, demographic, and/or biodiversity factors, coupled with many nonlinear relationships and heterogeneous spatial structures.

Drastic socioeconomic and demographic changes that have occurred in China over the last 2 decades may provide excellent opportunities (sometimes challenges) for researchers focusing on human–environment interactions. First, China has implemented an increasingly strict policy of family planning to curb its rapidly growing population. The 'later, longer, and fewer' (wan xi shao) campaign, implemented since the late 1970s, encouraged (required in some sense) couples to bear children at an older age (later), prolong the interval between two consecutive births if more than one child is allowed (longer), and have as fewer children as possible (fewer). This plan later developed into the more strict one-child policy (Feng and Hao 1992). As a result, China's total fertility rate (TFR) dropped greatly from 3.0 in 1979 (Hussain 2002) to 1.8 in the early 1990s, and could be as low as 1.6 in the near future (Wong 2001). Due to the big population base, China's total population reached 1.24 billion in 2000 (Liang and Ma in press) in spite of this decreasing fertility.

In addition to changes in population size, China's population structure has changed substantially, characterized by a decreased proportion of children (0–14) and an increased proportion of working-age (15–64 years old) groups over the past 3 decades (Hussain 2002). In parallel with this trend, another important phenomenon is the decline in household size, which has significant implications because smaller household size would cause higher per capita resource consumption (Liu et al. 2003a). Traditionally, Chinese people have been accustomed to a lifestyle of many generations under one roof (Liu et al. 1999a, 2001; An et al. 2003a), but this tradition has been increasingly challenged by the younger generation. In rural areas of China, the patrilineal extended family is still the prevailing order, and the majority of the elderly people tend to live with their children, with sons in particular (Cooney and Shi 1987). The research by An et al. (2003a), however, has shown that though the young adults care about the adverse effects associated with leaving their parental homes (such as housework and taking care of young children), many of them still prefer to live independently as long as resources (land and timber in particular) allow them to do so.

As the Chinese economy grows rapidly, cities continue to have a rising demand for migrant labor, resulting in a rapid rise of floating population (temporary migrants who stay at their places of destination over 6 months without permanent household registration status) that flows mostly from rural areas to coastal regions (Liang 2001). The floating population is estimated to be over 79 million in 2000, accounting for 6.34% of China's total population (Liang and Ma in press). On the one hand, this type of migration has provided a timely outlet for rural surplus labor and an opportunity for many farmers to earn much higher incomes than their original subsistence farming. On the other hand, it has led to a separation of temporary migrants' actual residence from their de jure residence (Yang 2000), which may affect both the destination and origin communities in many aspects such as environmental quality.

All the above-mentioned facts, to varying degrees, may have implications for biodiversity conservation. We are interested in how changes in some demographic features (e.g., age structure, fertility) and socioeconomic factors in a specific area could lead to changes in local biodiversity over time in a spatially explicit manner. A piecemeal treatment is obviously not effective because the underlying mechanisms and interrelationships among different subsystems are ignored or not paid sufficient attention. On the contrary, it is necessary to integrate various parts together and consider the interactions among various systems while developing policies or taking actions for conservation purposes. In this context, the questions of interest in this study include: (1) What demographic/socioeconomic factors would have significant impacts on the dynamics of local biodiversity? (2) Given changes in one factor or a combination of factors, how would local biodiversity respond accordingly over time and space?

Methods

Study site

An excellent site for studying these issues is the Wolong Nature Reserve (Figure 1). Designated in 1963 with an area of 200 km^2 and expanded to approximately 2,000 km^2 in 1975, Wolong Nature Reserve has a human settlement comprised primarily (approximately 75%) of Tibetan residents. The giant panda (*Ailuropoda melanoleuca*) has declined substantially in the reserve from 145 animals in 1974 (Schaller et al. 1985) to 72 in 1986 (China's Ministry of Forestry and World Wildlife Fund 1989) partly due to serious habitat degradation resulting from human deforestation. In addition to dislodging pandas from human residence areas, local inhabitants cut wood from surrounding forests for cooking and heating their households, while pandas depend on most of these forests as cover, shelter, and their understory bamboo as staple food (Liu et al. 2001). The past two decades have witnessed a continued

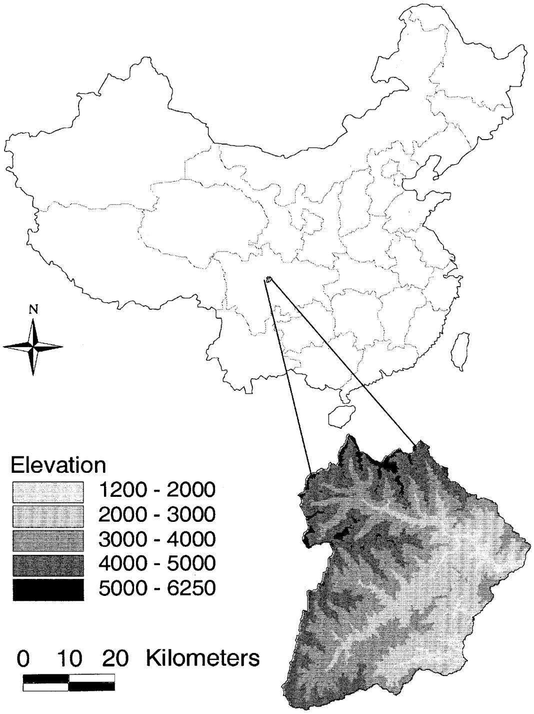


Figure 1. The location and elevation of Wolong Nature Reserve in China. The unit of elevation is meter.

increase in annual fuelwood consumption (from 4,000 to 10,000 m^3), which has caused a reduction of over 20,000 ha of panda habitat (Liu et al. 1999a). Panda habitat is used as an indicator of local biodiversity because over 2,200 animal/insect species and 4,000 plant species cohabit with the giant pandas in the reserve (Wolong Nature Reserve 1987).

The human population has increased at a rapid rate of 69% (from 2560 people in 1975 to 4320 people in 1998) despite the nationwide 'wan, xi, shao' campaign and the later one-child policy. Wolong Nature Reserve, as a rural area mostly composed of minority groups and a 'flagship' reserve in China, enjoys some special policies. For instance, it allowed three children per couple, especially in some remote areas in the reserve. Its fertility was 2.5 between 1975 and 1999 (Liu et al. 1999a). However, recent years have seen a draconian policy of two children per couple, even for minority groups in remote areas. Paralleling the increase in population, the number of households has escalated at an even higher rate (124%, from 421 households in 1975 to 942 households in 1998). The population age structure in Wolong, as in the entire country, has been characterized by an increased proportion of working-age (Figure 2a and b). It is reported that the more young adults live in Wolong, the more forest may be cut down and more habitat may be degraded (Liu et al. 1999a).

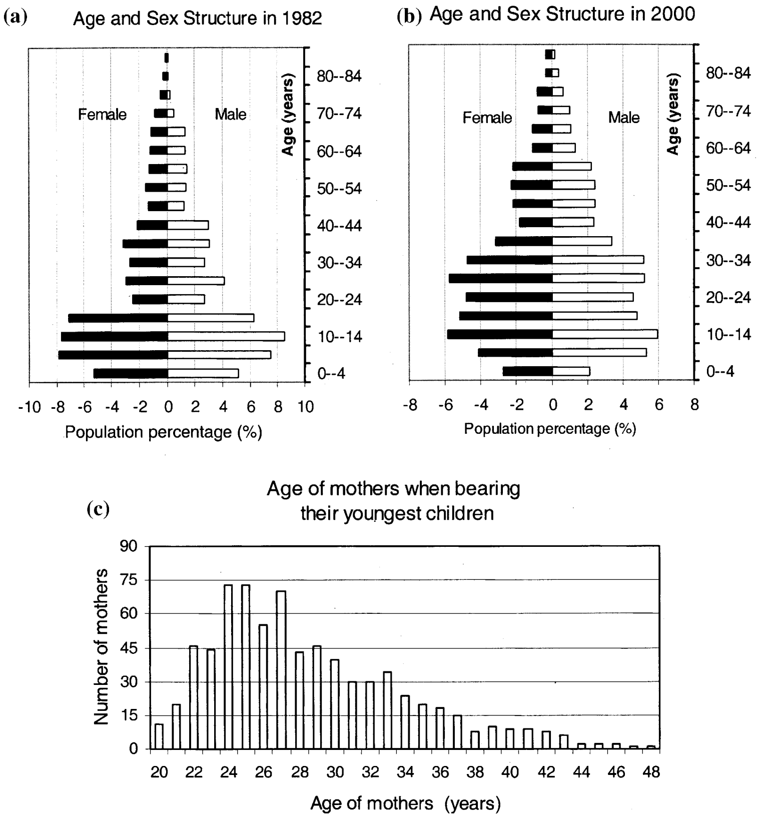


Figure 2. (a) Age and sex structure in 1982. (b) Age and sex structure in 2000. (c) Number of mothers who give birth to their youngest children at varying ages.

Temporary migration has occurred in Wolong as in other rural areas, characterized by the following facts. First, there are much fewer local residents (compared to other regions) who have temporary jobs in cities, which may arise from its special standing as a nature reserve. For instance, local people enjoy some special benefits (subsidies and lower taxes) and have less motivation to migrate to cities. Second, the rapidly growing local eco-tourism (centered on watching pandas in the reserve's breeding center) has provided some job opportunities for local residents. For instance, some young people work in local restaurants, some sell tourism souvenirs, and some collect Chinese medicine herbs and sell them to tourists. Last, most of the temporary workers with jobs in cities come back for the Chinese new year (spring festival), and some to help in agriculturally busy months. Therefore, these types of people are still considered as local population in this study because our major concern is the use of resources (land and forest in particular), and these people are still entitled to land and participate in most of the local resource use activities such as fuelwood collection and farming.

Some people (including a portion of these temporary workers) marry people in cities or other rural areas and move out permanently. This is the major form of out-migration in Wolong. Another form of out-migration is through young people's education: when young people who go to colleges or technical schools find jobs in cities after graduation, they settle down elsewhere (Liu et al. 1999a). According to Liu et al. (2001), elder people in Wolong do not want to relocate due to various reasons such as lack of skills to make a living in other areas and an inability to adapt to the outside environment. However, they encourage their children or grandchildren to emigrate through obtaining higher education. On the other hand, a small number of outside people move into the reserve each year and obtain permanent residence through marriage.

The local residents follow a rural lifestyle, characterized by satisfying their subsistence needs directly from, forests and cropland. They grow potatoes and corn primarily for pig fodders, and raise pigs for consumption and sale to tourists. Because of their belief that pig fodder should be well cooked prior to feeding pigs, they use a large portion of their fuelwood to cook pig fodder each year. Electricity, the likely substitute for fuelwood, is subject to problems such as relatively high price, unstable quality, and some degree of safety concerns. Our study of switch probabilities under different socioeconomic conditions shows that lowering price, increasing voltage, and decreasing outage frequency can encourage local residents to use electricity as a substitute for fuelwood, thus reducing forest degradation (An et al. 2002).

Model

With an excellent study site and a wealth of data (see Section 'Data preparation and integration'), we have developed an Integrative Model for Simulating

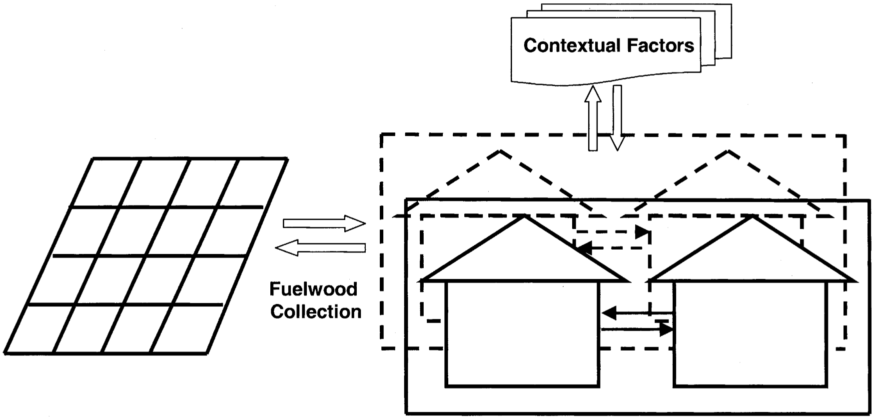


Figure 3. Model structure of IMSHED (modified from An et al. 2003b).

Household and Ecosystem Dynamics (IMSHED; see An et al. 2003b), which studies many complexities in the coupled human–environment system of Wolong by integrating agent-based modeling (ABM), traditional equation-based models, and geographic information systems (GIS). ABM is a methodology that predicts or explains emergent phenomena by tracking multiple microlevel 'agents' that constitute or at least impact the system behavior observed at higher levels (Jiang and Gimblett 2002). Agents, usually with some degree of self-awareness, intelligence, autonomous behavior, and knowledge of the environment and other agents, adjust their own actions in response to changes in the environmental or other agents' behavior (Lim et al. 2002).

The model structure is illustrated in Figure 3. IMSHED views individual persons, households, and land pixels as discrete agents or objects. The layer of dashed households in the dashed box represents households in the Wolong landscape at a past time, while the layer of solid ones represents households in the same landscape but at a later time (our introduction focuses on this layer). All the existing households come from the past and will move into the future, and many events (listed below) could happen during this process.

Birth and death

Based on the current family planning policy (2.0 children/couple) and our field observations (e.g., many couples prefer more than 2 children, but usually not more than 5), we set the average fertility to be 2.5 children/woman, while allowing couples to have 0, 1, 2, 3, 4, and 5 children with varying probabilities (for details see An et al. 2003b). When a specific female under consideration reaches a certain age (22, the average age at first marriage; see Hussain 2002) and finds a spouse (see Marriage below), she can give birth to a number of children (the number set by fertility as mentioned above) at appropriate times: the birth time of her first child is set by a parameter first kid interval, and the birth time of her other children (if possible) is set by a parameter birth interval (the time between two consecutive children).

People in Wolong at different age groups face different mortality rates (An et al. 2001). If the random number generator creates a number smaller than mortality rate corresponding to the age group that the person belongs to, he/she dies; otherwise the person survives and moves to the next year.

Marriage

Marriages occur when people reach 22 or above with a decreasing probability as they become older. When a female or male chooses to marry a person within the reserve, the resultant household location differs, and the specific rules are explained later in 'Household dynamics'. On a yearly basis, all the people are categorized into four groups: (1) young group for those under 22 years old and unmarried people (males and females), (2) single male group for all single males over 22 years old, (3) single female group for all single females over 22 years old, and (4) married group for all females and males who have spouses with them.

Migration

Based on the migration situation as mentioned in Section 'Study site', we consider three types of migrations: (1) local people marry people outside the reserve (usually people in richer areas) and move out permanently, (2) people outside the reserve marry local people and move into the reserve, and (3) young people go to college and reside elsewhere after graduation. Other types of migrations into Wolong are not allowed by law and local policy to conserve the giant panda. We use stochastic processes to control the number of out-migrants and in-migrants: if the random number generator produces a number smaller than any of the rates below in a given year, then the associated event would occur for that specific person under consideration.

The following rates control migrations in the model. (1) College attendance rate: the ratio between the number of people who go to college and the total number of people between 16 and 22 years of age in a given year. (2) Female marry-out rate: the ratio between the number of females between 22 and 30 years old who move outside the reserve through marriage and the total number of females between 22 and 30 years old in a given year. We use 22 as the lower limit because it is the average marriage age, and 30 as the upper limit because most of the people who migrate through marriage are young people not older than 30 years old (An, field observations). Some females marry people outside the reserve through a social network as mentioned above, e.g., introduction by relatives who migrated earlier. This is also true for other migration types as follows. (3) Male marry-out rate: the ratio between the number of males between 22 and 30 years old who move outside the reserve through marriage and the total number of males between 22 and 30 years old in a given year. (4) Female marry-in rate: the ratio between the number of males of 22 and 30 years old who bring outside females into the reserve through marriage and the total number of males of 22–30 years old in a given year. (5) Male marry-in rate: the ratio between the number of females of 22 and 30 years old who bring outside males into the reserve through marriage and the total number of males of 22–30 years old people in a given year.

Household dynamics

A parameter leave-home intention controls whether a 'parental-home dweller' establishes a new household after marriage. The parental-home dweller may be (1) a male who has no siblings, (2) a male who has only female siblings, (3) a male who is the youngest male sibling among brothers, (4) a female who has no siblings, or (5) a female who has only female siblings and is the youngest among these female siblings. We do not consider such situations as single-mothers or divorces because they are not that common in Wolong (An, field observations). Leave-home intention is determined or influenced by a set of psychosocial factors, including resource availability (primarily land and timber) and demographic structure of the parental household (An et al. 2003a). If a person is not a parental-home dweller, he/she leaves the parental home and establishes his/her own household after marriage; if he/she is, he/she does so with the probability specified by the parameter leave-home intention (with the default of 0.42 based on our field data). The new household is located in the vicinity of the parental household (the distance between the two households is controlled by a parameter with the default of 800 m) with appropriate elevation and slope (not over 2610 m and 37°, respectively, based on our field data).

The model updates the household dynamics (size and structure) at a yearly basis. Household size increases or decreases when people move into or out of the household under consideration through processes as described above (e.g., birth, death, move-in or move-out through marriage). When the number of people in a household becomes zero (for reasons like death and out-migration), the corresponding household becomes dissolved and removed from the model.

Resource demand

Given household structure and dynamics thus determined at each time step, the model predicts its fuelwood demand and probability to switch from fuelwood to electricity by a number of socioeconomic and demographic factors (An et al. 2001, 2002). The fuelwood demand for a household consists of three components: (1) fuelwood for cooking, which is a function of household size and calculated annually, (2) fuelwood for heating, which depends on if there is a senior person (60+ years old) in the household because a household with a senior person has to heat for a longer period of time in winter, and (3) fuelwood for cooking pig fodder, which is a function of land area for corn. This dependence on the area of corn land arises from the local lifestyle: local people use as much land as possible to grow corn (usually intercropped with potato), and cook the corn and potato using fuelwood to feed pigs and sell the extra pork or bacon (besides their own consumption) to tourists and local restaurants.

The probability of switching from fuelwood to electricity is determined by age, gender, and education of the household head, household annual income, current and hypothetical electricity prices, outage frequency levels, voltage levels, and so on (An et al. 2002). These variables are either updated yearly (e.g., age), remain unchanged (e.g., gender), or act as parameters subject to changes (e.g., outage frequency levels) in model tests or simulations.

Human–environment interactions

The interactions between humans and the environment are realized through fuelwood collection, as shown by the two horizontal block arrows in Figure 3. On the one hand, the trees on the landscape, given no human interference, grow and die by themselves. On the other hand, a household, given a certain amount of fuelwood demand, goes to a certain pixel to cut fuelwood. Because of ineffective enforcement of the habitat restriction policy (e.g., caused by the difficulty in monitoring due to the complex topographic conditions) and the common property nature of the forests, the model only considers geography of the forests in determining fuelwood collection sites. Specifically, it calculates the cost-distances (geographical distances corrected by slope) of all the locations within a certain buffer distance, and chooses the one with the smallest cost-distance.

Contextual factors

Government policies (e.g., fertility and migration regulations in the reserve) and environmental factors (e.g., tree species, volume, and growth rate in each pixel) play an important role in affecting the above human–environment system. Based on our goal in this study, we only focus on how policies in relation to the socioeconomic and demographic factors (Table 1) could be used to affect panda habitat through processes such as household formation and demand for electricity. Later in Section 'Simulations' we will show how we simulate the panda habitat dynamics by changing these factors.

Table 1. Two-sample paired *t*-test ($\alpha = 0.95$) results in population size, number of households and panda habitat in response to changes in the socioeconomic and demographic factors (the numbers are values of *t* statistic; double asterisks stand for significance at 0.95 level, and single asterisk at 0.90 level).

	Scenario	Variable	Value	Population size	Number of households	Panda habitat (km^2)
Status quo	1		Baseline	–	–	–
Socioeconomic	S2	Electricity price	0.05 Yuan decline	−0.02	−1.5	−30.29**
	S3	Electricity voltage level	One level increase	0.20	−1.86	−1.06
	S4	Electricity outage level	One level decrease	−0.33	−0.08	−18.38**
	S5	Leaving parental home intention	0.42 → 0.63	−0.20	−10.50**	6.17**
Demographic	D2	Fertility	2.5 → 3.5	−24.48**	−1.40**	0.57
	D3	Marriage age (year)	22 → 28	9.80**	3.69**	−2.76*
	D4	Birth interval (year)	3.5 → 5.5	1.55	−1.51	−5.05**
	D5	Upper birth age (year)	55 → 35	4.15**	−1.39	−0.96
	D6	College attendence rate (%)	1.92% → 5.76% (16–20 youth)	30.36**	9.49**	−1.73
	D7	Female marry-out rate (%)	0.28% → 20%	9.72**	9.97**	−1.49

Data preparation and integration

Our data used for model construction consist of the 1996 agricultural census data (Wolong Nature Reserve 1996) and 2000 population census data (Wolong Nature Reserve 2000). All these individual-based data are arranged by household, covering all rural people in the reserve, including name, ID of the household a resident belongs to, gender, age, education, kinship relation to the household head, and so on. But the 1996 data do not have interpersonal relations relative to the household head as the 2000 data do; we derive these relations based on the data in 2000, as shown below.

Based on the relations between individuals in the 2000 data, we derive the relations for the 1996 data. For example, household A had four individuals in 2000, and they were the household head, his wife, a child of 3 years old, and the household head's father. In 1996, there were also four individuals – but a woman 3 years younger than the household head with the same family name, not the child, was in the household. So we assume that the child was not born yet, and the woman was the sister of the household head who moved out of the household (or died) between 1996 and 2000. We are also interested in the reason why she was no longer in the household any more. It could be that she (1) moved out of the household and was relocated in another household in the reserve through marriage; (2) moved out of the reserve through marriage; (3) died; or (4) went to college. Only situation (1) can be determined based on our available population data of Wolong because the same person should be still registered in the reserve even though she was in another household. Situations (2), (3), and (4) are more difficult to address, though. We put all the people similar to this situation together (e.g., 30 people in total), and then used the age-based mortality rates to determine how many of them may have died, and used the rate of going to college to determine how many may have gone to college. The remaining number should be the number of people who went outside the reserve through marriage.

In this manner, we calculate the annual probabilities that a male would migrate into Wolong through marriage, that a female would migrate into Wolong through marriage, that a male would migrate to the outside of Wolong, and that a female would migrate outside Wolong between 1996 and 2000. The four rates thus derived, 0.043, 0.19, 0.043, and 0.28%, respectively, are used later in simulation.

Model test

We test our model by structural verification and empirical validation. For easiness of explanation, we still follow the traditional terms of verification and validation regardless of the debate about whether models (especially in complex systems) can be truly verified or validated (e.g., Oreskes et al. 1994; Rykiel 1996). Simply put, a verified and validated model is the one we fail to falsify using our available data and methods. Because the model has a number of stochastic processes, we run the model 30 times and compute the averages for each test or simulation. The length of demographic tests or simulations is normally 30 years for one run, though we run some simulations for 50 years to allow for some demographic factors' impacts to be demonstrated. For the socioeconomic simulations, we run the model over 20 years because such a time span is sufficient for the factors to exhibit their impacts on panda habitat.

The structural verification refers to the following processes: (1) the model passes both extreme tests (individual parameters taking maximal and minimal values) and combined extreme tests (a set of parameters taking maximal or minimal values simultaneously; these parameters are the most sensitive ones based on our sensitivity analysis, see details in An et al. 2003b); (2) the model gives expected spatial patterns of households and panda habitat over time under different scenarios; (3) the model gives stable but slowly increasing standard deviations in predicted panda habitat, number of households, and population size, and forms confidence envelops ($\alpha = 95\%$) with increasingly wider opening. This phenomenon is reasonable because uncertainties in demographic, socioeconomic, and ecological subsystems normally increase with time.

The empirical validation refers to: (1) our predicted rate of habitat loss is 1.45 km^2/year, very close to the rate of 123 km^2/year derived from findings of other researchers (Laurie and Pan 1991); (2) the paired two-sample *t*-test ($\alpha = 95\%$) between the predicted and observed population size from 1997 to 2003 gives a *p*-value of 0.88; and (3) the paired *t*-test between the predicted and observed household number from 1997 to 2000 gives a *p*-value of 0.89. The last two *t*-tests fail to reject the null hypothesis that the difference between the predicated and observed population sizes (or household number) is zero. In summary, the model works well and gives us reasonable confidence for later simulation and analysis.

Simulations

We simulate the impacts of socioeconomic factors for 20 years, and those for demographic factors for 30 years (Table 1). Two reasons account for doing so: (1) we have found that changes in many demographic factors require a longer time to impact panda habitat (An et al. 2003b). (2) Theoretically, 30 years could allow the young children (e.g., under 5 years old) to grow up and experience nearly all the important events, such as going; to college and getting married. In some situations where two generations are theoretically needed to examine the associated effects, we conduct the simulations for 50 years. For instance, if we increase the time (years) between births of two consecutive siblings, it lakes time for the birth-delayed sibling to experience all the possible events (e.g., going to college, deciding to leave parental household) and affect changes in habitat through increased/decreased fuelwood demand over time.

Electricity factors (price, outage level, and voltage level) are found to be significant in affecting fuelwood demand, and the default values for each household are set to be equal to the current values of these variables based on our survey data in 1999 (An et al. 2002). To test how changes in these three variables would impact panda habitat, we set a 0.05 Yuan (it represents a moderate change based on current electricity price) decrease for electricity price, a one level increase for voltage level (no more than level 2, the highest level in our study), and a one-level decrease for outage level (no less than 0; 0 for low, 1 for medium, and 2 for high for both voltage and outage levels). Also significant is the variable leave-home intention: the default value is set to be 0.42 based on our data, indicating that 42% of the 'parental-home dwellers' (See Section 'Model' under 'Household dynamics') would prefer to live separately. As a consequence of the decline in fertility, the proportion of elderly people will grow (Zimmer and Kwong 2003). Together with an increasing preference for initiating their own households, the pattern of an aging population (Figure 2a, b) may offset the decreasing trend in the number of households induced by the lowered fertility. We set the value of this parameter to be 0.63 (a 50% increase from the default value of 0.42) and test how the number of households and panda habitat would respond to this change.

A few demographic factors are worth testing for their potential impacts on panda habitat. One of them is total fertility rate (TFR) because controlling fertility is a major policy in China to control population. The default value is set to be 2.5 children per couple (Liu et al. 1999a). We change it to 3.5 for a lesser control, which could be caused by an ineffective government implementation of the policy. The motivation for more children lies in the fact that the more children a couple has, the more financial and instrumental (e.g., assistance to conduct daily house chore) support they may obtain from their children when they become old because there is no insurance or pension system for farmers in China (Zimmer and Kwong 2003).

In addition to fertility, a few other factors could affect population dynamics and panda habitat accordingly. (1) Marriage age: the higher the marriage age, the fewer births within a certain period of time given the same fertility rates. We change its value from the default (i.e., 22) to 28 years old, which is consistent with the 'later' component of the 'later, longer, and fewer' campaign. Some other developing countries (such as India; see Sushama 1996) have used this approach to curb population increase. (2) Birth interval (time interval between births of two consecutive siblings): the longer this interval, the fewer births within a certain period of time given the same fertility rates. This conforms to the 'longer' component of the 'later, longer, and fewer' campaign. We set its default to be 3.5 based on our data, and change it to 5.5 years as a policy test. (3) Upper birth age: as indicated by Figure 2c, the majority of the females have given birth to their last children prior to 50, so 50 is the default value for the maximal age to give births. However, as economic incentives and technical supports (such as contraceptives) are implemented, this number may undergo great decline. As such, we change it from 50 to 40.

Table 2. Definition of desirable and undesirable scenarios.

Factors	Variable	Desirable scenario	Undesirable scenario
Socioeconomic	Electricity price	0.05 Yuan decline	0.05 Yuan increase
	Outage levels	One level decrease	One level increase
	Voltage levels	One level increase	One level decrease
	Leaving parental home intention (probability)	0.42 → 0.21	0.42 → 0.95
Demographic	College attendance rate (%)	1.92 → 30% (16–20 years old youth)	1.92 → 0.0%
	Female marry-out rate (%)	0.28 → 20%	0.28 → 0.0%
	Fertility	2.5 → 1.5	2.5 → 5
	Birth interval (year)	3.5 → 5.5	3.5 → 1.5
	Marriage age (year)	22 → 28	22

The first numbers in the spaces below are the default values in the model, and the second values are those used in the associated scenarios.

Migration could also affect local population dynamics and household dynamics. First, we consider college attendance rate by changing it from 0.0192 to 0.05 to reflect a policy of more investment on local education in the hope of relocating more young people in the future. Second, we consider female marry-out rate (Table 1): we change it from 0.0028 to 0.20 to represent a possible social change that more local females would be attracted to marry people outside the reserve for purposes such as higher education opportunities and living standards.

In addition to studying the impacts of individual factors described above, we examine two scenarios, considering all of the above factors simultaneously: a desirable scenario with the factors taking values that would benefit panda habitat, and an undesirable scenario with the factors taking values that would degrade panda habitat. Table 2 summarizes what these two scenarios include. Doing so may provide some insight into the range of possible trajectories of panda habitat change.

Results

With changes in five socioeconomic factors (Table 1), the predicted population sizes do not have significant changes (Figure 4a). However, scenario S5 (an increase of leaving parental home intention) has a significant impact on the number of households (Figure 4b). Regarding panda habitat, only scenario S3 (a one level increase in electricity voltage level) does not cause significant changes (Figure 4c). Changes of demographic factors, except scenario D4 (an increase in birth interval from 3.5 to 5.5 years), have significant

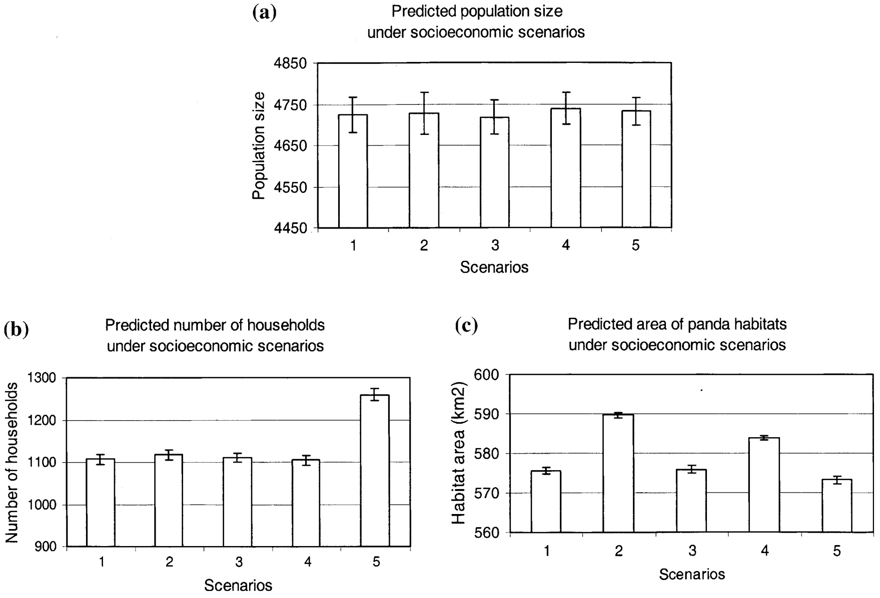


Figure 4. (a) Predicted population size, (b) number of households, and (c) the total amount of panda habitat under five socioeconomic scenarios (see Table 1 for definition of these scenarios).

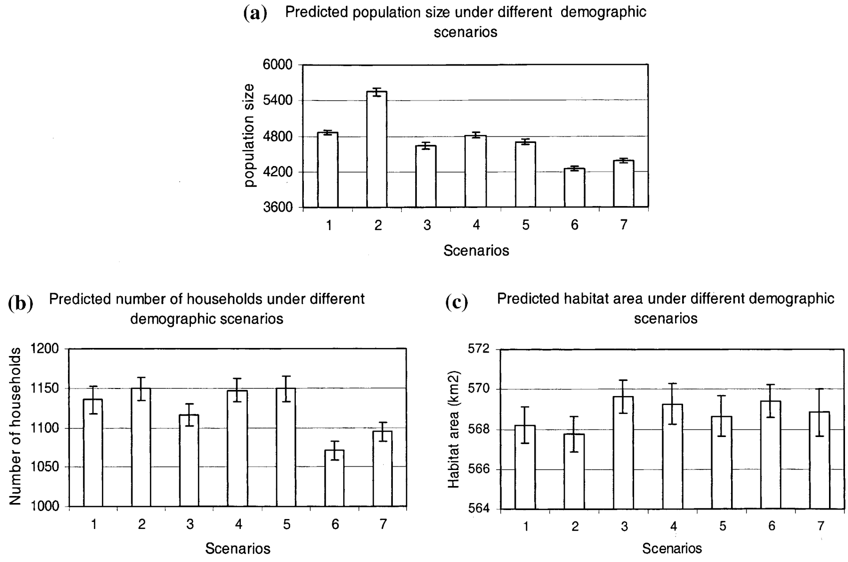
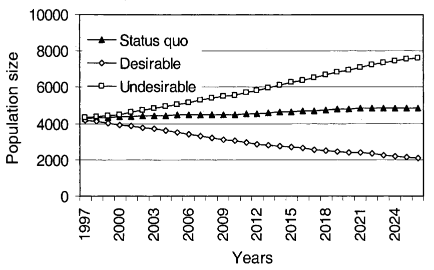
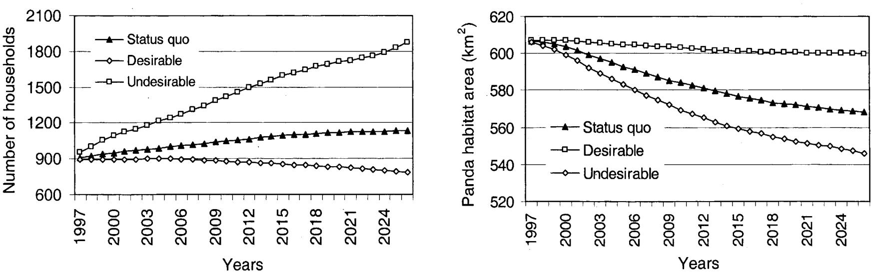


Figure 5. (a) Predicted population size, (b) the number of households, and (c) the total amount of panda habitat under seven demographic scenarios (see Table 1 for the definition of these scenarios).



(a) **Population size under different scenarios**



(b) **Number of households under different scenarios** **(c)** **Panda habitats over time**

Figure 6. Predicted (a) population size, (b) number of households, and (c) amount of panda habitat over time under status quo scenario, desirable scenario, and undesirable scenario. For definition of desirable and undesirable scenarios, see text in Section 'Simulations'.

impacts on human population size (Figure 5a). Scenarios D4 and D5 (an increase in upper birth age from 55 to 35; (Figure 5b), however, do not have significant impacts on the number of households. Regarding impacts on habitat, only scenarios D3 (an increase of marriage age from 22 to 28 years old) and D4 are significant at the 90 and 95% significance levels, respectively, though the absolute magnitudes are relatively small, ranging from 1.0 to 2.0 km^2 . The other four scenarios have not significantly changed the amount of panda habitat (Figure 5c).

The desirable and undesirable scenarios show that (1) the differences between the impacts on population size, number of households, and panda habitat between these two scenarios become increasingly large with time (Figure 6), and (2) At the end of 2026, there could be a difference of approximately 5550 people, 1100 households, and 54 km^2 panda habitat between these two scenarios. When the spatial distributions of panda habitat and households are considered (Figure 7), it is clearer to see the impacts caused by demographic and socioeconornic factors. Figure 7 shows that with outward expansion of households, the habitat is lost and fragmented over time. In addition, the spatio-temporal dynamics of panda habitat could differ substantially due to different values of the socioeconomic and demographic parameters in the two scenarios.

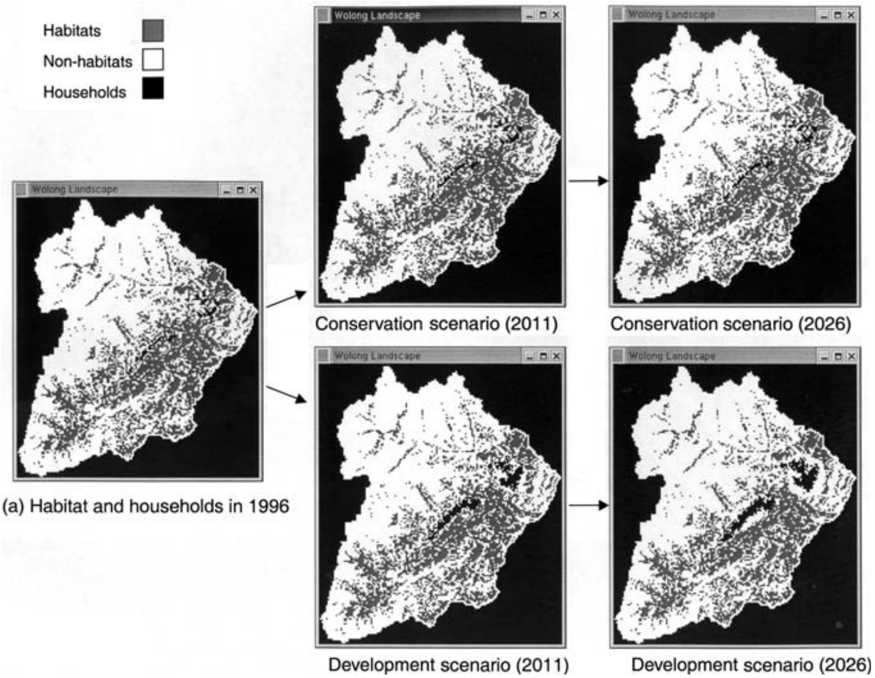


Figure 7. Snapshots of the spatio-temporal dynamics of panda habitat and households in 1996, 2011, and 2026 under conservation and development scenarios.

Conclusion and discussions

The above analyses show that socioeconomic factors play a very important role in affecting the spatio-temporal patterns of panda habitat, while some demographic factors do not have significant impacts on the panda habitat over 30 years. This phenomenon may arise from the cumulative effects of some demographic changes because the longer the time frame, the more differences will be made in human population size or number of households, and thus the more differences are likely to occur in panda habitat. From Figure 6(c), we can see an increasing difference in the impact of human factors between the two scenarios. This escalating-impact trend should be true for the four insignificant factors (D2, D5, D6, and D7) individually as time moves on. For instance, we run the model over a span of 40 years by setting upper birth age (D5) at 35 years old. It turns out that the average amount of panda habitat is 565.10 km^2, and the increase is significant at the 5% level compared to the baseline situation (564.15 km^2). On the other hand, the magnitude of habitat changes (approximately 1 km^2 over 40 years) in relation to the baseline situation may seem insubstantial when the distribution of panda habitat is not considered. Pandas usually prefer those areas that humans also tend to visit for

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fuelwood collection. So this decrease in habitat may occur in the panda's preferable habitat, which may considerably threaten panda survival.

In this study, we treat many demographic factors as exogenous factors (i.e., not explained or predicted by other factors). An example is fertility, which could be affected by many other socioeconomic and demographic factors as well. For instance, female education, economic equity (e.g., job opportunities) between males and females, household income, and financial equality between rich and poor households could affect fertility rates to varying extent (Daily 1996). In microeconomics where the concept of household production function is introduced and used, the incomes and time value of household members are combined to produce an array of commodities that yield utilities and welfare. As economy grows and the value of human time rises, households tend to have fewer but 'higher-quality' children who receive better health care and higher education (e.g., Schultz 1981). Household income, though a parameter included in the model, is not used in our simulations due to lack of household income data, though it is reported to be an important factor in determining many household decisions regarding fertility (e.g., Klawon and Tiefenthaler 2001) and land use (Perz 2001). In the future, inclusion of this factor may improve the analyses. However, as Wolong is a nature reserve where the primary goal is to protect giant pandas, other endangered species, and the associated ecosystems, economic growth should be encouraged elsewhere.

Our findings in this research are consistent with those of other researchers. First, as indicated by Liu et al. (1999a), human demographic factors (age structures in particular) play an important role in affecting biodiversity conservation in the long term. In our case, a decline in fertility or an increase in marriage age would save panda habitat in the long run. Second, migration (especially through higher education) is an ecologically effective, economically efficient, and socially acceptable approach to conserving wildlife habitat or biodiversity in a broader sense (Liu et al. 1999a). Our results show that an increase in college attendance rate would make substantial differences in panda habitat over 30 years. In the long run, it is worth considering other types of out-migrations aside from what have been included in this research (i.e., migration through marriage and education) because more young people may join the floating population in cities. As the economy in urban areas further grows, more migrants (including local residents in Wolong) may be attracted for higher incomes. Last, non-family organizations or services (electricity subsidy and assistance in our case) can reduce direct consumption of natural resources and could be integrated into programs in environmental protection and biodiversity conservation (Axinn and Barber 2003). We have shown that in the short run, providing subsidies for the use of electricity and increasing the quality of electricity would work well in conserving panda habitat.

Additionally, our findings suggest that family planning (e.g., controls in marriage age and birth time between consecutive children) is very important in conserving natural resources and thus has critical significance in human–

environment studies. This finding also has great policy implications in a developing rural setting such as Wolong, where people still follow a subsistence-oriented lifestyle and need more children as labor force. It may encounter social resistance if a policy of strict birth control (e.g., one child per couple) is implemented. However, policies encouraging later marriage and longer birth interval between children should have more public acceptance, especially when economic incentives (such as electricity subsidy or tax reduction) are tied to such a family planning program.

Based on the findings from our research and other studies, we recommend that a program for providing electricity subsidy and assistance and a policy of out-migration through higher education be implemented and initiated for panda conservation while the existing family planning policy continues to be monitored and implemented. While our research is in progress, the reserve government has built a new hydropower plant, and we hope cheaper electricity could be provided for local people. Aside from such practical purposes, this research is also oriented towards using an integrated approach to explore the impacts of socioeconomic and demographic factors on the environment. As is often the case in many other places or for other purposes such as protection of other species, complexities in many coupled society–biodiversity systems have kept some socioeconomic and demographic factors (often intertwined) and their interactions from being explicitly studied. Though socioeconomic and demographic factors and their specific interactions may differ from place to place, the perspectives and methods used in this research could still be useful. For more effective and efficient biodiversity conservation, it is crucially important, thus highly recommended, that socioeconomic and demographic factors, along with more individual-level information if possible, be integrated into more research and conservation activities.

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References

An L., Liu J., Ouyang Z., Linderman M.A., Zhou S. and Zhang H. 2001. Simulating demographic and socioeconomic processes on household level and implications on giant panda habitat. Ecol. Model. 140: 31–49.

An L., Linderman M.A., Qi J., Shortridge A. and Liu J. 2003b An agent-based spatial model for interdisciplinary and across-scale integration. Ann. Assoc. Am. Geogr. (in review).

An L., Lupi F., Liu J., Linderman M.A. and Huang J. 2002. Modeling the choice to switch from fuelwood to electricity: implications for giant panda habitat conservation. Ecol. Econ. 42(3): 445–457.

An L., Mertig A. and Liu J. 2003a. Adolescents' leaving parental home: psychosocial correlates and implications for biodiversity conservation. Popul. Environ.: J. Interdiscipl. Stud. 24(5): 415–444.

Axinn W.G. and Barber J.S. 2003. Linking people and land use. In: Fox J., Rindfuss R.R., Walsh S.J. and Mishra V. (eds), People and the Environment: Approaches for Linking Household and Community Surveys to Remote Sensing and GIS. Kluwer Academic Publishers, Boston, pp. 285–313.

Clark W.C. 2002. Research systems for a transition toward sustainability. In: Steffen W., Jäger J., Carson D. and Bradshaw C. (eds), Challenges of a Changing Earth, Proceedings of the Global Change Open Science Conference, Amsterdam, NL, 10–13 July 2001. Springer-Verlag, Berlin. http://ksgnotes1.harvard.edu/BCSIA/sust.nsf/pubs/pub54.

Cooney R.S. and Shi J. 1987. Household extension of the elderly in China. Popul. Res. Policy Rev. 18(5): 451–471.

Daily G.C. 1996. Socioeconomic equity, sustainability, and earth's carrying capacity. Ecol. Appl. 6(4): 991–1001.

Ehrlich P.R. and Wilson E.O. 1991. Biodiversity studies: science and policy. Science 253: 758–762.

Feng G. and Hao L. 1992. Summary of 28 regional birth planning regulations in China. Population Res. (Renkou Yanjiu; in Chinese) 4: 28–33.

Gimblett H.R. 2002. Integrating geographic information systems and agent-based technologies for modeling and simulating social and ecological phenomena. In: Gimblett H.R. (ed.), Integrating Geographic Information Systems and Agent-Based Techniques for Simulating Social and Ecological Processes. Oxford University Press, New York, pp. 1–20.

Grimm V. 1999. Ten years of individual-based modeling in ecology: what have we learned and what could we learn in the future? Ecol. Model. 115: 129–148.

Gulyáa L. 2002. On the transition to agent-based modeling: implementation strategies from variables to agents. Soc. Sci. Comput. Rev. 20(4): 389–399.

Hussain A. 2002. Demographic transition in China and its implication. World Dev. 30(10): 1823–1834.

Jiang B. and Gimblett H.R. 2002. An agent-based approach to environmental and urban systems within geographic information systems. In: Gimblett H.R. (ed.), Integrating Geographic Information Systems and Agent-Based Techniques for Simulating Social and Ecological Processes. Oxford University Press, New York, pp. 171–189.

Klawon E. and Tiefenthaler J. 2001. Bargaining over family size: the determinants of fertility in Brazil. Popul. Res. Policy Rev. 20: 423–440.

Lambin E.F. 2003. Linking socioeconomic and remote sensing data at the community or at the household level: two case studies from Africa. In: Fox J., Rrndfuss R.R., Walsh S.J. and Mishra V. (eds), People and the Environment: Approaches for Linking Household and Community Surveys to Remote Sensing and GIS. Kluwer Academic Publishers, Boston, pp. 223–240.

Laurie A. and Pan W. 1991. Working group report on giant pandas in the wild. In: Klerman D. and Roberts M. (eds), Giant Panda and Red Panda Conservation Workshop, Working Group Reports, National Zoological Park. Smithsonian Institution, Washington, DC, pp. 5–12.

Liang Z. 2001. The age of migration in China. Popul. Dev. Rev. 27(3): 499–524.

Liang Z. and Ma Z. China's floating population: new evidence from the 2000 census. Population and Development Review. (in press).

Lim K., Deadman P.J., Moran E., Brondizio E. and McCracken S. 2002. Agent-based simulations of household decision-making and land use change near Altamira, Brazil. In: Gimblett H.R. (ed.), Integrating Geographic Information Systems and Agent-Based Techniques for Simulating Social and Ecological Processes. Oxford University Press, New York, pp. 277–308.

Liu J. 2001. Integrating ecology with human demography, behavior, and socioeconomics: needs and approaches. Ecol. Model. 140(1–2): 1–8.

Liu J, Daily G.C., Ehrlich P.R. and Luck G.W. 2003. Effects of household dynamics on resource consumption and biodiversity. Nature 421(6922): 530–533.

Liu J., Linderman M., Ouyang Z., An L., Yang J. and Zhang H. 2001. Ecological degradation in protected areas: the case of Wolong Nature Reserve for giant pandas. Science 292: 98–101.

Liu J., Ouyang Z., Tan Y., Yang J. and Zhang H. 1999a. Changes in human population structure: implications for biodiversity. Popul. Environ.: J. Interdiscipl. Stud. 21: 46–58.

Liu J., Ouyang Z., Taylor W.W., Groop R. and Zhang H. 1999b. A framework for evaluating the effects of human factors ob wildlife habitat: the case of giant pandas. Conserv. Biol. 13: 1360–1370.

Malthus T.R. 1798. An essay on the principle of population it affects the future improvement of society. Reprint, Pelican Books (1970). Harmondsworth, England.

Merli M.G. and Smith M.L. 2002. Has the Chinese family planning policy been successful in changing fertility preferences? Demography 39(3): 557–572.

Oreskes N., Shrader-Frechette K. and Belitz K. 1994. Verification, validation, and confirmation of numerical models in the earth sciences. Science 263(5147, Feb. 4, 1994): 641–646.

Pebley A.R. 1998. Demography and the environment. Demography 35(4): 377–389.

Perz S.G. 2001. Household demographic factors as life cycle determinants of land use in the Amzon. Popul. Res. Policy Rev. 20: 159–186.

Rykiel E.I. Jr. 1996. Testing ecological models: the meaning of validation. Ecol. Model. 90(1996): 229–244.

Schaller G.B., Hu J., Pan W. and Zhu J. 1985. The Giant Pandas of Wolong. The University of Chicago Press, Chicago and London.

Schultz T.P. 1981. Economics of Population. Addison-Wesley, Reading, Massachusetts.

Sushama P.N. 1996. Transition from high to replacement-level fertility in a Kerala village. Health Trans. Rev. 6: 115–136.

Turner B.L. (ed.) 1990. The Earth As Transformed by Human Action: Global and Regional Changes in the Biosphere over the Past 300 Years. Cambridge University Press, Cambridge and New York.

United States National Research Council Boardon Sustainable Development. 1999. Our Common Journey: A Transition Toward Sustainability. National Academy Press, Washington, DC.

Wilson E.O. 1988. The current state of biological diversity. In: Wilson E.O. (ed.), Biodiversity. National Academy Press, Washington, DC.

Wolong Nature Reserve. 1987. Wolong Vegetation Cover and Plant Resources. Sichuan Science and Technology Press, Chengdu (China).

Wolong Nature Reserve. 1996. Agricultural Census. Wolong (unpublished, in Chinese).

Wolong Nature Reserve. 2000. The 2000 Nationwide Population Census. Wolong (unpublished, in Chinese).

Wong J. 2001. China's sharply declining fertility: implications for its population, policy. Issues Stud. 37(3): 68–86.

Yang X. 2000. The fertility impact of temporary migration in China: a detachment hypothesis. Eur. J. Popul. 16: 163–183.

Yang Y. and Li C. (eds) 1992. Sichuan Forests. China Forestry Press, Beijing, China.

Zimmer Z. and Kwong J. 2003. Family size and support of old adults in urban and rural China: current effects and future implications. Demography 40(1): 23–44.

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Avian species richness and numbers in the built environment: can new housing developments be good for birds?

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Abstract. Bird species richness (S) and numbers (N) were studied in the breeding season in housing developments of different ages in a small English town and compared with village sites, urban green corridors and adjacent arable farmland. S and N were highest in village and green corridor sites. S in urban plots ranged from 13 to 18 species, similar to farmland, but N was much lower in farmland. Marked differences in the number of individual species between plots were recorded. S and N were independent of age of development and area of gardens within plots but both were correlated with the area of greenspace. Greenspace alone and combined with gardens was correlated with the numbers of several individual species. The results are discussed in relation to proposed new large-scale housing developments in England.

Introduction

It is now well known that bird populations on farmland in the UK have suffered major declines over the past two decades (Fuller et al. 1995; Siriwardena et al. 1998). Some species which have largely disappeared from farmland in eastern England, such as the thrushes, appear to be thriving in the built environment (Mason 1998, 2000, 2003), while it has been estimated that habitats associated with human habitation hold more than 20% of the total population of some species in Britain (Gregory and Baillie 1998). Nevertheless, two typically urban species, starling *Sturnus vulgaris* and house sparrow *Passer domesticus*, have been added to the red list of birds of conservation concern in the UK because of strong population declines (Gregory et al. 2003). However there has been very little study of the bird communities and populations within towns, or of the factors that might influence them (Marzluff et al. 1998; Clergeau et al. 1998; Niemelä 1999). This is surprising in view of the fact that the built environment occupies 14% of the land surface of England, 10% being classified as urban. Furthermore there are intense development pressures facing regions such as southeast England. For example, it is proposed to build 120,000 new homes along the Thames estuary (some 75 km southwest of the study area reported here) over the next 13 years to relieve housing shortage in the London area. Many more developments are planned in England, including the creation of new towns. While at first glance such urban development might seem inimical to the conservation of birds, it might, if properly designed, greatly increase avian diversity compared to that currently supported by the intensely managed farmland that surrounds the majority of English towns.

I report here on avian species richness and numbers in various urban developments of different ages in a small coastal town in eastern England and relate differences between them to several attributes of the built environment. In addition, I examine the role of garden area and the area of open space in developments in relation to avian richness and numbers. Comparisons are made with village sites (where individual gardens are often large), urban green corridors (which may provide additional habitat to enhance urban bird diversity) and adjacent farmland (on which future housing projects will be developed). The results may go some way to inform the design of new developments in enhancing avian diversity.

Study area and methods

The study area was centred on the coastal town of Harwich, Essex, eastern England (51°56′N, 1°18′E), with a human population of 17,000 (39 persons/ha). The 12 urban study plots were a subset of those studied by Mason (2003) and represented two of each type and age of building development, the categories determined from the local plan of Tendring District Council (Table 1). Formed from the coalescence of two settlements, the town has two centres, one primarily

Table 1. Statistics of the study plots containing housing.

Development type	Code	Area (ha)	Percent			House density/ha
			Garden	Greenspace	Total	
Historic/Victorian terrace	HV1	16.1	26.2	4.0	30.3	52.4
Historic/Victorian terrace	HV2	16.2	27.0	1.3	29.2	38.6
Town centre	TC1	9.3	5.5	7.1	12.6	48.8
Town centre	TC2	9.9	16.3	0	16.3	28.8
Interwar, predominantly semi-detached	IW1	9.7	76.9	6.6	83.6	17.1
Interwar, predominantly semi-detached	IW2	19.6	64.0	3.6	67.6	11.5
Bungalows (interwar)	BD1	8.6	66.6	1.9	68.5	29.9
Bungalows (1990s)	BD2	7.3	27.8	53.0	80.8	23.8
Post-war suburban (1960s/70s)	SI1	31.0	55.8	19.3	75.1	34.4
Post-war suburban (1960s/70s)	SI2	8.2	60.5	10.9	71.4	39.9
1990s	NI1	3.4	63.1	3.9	67.0	35.7
1990s	NI2	8.5	74.2	12.7	86.9	21.2
Village	VI1	51.4	58.6	33.8	92.4	4.3
Village	VI2	15.9	41.8	50.3	92.1	4.7

of medieval construction, the other Victorian. Of the urban green corridors, one (plot code GR1) consisted of scrub of various ages, with mature trees and rough grassland, some on a steep slope, between a 1960s housing development (SI2) and an industrial area; the level ground of this plot is ear-marked for development. The other green corridor (GR2) is a narrow strip of grassland and scrub between two 1960s developments, used to take storm-water drainage. The two villages, Bradfield (VI1) and Ramsey (VI2), were 8 km and 0.5 km respectively from the edge of the town. The two predominantly arable farmland areas (AR1 and AR2) were within 3 km of the edge of the town.

Transects, of variable lengths (500–1700 m, depending on the area of development) were walked on three occasions (in the second half of April, first half of May and second half of May/first week of June) in 2003. All birds seen (excluding gulls and over-flying individuals) were counted. Starlings were not counted during the final survey as young had fledged and were ranging widely. Species richness (S) was taken as the total of the number of species seen during the three surveys. The number of each species on transects was taken as the largest count recorded from the three surveys, adjusted to birds/km. These were summed to give the total number of individuals (N).

For each built development, the percentage of the area occupied by gardens and greenspace was measured from large-scale maps. Greenspace consisted of areas within developments of mown grass, with shrubberies and scattered trees, but excluded any parks/recreation grounds adjacent to developments. In villages, horse-pasture within the built envelope was included within greenspace. The density of houses was also determined (Table 1). The area occupied by the hard surfaces of roads was excluded from the total plot area prior to calculations on the basis that it offered neither feeding nor nesting opportunities for birds.

Within the 14 built study plots (urban plus village), relationships between S, N, the numbers of individual species and the percentages of the plot occupied by gardens (G), by open greenspace (O), by total garden plus greenspace (O + G) and with house density (D) were examined using Spearman rank correlation.

Biomass can be used as a measure of the dominance of individual species within developments. Average weights of birds were taken from Hickling (1983) and multiplied by the number of individuals/km to give an estimate of biomass.

Results

There was no relationship between species richness (S) or the total number of birds/km (N) and the length of transect in either the built study plots ($r_s = 0.12$, -0.15 respectively, $n = 14$, ns) or in all study plots ($r_s = 0.03$, -0.27 respectively, $n = 18$, ns). Similarly there was no relationship between S or N and the area of development ($r_s = 0.45$, 0.18 respectively, $n = 14$, ns). Thus both S and N were independent of transect length and plot area.

A complete list of species recorded, including scientific names and the plots in which they occurred is given in Appendix 1. Species richness and number of birds/km in the different plots is shown in Figure 1. S was highest in the villages (21, 28 species) and urban green corridors (23, 24). Within the town S ranged from 13 to 18 species, similar to that in farmland (14, 16). N was greatest in the villages (123, 158 birds/km) and lowest in farmland (26, 31), historic/Victorian (43, 55) and town centre (53, 58). Apart from swift and house martin, nesting on buildings, all species recorded within urban developments were resident species or short-distance migrants such as goldfinch. Both village and urban green corridor plots included small numbers of five long-distance summer visitors.

The numbers of the five most widespread species within the different developments are shown in Figure 2. Marked differences were recorded. The highest densities of house sparrows were found in interwar (30, 31 birds/km) and 1960s/70s (28, 28) developments and in villages (27, 43), while lowest densities were in 1990s developments (2, 10). The numbers of starlings were less clearly associated with development. Highest densities were in one each of the interwar (24), 1960s/70s (28) and 1990s (32) and 1990s bungalow (46) developments, with lowest numbers in the other (interwar) bungalow (4) and historic/Victorian (13, 14) developments. The highest densities appeared to be associated with houses with non-functional chimneys.

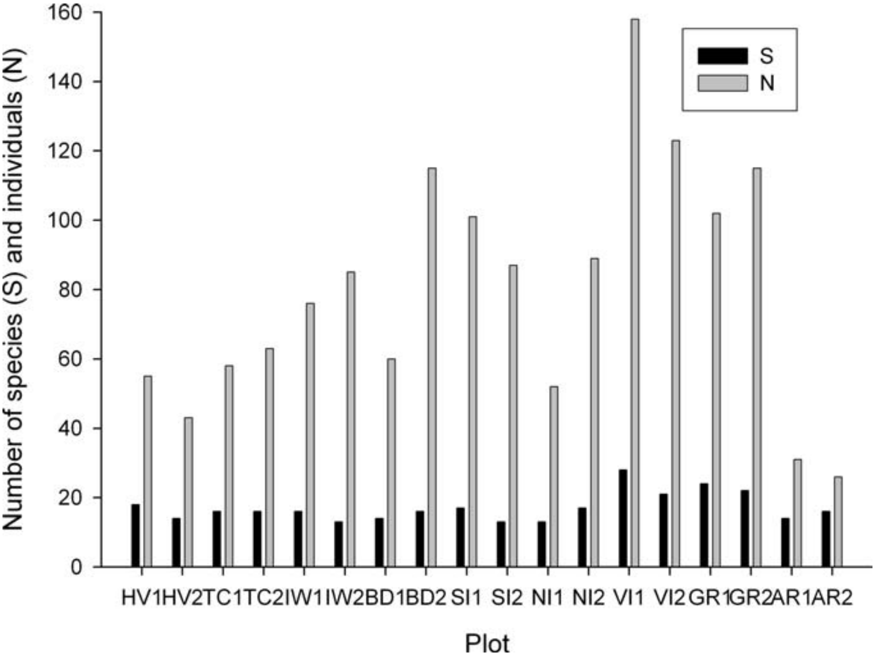

Figure 1. Species richness and total number of birds recorded in individual plots (see Table 1 for plot codes and description of plots).

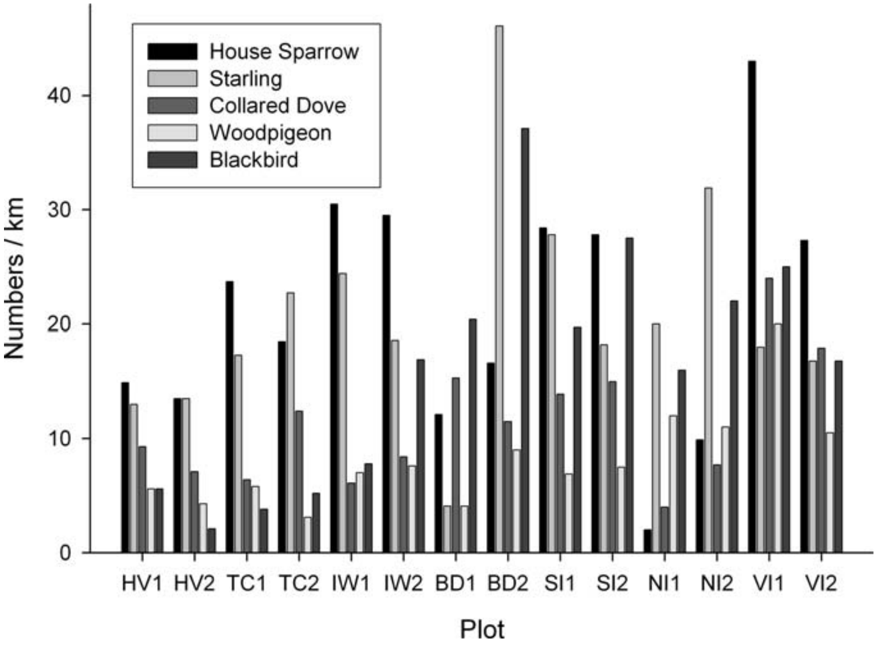

Figure 2. Numbers of the five most common bird species in the 14 built plots (see Table 1 for plot codes).

Of other birds nesting on buildings, feral pigeons were found only in historic/Victorian and town centres, outnumbering woodpigeons in the latter. Swifts were found only in historic/Victorian terrace and town centre sites, and in one of the villages. The density of house martins was markedly higher in village plots, and they were not recorded at all in town centre, bungalow developments or 1960s/70s housing.

The highest numbers of collared doves were in village (18, 24 birds/km) and 1960s/70s (14, 16) developments, with lowest numbers in historic/Victorian (7, 9), inter-war (6, 8) and 1990s (4, 8) developments (Figure 2). Woodpigeon numbers were highest in village (11, 12) and 1990s (11, 12) developments, with fewest birds in historic/Victorian (4, 6) and town centre (3, 6) developments. The smallest numbers of blackbirds were located in historic/Victorian (2, 6) and town centres (4, 5) with most in bungalow (20, 37) and 1960s/70s (20, 23) developments and single 1990s (22) and village (25) sites.

Song thrushes were absent from historic/Victorian and town centres and were most numerous in the village sites. There were eight other species that occurred in at least 12 of the 14 built sites (Appendix 1). Of these, wren, robin, blue tit, great tit, chaffinch and greenfinch were more numerous in the village sites. Dunnock achieved higher densities in the two bungalow sites and single 1960s/70s, 1990s and village sites. There was no obvious pattern in the distribution of magpies, which may have been entering developments to forage.

In terms of biomass, woodpigeon was the dominant species in all but two developments, where collared dove was the dominant species. Woodpigeon biomass ranged from 15.1 to 56.8% of total biomass (average 34.1%, $n = 14$). The Columbidae (pigeons and doves) as a group made up 43.6–65.3% of the total bird biomass (average 55.9%).

The two green corridors introduced species into the urban environment that were not recorded in the built sites. These comprised mallard, moorhen, pheasant, turtle dove, four warblers and bullfinch. Four species were found in the farmland plots that did not occur elsewhere: red-legged partridge, skylark, yellowhammer and corn bunting. The densities of all other species on farmland were lower than recorded in other plots.

Within the 12 urban plots there was no relationship between age of development and either S or N ($r_s = 0.16, -0.51$ respectively, ns). Neither S nor N was related to percentage of plots occupied by gardens (G) ($r_s = -0.24, 0.24$ respectively, ns). Feral pigeon and swift were significantly negatively associated with G ($r_s = -0.71, -0.77$ respectively, $p < 0.01$). Sixteen of 17 other species were positively associated with G but none approached significance. However, if the village sites were excluded, greenfinch showed a significant positive relationship with G ($r_s = 0.66$, $p < 0.05$).

There were significant relationships between S and the percentage of plots occupied by open greenspace (O), and between N and O, O + G and house density (D) (Table 2). The relationship between N and O is shown in Figure 3, and between N and D in Figure 4. Feral pigeon and swift were negatively associated with O and O + G, and positively with D, though only those with O + G were significant. All other species showed positive association with O and O + G, six significantly with O and 10 species with O + G (Table 2). Nineteen species showed negative correlations with D, six of them significant. The two characteristic urban species, house sparrow and starling, showed no relation between numbers and the habitat variables, though if village sites were excluded starlings were positively associated with O and O + G ($r_s = 0.59$, 0.62 respectively, $p < 0.05$).

It has been suggested that pigeon and doves could be implicated in the decline of house sparrows through competition for food (Summers-Smith 2003). A negative correlation between house sparrow numbers and those of pigeons and doves might therefore be expected. The numbers of house sparrows was positively correlated with numbers of collared doves ($r_s = 0.61$, $p < 0.05$) in the built study plots, and independent of numbers of feral pigeons ($r_s = -0.49$, ns), woodpigeons ($r_s = 0.38$, ns) and combined doves and pigeons ($r_s = 0.31$, ns).

Discussion

Some studies have shown that progressive urbanization often leads to biotic homogenization (e.g. McKinney and Lockwood 2001; Crooks et al. 2004),

Table 2. Spearman rank correlations between birds (numbers/km) and proportion of Greenspace (O), Greenspace + Garden (O + G) and House density (D) within developments.

Species	Greenspace (O)	Total open space (O + G)	House density (D)
Feral pigeon	– 0.35	– 0.68**	0.33
Woodpigeon	0.65*	0.68*	– 0.53*
Collared dove	0.36	0.45	– 0.33
Swift	– 0.37	10.61	0.32
House martin	0.26	0.24	– 0.28
Wren	0.41	0.70**	– 0.73**
Dunnock	0.48	0.54*	– 0.16
Robin	0.68**	0.72**	– 0.39
Blackbird	0.64*	0.72**	– 0.43
Song thrush	0.58*	0.69*	– 0.50
Blue tit	0.48	0.64*	– 0.72**
Great tit	0.43	0.44	– 0.41
Magpie	0.01	0.21	– 0.06
Carrion crow	0.15	0.18	– 0.33
Starling	0.36	0.29	– 0.20
House sparrow	0.34	0.37	– 0.45
Chaffinch	0.52	0.58*	– 0.63*
Greenfinch	0.76**	0.60*	– 0.71*
Goldfinch	0.57*	0.77**	– 0.55*
S	0.56*	0.49	– 0.32
N	0.86**	0.86**	– 0.64*

*$p < 0.05$; **$p < 0.01$.

whereby a few widespread and successful species replace a diverse avifauna. Such studies, though, have examined the spread of towns into natural habitats. In the present study, the hinterland was modified for agriculture many centuries ago and is currently farmed so intensively that few species thrive, the built environment providing a better habitat for the majority of species.

Villages had the highest diversity and density of breeding birds, while bird density was markedly higher in urban developments than in farmland, though species richness was similar in the two habitats. There was no apparent decline in species richness with degree of urbanization, as reported for example by Clergeau et al. (1998). This may have been due to the relatively small size of Harwich compared to the cities of Rennes and Quebec studied by Clergau et al. and even housing in the most urbanized plots had some garden area and open space. Harwich is, however, typical of many small towns across England.

Farmland held four species not occurring in other study plots but of species occurring across habitats, farmland had the lowest numbers. Residential areas are likely to provide both greater structural diversity and greater diversity of feeding opportunities (Blair 1996). Three of the five commonest species on urban plots were not recorded in farmland – collared dove, starling and house sparrow. Urban green corridors also held more species and higher numbers of birds than all sites other than villages.

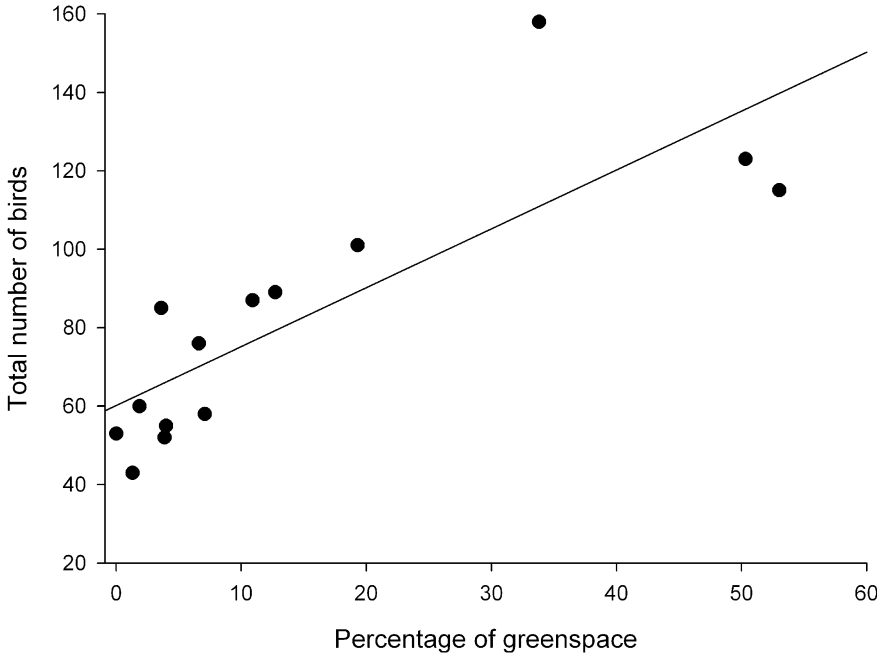

Figure 3. Relationships between the total numbers of birds (N) recorded in built plots and percentage of greenspace (O).

Both house sparrow and starling are currently red-listed, their populations having declined by more than 50% in the last 25 years (Gregory et al. 2003). Both primarily use buildings for nesting. The decline in house sparrows has occurred in both rural (Hole et al. 2002) and urban areas (Bland 1998; Dott and Brown 2000; Summers-Smith 2003). In the present study villages had the highest densities of house sparrows, as also suggested by the questionnaire survey of Wotton et al. (2002). Within the town the highest densities of house sparrows were found in interwar and post-war developments, with fewest in the most modern developments, a pattern similar to that found in Bristol (Bland 1998). House Sparrow density was not significantly related to any of the habitat variables, suggesting that the availability of suitable sites in buildings for nesting may be the most important factor in determining numbers. Some earlier studies have suggested that building design could be modified to exclude house sparrows and starlings (Lancaster and Rees 1979; Beissinger and Osborne 1982). Clearly in Great Britain the opposite approach may now be required. It has been suggested that competition with doves and pigeons for food might be a contributory factor in house sparrow declines (Summers-Smith 2003). The lack of any negative relationship between house sparrow numbers and those of columbid populations, separately or combined, does not lend support to this hypothesis.

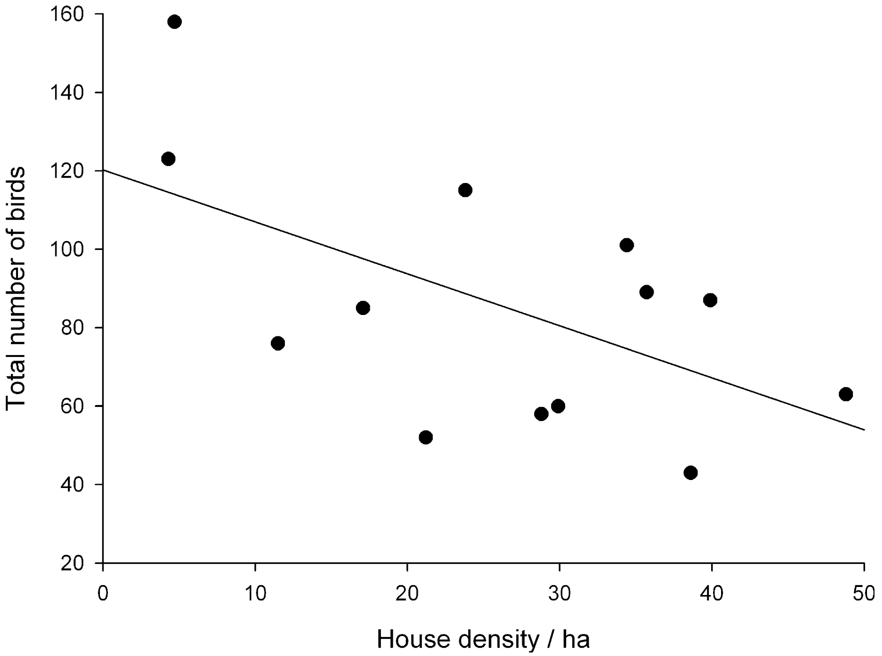

Figure 4. Relationships between the total numbers of birds (N) recorded in built plots and house density (D).

The preference of starlings for old houses, as found by Wotton et al. (2002), was not apparent in the present survey, with Victorian developments having relatively few birds. Similarly villages were not especially favoured. Starlings primarily forage in areas of short grass (Bruun and Smith 2003) and numbers were positively associated with greenspace within developments, but only if village sites were excluded; presumably there were suitable feeding sites on farmland close to, but outside of, the village envelope. Three other species used buildings for nesting – feral pigeon, swift and house martin. Feral pigeons were restricted to town centre and historic/Victorian sites and swifts were largely so, with a single village plot being utilized, while house martins were mainly village nesters. The preferences for older houses by swifts and village sites by house martins largely confirm the pattern reported by Wotton et al. (2002).

The majority of other species in the urban environment are birds of woodland or open country. Some species, such as song thrush and blackbird, have largely disappeared from farmland (Mason 1998, 2000) and the present study confirms this situation, with song thrush being absent from farmland and blackbird scarcer here than in all other plots. Song thrushes were most numerous in village and urban green corridor plots. The importance of gardens, especially in villages, for this species is increasingly recognized (Mason 2000; Peach et al. 2002; Snow 2003).

It was notable that, apart from swift and house martin, exploiting buildings as nest sites and feeding aerially, there were no summer migrants present in urban plots, while, apart from swallow with behaviour similar to the previous two species, migrants were scarce in village plots. O'Connor (1985) has argued that migrants are competitively inferior to residents so that habitat use is restricted when resident populations are high. Within residential areas, artificial feeding in winter may buffer resident populations against inclement conditions, thus excluding migrants.

While artificial feeding will be beneficial to many bird species in towns (Cowie and Hinsley 1988), a number of features may mitigate against success. Predation by domestic cats may be of especial importance (Churcher and Lawton 1987; Lepczyk et al. 2003). There are estimated to be some 9 million cats in Great Britain, by far the most abundant carnivore in the country, killing an estimated 27 million birds each year (Woods et al. 2003). This loss, together with factors such as disturbance by humans (Fernández-Juricic 2000; Fernández-Juricic and Telleria 2000), intensive use of pesticides (Ansell et al. 2001), and poor quality of food before the breeding season (Solonen 2001) may all influence success. Despite this the high densities of some species in residential areas compared with other habitats, especially farmland, suggest that the benefits of living in close proximity to humans may outweigh the costs (Mason 2003).

There were no consistent patterns of S in urban sites, but distinct differences in N. Surprisingly, N does not appear to be influenced by the area occupied by gardens considered alone within developments. This differs from the findings of Mason (2003) for blackbirds in the same general study area. However the present study excluded surveys of urban residential areas with very large garden plots because these will not be a feature of future urban developments. Average garden size in the urban plots ranged from 0.001 ha (town centre) to 0.06 ha (interwar housing), based on the dwelling density and proportion of plot devoted to gardens (Table 1). Village gardens averaged 0.09 and 0.14 ha in the two plots, considerably larger than urban gardens. Much has been written about the value of gardens as bird habitats and the way they can be enhanced for birds (e.g. Cannon 1998, 1999) and much of the information on the value of gardens as been gained from those with an interest in birds and catering for their needs (Cannon 1998). Individual gardens will, of course, vary greatly in the amount and structure of vegetation they contain and the way in which they are managed, influencing their suitability to individual bird species. Such features were not measured in this study. Differences in structure and management might tend to be repeated, more or less, across developments, depending for example on the general level of affluence within its community. Small gardens will suffer a much greater general level of disturbance from householders, their children and pets, than large gardens, likely reducing breeding success, feeding opportunities, and increasing predation.

Bird numbers overall (N) were strongly associated with the area of communal greenspace within developments, and with combined greenspace and gardens. None of these greenspace areas consisted of parks in the traditional sense, parks being especially important to enhancing avian diversity within towns (Fernández-Juricic and Jokimäki 2001). The significance of O + G for blackbird confirms the observations of Mason (2003), while the relative importance of O and O + G varied between species.

New housing developments in the UK are built at an average density of 22 dwellings per ha (DEFRA 2001). It is estimated that an additional 4.4 million houses will be required by 2016. The two 1990s developments in this study, with housing densities of 21 and 36 dwellings/ha (excluding roads), are likely to be fairly typical of future developments. Plot NI2, with the lower housing density had 17 species of birds and a relatively high total number of birds, both of which may increase as the development matures. This plot is characterized by greenspace areas of communal mown grass, shrubberies and trees. An examination of Figure 3 would suggest that a housing density of 22 dwellings/ha, combined with greenspace of at least 20% (excluding road area) would result in good numbers of a typical range of some 16–18 species of birds, which will not be unduly influenced by the current propensity for small gardens. The two areas of green corridors added additional species to the urban bird community which did not occur in built developments, including two species currently red-listed as of conservation concern in the UK – turtle dove and bullfinch (Gregory et al. 2003). Often such areas develop on brownfield sites previously used for industrial purposes and are frequently considered by planners as ideal sites for development. Such sites need evaluation for their nature conservation potential as development plans are formulated. Natural habitat (woodland patches, isolated mature trees etc.) should be retained (Beissinger and Osborne 1982; Moore 1990; Mortberg and Wallentinus 2000) and indeed linked by corridors to open country. Site specific actions can provide diverse habitats which will increase bird diversity (Clergeau et al. 2001).

In conclusion, new and large housing developments are inevitable. The built environment has the potential to hold greater biodiversity than the arable farmland it will largely replace in lowland England. However to achieve this diversity, wildlife conservationists must insist on being involved from the earliest stages of planning so that valuable sites are retained and new ones are created within the housing matrix, to the benefit of both wildlife and the future human inhabitants.

Appendix 1. Bird species recorded on study plots.

Species	Plots recorded in
Mallard *Anas platyrhynchos*	GR2
Sparrowhawk *Accipiter nisus*	HV1, VI2
Red-legged Partridge *Alectoris rufa*	AR2

Appendix 1. Continued.

Species	Plots recorded in
Pheasant *Phasianus colchicus*	VI1, GR1, AR1, AR2
Moorhen *Gallinula chloropus*	GR2, AR1
Feral pigeon *Columba livia*	HV1, TC1, TC2
Stock dove *Columba oenas*	VI1
Woodpigeon *Columba palumbus*	All plots
Collared dove *Streptopelia decaocto*	All plots except AR1, AR2
Turtle dove *Streptopelia turtur*	VI1, GR1, GR2
Swift *Apus apus*	HV1, HV2, TC1, TC2, VI1
Green woodpecker *Picus viridis*	BD2, VI1, GR1
Skylark *Alauda arvensis*	AR1, AR2
Swallow *Hirundo rustica*	VI1, VI2
House martin *Delichon urbica*	HV1, NI2, IW1, VI1, VI2
Wren *Troglodytes troglodytes*	All plots
Dunnock *Prunella modularis*	All plots except NI1, AR1, AR2
Robin *Erithacus rubecula*	All plots except NI1, TC1, IW2, AR1, AR2
Blackbird *Turdus merula*	All plots
Song thrush *Turdus philomelos*	NI2, IW2, SI1, SI2, VI1, VI2, GR1, GR2
Mistle thrush *Turdus viscivorus*	VI1, VI2, GR2
Lesser whitethroat *Sylvia curruca*	GR1, GR2, AR2
Whitethroat *Sylvia communis*	VI1, VI2, GR1, AR1, AR2
Blackcap *Sylvia atricapilla*	GR1, GR2
Chiffchaff *Phylloscopus collybita*	VI1, GR1, GR2
Goldcrest *Regulus regulus*	VI1
Spotted flycatcher *Muscicapa striata*	VI1
Long-tailed tit *Aegithalos caudatus*	NI1, GR1, GR2, AR2
Blue tit *Parus caeruleus*	All plots
Great tit *Parus major*	All plots except BD1, SI2
Magpie *Pica pica*	All plots except TC1, VI1
Jackdaw *Corvus monedula*	VI1
Carrion crow *Corvus corone*	All plots except NI1, NI2, IW2, GR1, GR2, AR2
Starling *Sturnus vulgaris*	All plots except AR1, AR2
House sparrow *Passer domesticus*	All plots except AR1, AR2
Chaffinch *Fringilla coelebs*	All plots except HV2, NI1, SI2
Greenfinch *Carduelis chloris*	All plots except AR1, AR2
Goldfinch *Carduelis carduelis*	NI1, NI2, TC1, IW1, BD1, BD2, SI1, VI1, VI2, GR2
Linnet *Carduelis cannabina*	NI2, BD2, SI1, GR1, AR1
Bullfinch *Pyrrhula pyrrhula*	GR1
Yellowhammer *Emberiza citrinella*	AR1, AR2
Corn bunting *Miliaria calandra*	AR1, AR2

Plot codes as in Table, plus green corridor plots (GR1, GR2) and farmland plots (AR1, AR2).

References

Ansell R., Baker P. and Harris S. 2001. The value of gardens for wildlife – lessons from mammals and herpetofauna. British Wildlife 13: 77–84.

Beissinger S.R. and Osborne D.R. 1982. Effects of urbanization on avian community organization. Condor 84: 75–83.

Blair R.B. 1996. Land use and avian species diversity along an urban gradient. Ecol. Appl. 6: 506–519.

Bland R.L. 1998. House sparrow densities in Bristol. Avon Bird Report 145–148.

Bruun M. and Smith H.G. 2003. Landscape composition affects habitat use and foraging flight distances in breeding European starlings. Biol. Conserv. 114: 179–187.

Cannon A. 1998. Garden BirdWatch Handbook. BTO, Thetford.

Cannon A. 1999. The significance of private gardens for bird conservation. Bird Conserv. Int. 9: 287–297.

Churcher P.B. and Lawton J.H. 1987. Predation by domestic cats in an English village. J. Zool., London 212: 439–455.

Clergeau P., Jokimäki J. and Savard J.-P. L. 2001. Are urban bird communities influenced by the bird diversity of adjacent landscape? J. Appl. Ecol. 38: 1122–1134.

Clergeau P., Savard J.-P.L., Mennechez G. and Falardeau G. 1998. Bird abundance and diversity along an urban-rural gradient: a comparative study between two cities on different continents. Condor 100: 413–425.

Cowie R.J. and Hinsley S.A. 1988. The provision of food and the use of bird feeders in suburban gardens. Bird Study 35: 163–168.

Crooks K.R., Suarez A.V. and Bolger D.T. 2004. Avian assemblages along a gradient of urbanization in a highly fragmented landscape. Biol. Conserv. 115: 451–462.

DEFRA 2001. Digest of Environmental Statistics. www.defra.gov.uk/environment/statistics/des/chap08/ch080217.htm.

Dott H.E.M. and Brown A.W. 2000. A major decline in house sparrows in central Edinburgh. Scottish Birds 21: 61–68.

Fernández-Juricic E. 2000. Local and regional effects of pedestrians on forest birds in a fragmented landscape. Condor 102: 247–255.

Fernández-Juricic E. and Jokomäki J. 2001. A habitat island approach to conserving birds in urban landscapes: case studies from southern and northern Europe. Biodiv. Conserv. 10: 2023–2043.

Fernández-Juricic E. and Telleria J.L. 2000. Effects of human disturbance on spatial and temporal feeding patterns of Blackbird *Turdus merula* in urban parks in Madrid, Spain. Bird Study 47: 13–21.

Fuller R.J., Gregory R.D., Gibbons D.W., Marchant J.H., Wilson J.D., Baillie S.R. and Carter N. 1995. Population declines and range contractions among lowland farmland birds in Britain. Conserv. Biol. 9: 1425–1441.

Gregory R.D. and Baillie S.R. 1998. Large-scale habitat use of some declining British birds. J. Appl. Ecol. 35: 785–799.

Gregory R.D., Eaton M.A., Noble D.G., Robinson J.A., Parsons M., Baker H., Austin G. and Hilton G.M. 2003. The State of the U.K.'s Birds 2002. RSPB, BTO, WWT and JNCC, Sandy.

Hickling R. 1983. Enjoying Ornithology. Poyser, Calton.

Hole D.G., Whittingham M.J., Bradbury R.B., Anderson G.Q.A., Lee P.L.M., Wilson J.D. and Krebs J.R. 2002. Agriculture: widespread local house-sparrow extinctions. Nature 418: 931–932.

Lancaster R.K. and Rees W.E. 1979. Bird communities and the structure of urban habitats. Can. J. Zool. 57: 2358–2368.

Lepczyk C.A., Mertig A.G. and Liu J. 2003. Landowners and cat predation across rural-to-urban landscapes. Biol. Conserv. 115: 191–201.

Marzluff J.M., Gehlbach F.R. and Manuwal D.A. 1998. Urban environments: influences on avifauna and challenges for the avian conservationist. In: Marzluff J.M. and Sallabanks R. (eds), Avian Conservation. Island Press, Washington, DC, pp. 293–299.

Mason C.F. 1998. Habitats of the song thrush *Turdus philomelos* in a largely arable landscape. J. Zool. Lond. 244: 89–93.

Mason C.F. 2000. Thrushes now largely restricted to the built environment in eastern England. Biodiv. Distrib. 6: 189–194.

Mason C.F. 2003. Some correlates of density in an urban Blackbird *Turdus merula* population. Bird Study 50: 185–188.

McKinney M.L. and Lockwood J.L. 2001. Biotic homogenization: a sequential and selective process. In: Lockwood J.L. and McKinney M.L. (eds), Biotic Homogenization. Kluwer, New York, pp. 1–17.

Moore N.W. 1990. From arable farm to new town: changes in flora and fauna during the development of Bar Hill, Cambridgeshire, from 1966 to 1988. Nature Cambridgeshire 32: 27–58.

Mortberg U. and Wallentius H.G. 2000. Red-listed forest birds in an urban environment-assessment of green space corridors. Landscape Urban Plan. 50: 215–226.

Niemelä J. 1999. Ecology and urban planning. Biodiv. Conserv. 8: 119–131.

O'Connor R.J. 1985. Behavioural regulation of bird populations: a review of habitat in relation to migration and residency. In: Sibly R.M. and Smith R.H (eds), Behavioural Ecology: Ecological Consequences of Adaptive Behaviour. Blackwell, Oxford, pp. 105–142.

Peach W., Taylor R., Cotton P., Gruar D., Hill I. and Denny M. 2002. Habitat utilization by song thrushes *Turdus philomelus* on lowland farmland during summer and winter. Aspects Appl. Biol. 67: 11–20.

Siriwardena G.M., Baillie S.R., Buckland S.T., Fewster R.M., Marchant J.H. and Wilson J.D. 1998. Trends and abundance of farmland birds: a quantitative comparison of smoothed Common Birds Census indices. J. Appl. Ecol. 35: 24–43.

Snow D.W. 2003. Song and territories of Song Thrushes in a Buckinghamshire village: a ten-year study. British Birds 96: 119–131.

Solonen T. 2001. Breeding of the great tit and blue tit in urban and rural habitats in southern Finland. Ornis Fennici 78: 49–60.

Summers-Smith J.D. 2003. The decline of the house sparrow: a review. British Birds 96: 439–446.

Woods M., McDonald R.A. and Harris S. 2003. Predation of wildlife by domestic cats *Felis catus* in Great Britain. Mammal Rev. 33: 174–188.

Wotton S.R., Field R., Langston R.H.W. and Gibbons D.W. 2002. Homes for birds: the use of houses for nesting by birds in the UK. British Birds 95: 586–592.

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Indigenous knowledge and traditional conservation of fonio millet (*Digitaria exilis*, *Digitaria iburua*) in Togo

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Abstract. Fonio millet (*Digitaria exilis* Stapf, *Digitaria iburua* Stapf) is known in Togo far several centuries and has played a strategic role in the household food security mainly in rural areas. Using Participatory Research Appraisal (PRA) tools and techniques, 55 villages randomly selected in the two production zones of Togo were surveyed to document the ethnobotanical and indigenous knowledge related to its production, diversity, use and conservation. For all of the ethnic groups involved in fonio production in Togo (Akposso and Akébou in the south; Losso-Nawda, Lamba, Tamberma, Tchokossi and Gangan in the north), the crop has a high sociocultural value. The fonio genetic diversity being managed by the farmers seems important as 42 landraces were recorded. Two lines of origin that contributed to this current genetic diversity (local domestication or introduction from neighbouring countries) were reported by the farmers. Cooking qualities, growth cycle, colour and size of the grains are the main criteria used by farmers to describe varieties. According to farmers, fonio production and diversity are being regressing because of several constraints of which the most important are lack of adequate harvest, threshing and processing technologies and development of pests and diseases. The important ethnobotanical and indigenous data recorded will be useful in accessing the genetic diversity of the crop in Togo and in defining appropriate strategies for its conservation on farm.

Introduction

The cosmopolitan genus *Digitaria* (Gramineae, Poaceae) includes 230 species that are widely distributed in the tropics and in the subtropics (Clayton and Renvoze 1986). Among them, *Digitaria exilis* and *D. iburua*, known respectively as white and black fonio, are domesticated and cultivated in West Africa (Portères 1976) where they are staple food for several millions of people.

According to Bezpaly (1984) and Vietmeyer et al. (1996), the total area cultivated by year is estimated at about 300,000 ha. Fonio is one of the most nutritious and best-tasting of African cereals (Jideani 1990). Its seeds are rich in methionine and cystine, two vital amino acids in human nutrition that are lacking in some major cereals such as rice, wheat, sorghum, barley and rye (Vietmeyer et al. 1996). The crop withstands drought and floods and flourishes in poor soils. Therefore, it has a potential of playing future role in agriculture and food security in West-Africa. However, this potential cannot be exploited to advantage if the basic information related to the production, use and diversity are not well understood.

In Togo, a long history of cultivation and tradition coupled with high landraces diversity (19 ecotypes reported by Clément and Leblanc 1984) of fonio has surely led to important amount of indigenous knowledge. Because of scientific neglect, this has never been documented for use by scientific research and development agencies. In order to fill this gap, a survey was conducted throughout the production zones of the country. The study mainly aimed at understanding the socio-economic characteristics of the producers; the agricultural practices used; the production constraints; the landraces diversity, origin, naming, traditional description and classification; the indigenous uses and the traditional diversity management and conservation practices. The finding reported here will further guide genetic diversity studies on this crop and help formulating sustainable promotion and conservation strategies, both *in situ* (on-farm) as well as *ex situ*.

Methodology

Fifty-five villages randomly selected in the two fonio production zones of the country were surveyed in 2003 (Figure 1). Main criteria used for selecting villages are production, ethnic group and cultural value. Randomness was practiced after selecting the villages that met these criteria. Data were collected during expeditions from the different sites (villages) through the study. Participatory Research Appraisal (PRA) tools and techniques (direct observation, focus group and individual discussions, field visits, administration of questionnaire, etc.) was used, following Guarino and Friis-Hansen (1995) and Christinck et al. (2000). Interviews were conducted with the help of translators from each area. Four-hundred and eighty-seven randomly selected producers (seven to nine males and females per village) were surveyed in the different production zones.

Information collected were related to the socio-economic characteristics of the producers, the agricultural practices, the production constraints, the existing landraces (diversity, origin, naming, traditional description, and classification) and their traditional management, conservation and uses.

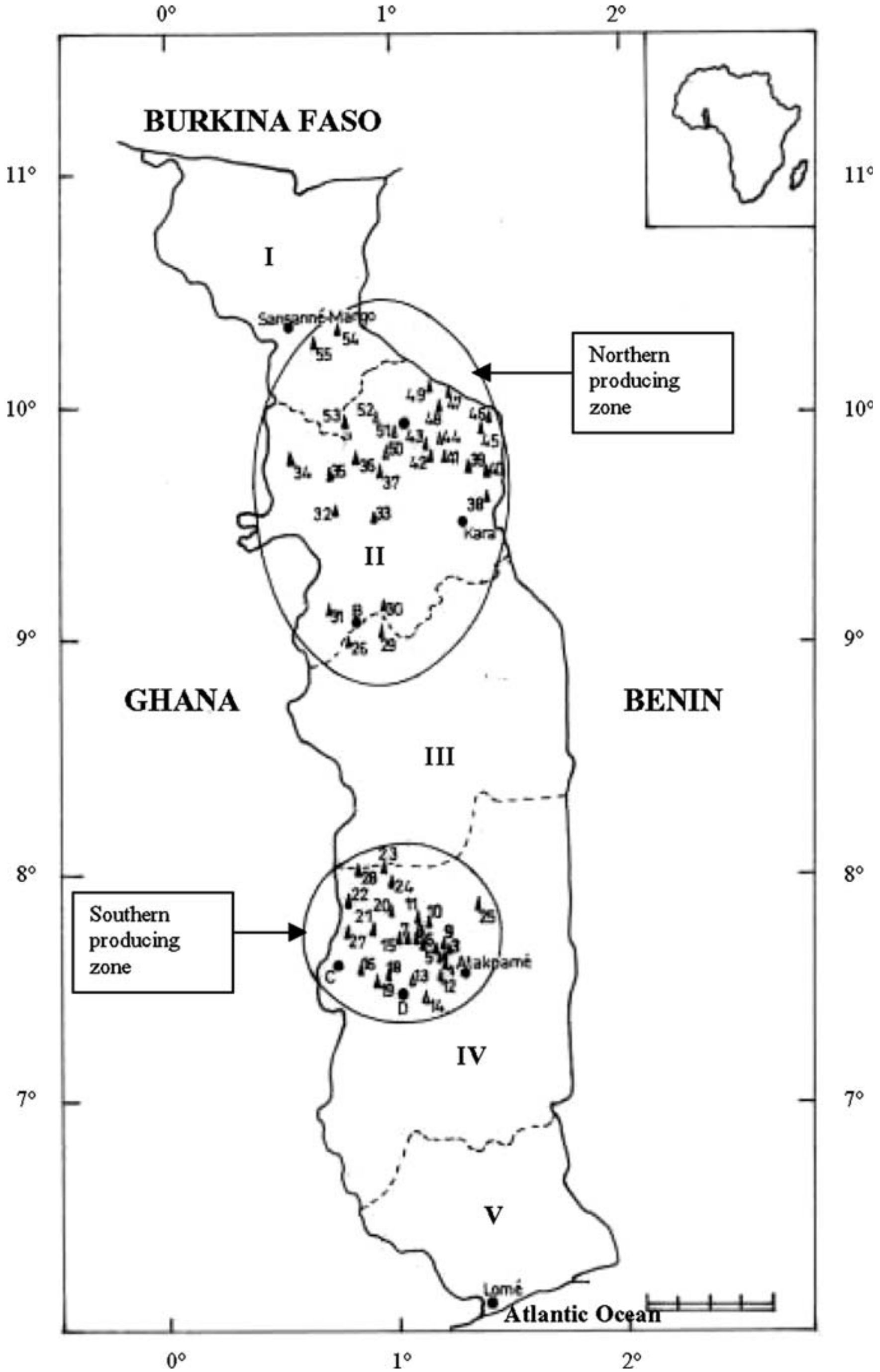

Figure 1. Fonio producing zones and villages surveyed during the study in Togo.

Results and discussions

Current status of fonio production in Togo

In Togo, fonio millet is produced in three administrative regions organised in two zones: Kara and Savanes regions in the north and Plateaux region in the south (Figure 1). Information (unpublished data) gathered from the National Office of Agricultural Statistics and Documentation of Togo (DSID) places fonio in fifth position among cereal crops after maize, sorghum, pearl millet and rice. The evolution of its production was erratic during the last 20 years when considering the total area cultivated (Figure 2). Since 1996, the total area devoted to the crop has regularly declined (Figure 2) at an average rate of 17% a year. Hence, only 3521 ha were recorded in year 2000 against 11136 ha in 1996.

According to the discussion we had with the farmers during the survey, three major reasons were presented to explain this worrying situation. These are: poor market demand, difficult production and post harvest processing, and rural depopulation. In the northern production zone, many farmers have completely or partially replaced fonio by maize (recently introduced by the national agricultural extension services) for its higher yield and easier production, harvesting, processing and commercialising. In the southern production zone, the reduction of labour supply has led many elder producers to abandon this high labour-consuming fonio crop and devoting themselves to other cash income crops (coffee, cacao, banana, etc.) they normally produce along with fonio as secondary crops.

Contrary to the general situation, fonio production is still very active in certain villages (Défalé and Kadjala in the north; Eliko, Edoko and Ouanibè in the south) where it remains the major food and has a higher sociocultural value.

Characteristics of the fonio producers

Among the 487 farmers interviewed, 11 (2.3%) were less than 30 years old, 196 (40.2%) were in the age group of 30–50 years and 280 (57.4%) were above 50 years old. They belong to seven ethnic groups (Akposso and Akébou in the south; Losso-Nawda, Lamba, Tamberma, Tchokossi and Gangan in the north) of which two (Akposso and Lamba) are known as the most important producers (Adoukonou-Sagbadja et al. 2003).

Fonio growers encountered have very low educational level. Most of them (63.3%) have never been to school, only 9.1% have reached secondary school and the remaining (27.6%) have been to primary school. The great majority (96.7%) of them have farming as the main occupation. Only few farmers (3.3%) are civil servants. A little more than two-thirds (67.8%) of the fonio producers encountered were animists and about one-third (32.2%) were

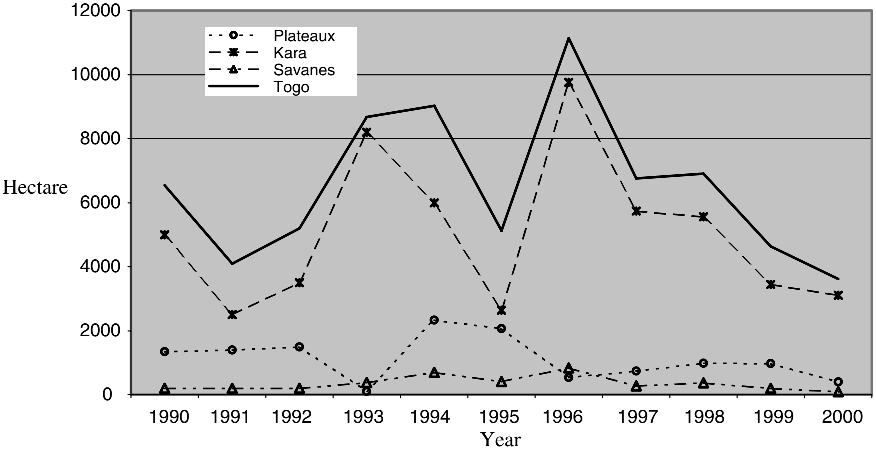

Figure 2. Evolution of area devoted to fonio cultivation in the three administrative regions.

Christians. Such predominance of animists is not surprising as in Togo the crop is associated with numerous traditional beliefs.

Although fonio is known as men crop, an important proportion (39.1%) of women (members or heads of household) where found among the growers. Women heads of household are either widows or divorced.

Agricultural practices

In Togo, fonio is mainly cultivated in marginal, mountainous and hilly zones and on sandy, poor and degraded soils. Many farmers (51.7% of respondents) used rotation cropping system in which fonio, which is more adapted to poor soils, occupies mostly the last place after maize and pearl millet or sorghum. In spite of its high adaptability to poor soils, fonio is rarely cultivated successively more than twice in the same field. Generally, field previously cultivated in fonio is allowed to fallow for 1–2 years. The field left fallow develops weeds and serves as pasture land for livestock in the north (ethnic zones Tamberma and Tchokossi).

In the majority (78.1%) of the fields visited, fonio was found in pure culture. In some cases, fonio was grown in association with other crops such as Bambara groundnut, pigeon pea, pearl millet, sorghum, cassava and okra. In these associations, fonio was the main crop. In only rare case (Tamberma tribe), fonio and pearl millet seeds were directly mixed and sown together: fonio will be harvested first and the pearl millet later.

The sowing time varies among producing zones and depends on the onset of the rainy season. Seed broadcast is the unique sowing method used by the farmers. No fertilizers and pesticides are used by the farmers as fonio flourishes in poor soils and is, in general, resistant to pests and diseases. In contrast, more attention is paid to weeding because fonio plants are low weed competitors. In most of the cases, weeds are removed (manually) four to five weeks after sowing. The harvest which is the most labour consuming activity occurs between August and October. The harvesting methods vary with the producing zones and the ethnic groups. With the Akposso and Akébou ethnic groups in the south, mature fonio plants are uprooted while in the north, traditional tools (home knives and sickles) are used by farmers to cut straw with mature panicles during harvesting. The Lamba tribe straw cutters for example, use a special craft thimble made with a particular variety of calabash to protect their index fingers against injuries.

Threshing method used to extract grains after harvesting also depends on the producing zones. In the south, fonio is threshed by beating the straw while in the north grains are extracted by trampling dry straw. Because of the intense sunshine during the harvesting period, threshing is done overnight. After threshing, grains are dried 3–4 days and stored in barn. According to farmers the storage duration is about 5–10 years but the seed viability (germination rate) decreases considerably after 2 years of storage.

Gender role in fonio production

Male and female farmers contribute differently to fonio production activities (Table 1): 50% of the activities (weeding, collecting panicles after harvesting, threshing by trampling, cleaning, drying, processing, and selling) are exclusively done by women while only 14.28% (harvesting and threshing by beating) are exclusively done by men. Therefore, women contribute much more to the activities than men. According to farmers, men do most work that needs more

Table 1. Gender importance in fonio production activities.

Activities	Male	Female
Land preparation	High	Low
Broadcasting (sowing)	High	Medium
Weeding	None	High
Harvesting (cutting or uprooting)	High	None
Collecting harvested fonio	None	High
Threshing by beating (south)	High	None
Threshing by trampling (north)	None	High
Cleaning	None	High
Transporting	High	High
Drying	None	High
Keeping seeds for next season	High	Low
Storing for consumption	Low	High
Processing	None	High
Selling (in market)	None	High

Table 2. Major constraints reported in fonio production in Togo (% of responses).

Constraints	Men (%)	Women (%)
Lack of improved harvesting technologies	62.5	2.6
Lack of modern tools for post-harvest processing	10.8	64.2
Insufficient knowledge in weeding system	1.3	11.1
Pests development	15.2	3.7
Attack by wild animals (birds, rats)	0.3	0.5
Insufficient rainfall	9.1	3.2
Decline of the traditional self-help groups	10.8	6.8
Lack of organised market	2.0	7.9
Total	100	100

strength and energy while activities that need more skills and patience are mostly left to women. Because the crop is labour consuming, farmers having large fields of fonio and household of small size always call for assistance. The lack of financial means for labour hiring coupled with task distribution has led to the development of both men and women self-help groups mainly for weeding and harvesting.

Production constraints

The major constraints reported by farmers are summarised, according to gender, in Table 2. For the majority of men (62.5% of responses), lack of improved harvesting technologies was the most important followed by development of insect pests management (15.2% of responses). For women, the most important constraints were the inexistence of modern tools for post-harvest processing (64.2% of responses) and the insufficient knowledge in weeding systems (11.1% of responses). This gender differences in appreciating constraints in fonio production confirms the distribution of tasks according to the sex as described above. Among the other constraints reported, pest development was the most prominent. Two insects (not found during the survey) that cause at times severe leaf and stem damages in the fields were pointed out by farmers for whom the promotion of the crop should necessarily pass through the improvement of the constraints.

Folk taxonomy and landraces diversity

In all the producing zones explored, the crop was designated by a generic name (Table 3). These generic names which vary with the ethnic groups mainly highlight the origin of the crop (food from the bush, bush grains for birds) and the quality of the food (good food, small quantity for enough food) it gives (Table 3).

Table 3. Generic names of fonio within the different ethnic groups in Togo.

Ethnic group	Generic name of fonio millet	Meaning of the name
Akposso	Ova	A new food from the bush
Lamba	Afiôhoun	—
Losso Nawda	Kafia / Figm	Small quantity for enough food
Bassar*	Ipibim (Ipi)	Bush grains for bird
Tamberma	Iponaka	—
Tchokossi	Ounvoni	Good food from the bush
Gangan	Ifi	—
Mina, Ewe*	Woxè, Gbekoui	Bush grains for bird

*doesn't cultivate fonio

In total, forty-two fonio landraces, traditionally classified in three groups according to the growth cycle (early maturing, intermediates and late maturing), were identified in all the different agro-ecological and ethnic zones surveyed (Table 4). To describe and name landraces, farmers use diverse traits. These are related to the growth habit (height and vigour) of the plant, the colour of the shoot, leaves and young panicles, seed characteristics (colour, size, form, brightness and hardness), the growth cycle, and the organoleptic characters. The meanings of local names of most of the landraces were presented in Table 4.

From name meaning and key agro-morphological traits of the landraces (Table 4), it appeared that Lamba (northern zone) and Akposso (southern zone) ethnic zones are the richest in landraces' diversity. On the other hand, the northern production zone with 33 landraces out of the 42 reported by farmers is the part of the country where most of the landraces diversity is concentrated. This finding is in agreement with the report of Portères (1955, 1976) according to which this zone of Togo is one of the important centres of diversification of fonio in West-Africa.

The value of folk taxonomy in plant genetic resources conservation was highlighted by many authors (Van Oosterhout 1990; Berlin 1992; Uguru 1998; Sambatti et al. 2001). Recognising the names farmers give to varieties and understanding the traditional system of classification (folk taxonomic classification) are important because the 'farmer-named variety' is the unit that farmers manage and select over time and the skills with which farmers recognize and manage a given amount of diversity may have important evolutionary consequences for the crop.

Origin of the landraces

Following Dalziel (1937), Henrard (1950), Portères (1976), Zeven and de Wet (1982), Haq and Ogbe (1995), and Hilu et al. (1997), fonio millet is indigenous to West Africa. Based on the discussion we had with farmers, two schools of thought contribute to explain the current genetic diversity found in Togo (figure 3). For the farmers of the first school, the existing fonio landraces were

Table 4. Fonio landraces inventoried in the different ethnic groups surveyed in Togo and their local name significance and characteristic traits.

Local name	Ethnic group	Significance of the name	Morpho-agronomic traits reported
Afio	Lamba	White fonio	Early maturing landrace (3 months); white seeds.
Adjougouri	Lamba	Produce many tillers	–
Angim	Lamba	–	Late maturing landrace (4 months).
Avècasho	Akébou	Mature quickly	Early maturing landrace (3 months).
Awèrô	Lamba	–	Early maturing landrace
Ayôrô (yôrô)	Lamba	Mature quickly	Early maturing landrace (less than 3 months); white seeds.
Djibiga	Nawda	–	Late maturing landrace (4 months).
Egniva	Akposso	–	Intermediate landrace (3.5 months)
Ezio	Akposso	Easy to husk	Early maturing landrace (less than 3 months); white seeds.
Fig'm Nawda	Nawda	Small quantity for enough food	Early maturing landrace (3 months);
Folom	Lamba	Hairy and irritated grains	Late maturing landrace (4 months); tiny, rounded and white grains
Foukmum	Nawda	Produce many tillers	Late maturing landrace (4 months)
Gnimimbi	Akébou	Sparkly (grains) fonio	Early maturing landrace (3 months); tiny and easy husking grains.
Hobi	Lamba	–	Late maturing landrace (4 months).
Ipibim (Ipi)	Lamba	Bush grains for birds	Late maturing landrace (4 months)
Ipoaga*	Otamari	–	Early maturing landrace ?
Ipoeda*	Otamari	–	Late maturing landrace (4 months)
Iporlepiah	Tamberma	White fonio	Early maturing landrace (3 months); white gains.
Iporni	Tamberma	Female fonio	Late maturing landrace (4 months)
Ipowan	Tamberma	Red fonio	Intermediate landrace (3.5 months) with reddish grains.
Itamali	Tamberma	–	Intermediate landrace (3.5 months); tiny, rounded and reddish grains.
Ipoyè (Iyè)*	M'bermè	Mature quickly	Early maturing landrace (3 months).
Kantonga	Gangan	–	Early maturing landrace (3 months).
Kayara (yara)	Lamba	–	Late maturing landrace (4 months)
Kiwo	Lamba	–	Early maturing landrace (3 months); rounded, hairy (?) and reddish grains.
Kopordagou	Tamberma	Male (vigour) fonio	Late maturing landrace (4 months); rounded and reddish grains.
Kpéntiki	Tchokossi	–	Early maturing landrace.
Lamfig'm	Nawda	Fonio of Lamba (origin)	Late maturing landrace (4 months), and reddish grains.
Namba	Nawda	Mature quickly	Early maturing landrace (3 months).

Table 4. Continued.

Local name	Ethnic group	Significance of the name	Morpho-agronomic traits reported
Nanam*	Otamari	–	Intermediate landrace (3.5 months)
Oufapôh	Akébou	–	Late maturing landrace (4 months)
Ougniva	Akposso	Fonio with big grains (size)	Intermediate landrace (3.5 months).
Ounfissa	Gangan	Red like blood (grains' colour)	Early maturing landrace (3 months), reddish grains.
Ounvonikpa	Tchokossi	Good cooking quality	Late maturing landrace (4 months).
Ova	Akposso	A new food from a bush (origin)	Late maturing landrace (4–5 months).
Sammao	Lamba	–	Late maturing landrace (4 months).
Sèmbre	Lamba	Hard but good for food	Intermediate landrace (3.5 months), big and reddish grains.
Tchabigô	Lamba	Mature lately	Late maturing landrace (4 months).
Tchapionga	Nawda	–	Late maturing landrace (4 months)
Tchibam or Tipon	Lamba	Hard to husk	Late maturing landrace (4 months), black grains.
Trikpa	Akposso	Difficult to husk	Late maturing landrace (4 months), big and black grains, difficult cultivation.
Vafoo	Akposso	Easy to husk	Early maturing landrace (less than 3 months); easy cultivation.
Vitchi	Akposso	Fonio of twins (cultural role)	Dwarf; early maturing landrace (less than 3 months); reddish grains.
Yaarang	Nawda	–	Early maturing landrace (3 months) rounded, hairy and reddish grains.
Yolum	Lamba	Fonio harvested in raining period	Intermediate landrace (3.5 months).
Waareh or Waaro	Lamba	Difficult to husk	Late maturing landrace (4 months), big and black grains, difficult cultivation.

*Landraces documented from some Beninese farmers newly installed in the northern producing zone in Togo.

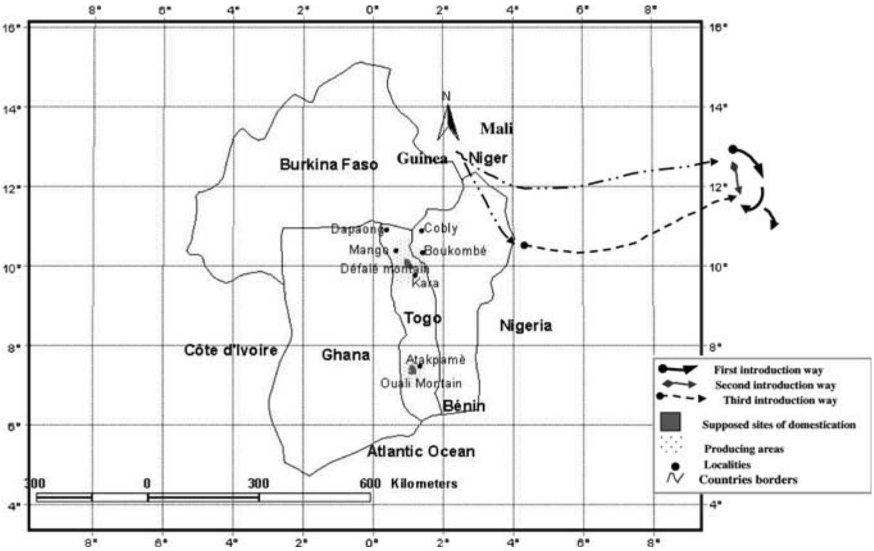

Figure 3. Proposed origins of fonio germplasm cultivated in Togo.

formerly domesticated locally around the mountains of Ouali (near Atakpamé in the South) and Défalé (Doufelgou district in the North) by Akposso and Lamba ancestors who respectively occupied these sites. According to them, wild species known as 'Birds' fonio' (*Djigbla* and *Ovahoui* in Akposso, *Sôhia* in Akébou, *Léto* and *Kanéra* in Lamba, *Gniwinou* in Nawuda, and *Oudjaloun* in Gangan) and consumed in the past as food by the hunters during long hunting trips were used and still exist in the bush (savannah or ancient fallow).

For the farmers of the second school of thought landraces were introduced to Togo from the neighbouring countries (Burkina Faso, Benin, Ghana and Côte d'Ivoire). Three lines of introductions linked to the peoples' immigration and establishment were reported. The first line was Burkina Faso – Benin – Togo and concerns the ethnic group Tamberma (equivalent of Otamari in the north-west of Benin) located at Nadoba in the north-east of Togo (Figure 3). Farmers reported that ancestors of Tamberna people came from Dinaba in Burkina Faso with some fonio landraces and first established themselves respectively at Cobly and Boukoumbé in Benin before entering Togo by Nadoba where they are since established. The second introduction line reported was linked to the immigration of Gangan people originated from the south of Burkina Faso. With their series of landraces, these people would have entered Togo by Dapaong in the North (Figure 3) and established themselves in the region of Gando (North). Tchokossi ethnic group established in Mango region was concerned with the third introduction line reported. Their ancestors would be some Baoulé of Côte d'Ivoire who came to Togo via Ghana with their fonio landraces.

Taking into account the two types of explanation, one can hypothesise that fonio landraces cultivated in Togo are derived from both indigenous domestications and introductions from neighbouring countries (Burkina Faso, Benin, Ghana and Côte d'Ivoire). Similar situation was reported with yam which is also indigenous of the region (Dansi et al. 1999; Dumont and Vernier 2000; Mignouna and Dansi 2003). The historical-ethnobotanical meanings of the generic names given to the crop (Table 3) are in favour of the domestication hypothesis. According to Portères (1976), this domestication occurred in many regions of West-Africa. Therefore, landraces introduced in Togo, as reported by farmers, were also probably domesticated in their countries of origin. A germplasm survey is being organised to identify and collect (with farmers' collaboration) the related wild species of fonio, as these may be sources of useful genes for the genetic improvement of the crop.

Indigenous uses

Fonio as religious and cultural crop

Like yam in West-Africa (Orkwor 1998) and taro in Hawaii (Matthews 1998), fonio has an important religious and cultural value for its producers. In all the communities surveyed, fonio is the food eaten during the traditional ceremonies. In Akposso and Akébou communities some rituals should be done before sowing, harvesting and eating the new harvested fonio. In these two communities, an important traditional festival called *Ovazu* takes place each year to celebrate their multi-secular cultural links with this crop. In Lamba and Tamberma communities, fonio grains are the most important ingredients in women initiation ceremonies and for the traditional baptism of newborn child. It also plays an important role in the wedding process. To request young woman's hand, a given quantity of fonio should be sent by the man to the family in law. The bigger the quantity of fonio offered, the most sincere and valuable is the bridegroom.

In Akposso and Akébou communities, newly married couple should take together fonio food during the first wedding night and this is done with rituals placed under the auspices of an ancestral fetish named *Kolissa*. This ceremony is seen as a contract of fidelity of the lady to her new husband, and of the man to his family in law. The fetish *Kolissa* is chosen because peoples of these communities believe that fonio was a gift of that ancestral divinity to their ancestors. In fact, according to the history, it is *Kolissa* that indicated bush fonio to their ancestors as good food. This last information is another element that is in favour of the domestication hypothesis highlighted above.

Fonio as food

Fonio is essentially cultivated for home consumption. It is the staple food crop for most of the ethnic groups surveyed. In Akposso and Lamba communities, fonio can be eaten three-times a day in various ways. It is also the most important meal used during celebrations or when having guests to lunch or diner. Five different fonio-based diets were recorded during the survey and described in Table 5. The most popular fonio food reported by the farmers (78.2% of respondents) was 'Fonio-beans' or *Ayè* in Akposso language. It is the dish mostly prepared at special occasions for chiefs, dignitaries or guests. The next common fonio meals are fonio couscous (60.5% of respondents), 'fonio-rice' (59.1% of respondents) and fonio porridge (42.7% of respondents). Fonio paste (23.6% of respondents) was mostly consumed in the northern zone. In this zone, fonio is also used, solely or in mixture with sorghum, pearl millet and rarely maize to prepare the local beer named *Tchoukoutou*. As in the tradition high quality *Tchoukoutou* is produced only with sorghum, fonio-based *Tchoukoutou* is seen as low quality drink and is specially prepared for, and use as drink by the farmers (hired labour or self-help group) during the harvest.

Fonio as medicine

According to farmers, fonio has some medicinal values. It is used to treat or eliminate blood clots resulting from accidents and roughed up injuries or accumulated in the uterus after women deliveries (12.3% of respondents). Fonio is also used to treat chronic diarrhoea (5.7% of respondents), loss of appetite (5.7% of respondents), dysentery (2.3% of respondents), chickenpox (2.3% of respondents), stomach-ache (1.1% of respondents), and asthma (1.1% of respondents). Some people consider fonio as useful diet for those suffering from diabetes.

Other uses

Fonio's straw is used as a fodder for ruminants, mainly sheep, cattle and goat. It is also used in protecting plant nursery against sun, making mattresses and hay, confecting kitchen, barn roof and jars and in building walls. Some farmers use the ash of the straw as potash for cooking. Some (5% of respondents) also reported the use of fonio grains in feeding poultry, especially young Guinea fowl. According to them, a daily feeding of young guinea Fowl with fonio grains orients their sex differentiation in favour of male.

Traditional conservation of fonio biodiversity on farm

At the household or farmer level, the number of landraces maintained varies from one to three. In the entire producing zone explored, 85% of the farmers produced only one variety, 10% cultivated two varieties and only 5% had three varieties.

Table 5. Major fonio food products in Togo.

Food forms	Local name (ethnic group)	Freq.in %	Processing description
Fonio-beans	*Ayè* (Akposso), *Warreh* (Akébou), *Ounvoenialoa* (Tchokossi), *Fig'm tiram* or *Dabla* (Nawda), *Ounkoussissi*(Lamba)	78.2	Fonio grains are added to boiling pulse and cooked for 10 min. The food obtained is eaten with red oil palm.
Fonio couscous	–	60.5	Fonio couscous is cooked in ready soup, fish or meat could be added.
Fonio-rice	*Epoéta* (Akposso), *Wayôloow* (Akébou)	59.1	Fonio is cooked in steam salt water with vegetables (eggplant, cabbage, etc). Red oil palm could be occasionally added before consumption.
Thick and thin porridge	*Ounvoenibaca* (Tchokossi), *Kafuia ndôro* (Lamba)	42.7	Fonio grains are boiled in water to obtain a consistence gruel and eaten mixed with honey or sugar.
Paste	*Farienpôh* (Akébou), *Fig'm hag'm* (Nawouda), *Kafuia moto* or *Gnabre* (Lamba), *Ounvoenito* (Tchokossi)	23.6	Paste is prepared using fonio grains solely or in mixture with flour of other cereals (sorghum, pearl millet, finger millet but rarely maize).

Each year, farmers' decision-making in the choice of how many and which varieties to grow is influenced by diverse socioeconomic (food availability in the barns, availability of labour), agronomic (grow cycle, yield, easiness in processing, cooking qualities, ability of supporting late harvesting) and cultural (use for special ceremonies as in the case of landrace *Vitchi* in Akposso tribe) factors. Because early maturing landraces mature during the rainy period and must be harvested immediately, farmers producing several crops and having insufficient labour, generally adopt late maturing landraces. Farmers who grew two to three landraces used different fields or different plots within the same field.

Varieties are either inherited from parents and conserved with great care (87.4% of the respondents) or obtained from friends (8% of the respondents) or from local markets (4.6% of the respondents). Each of the households interviewed was self-sufficient in term of seeds. Each year, a certain quantity of seeds is determined per variety and retained on farm from the new harvest to serve for the next sowing. Selected seeds are sun dried and stored in granaries in specific storing jars (that will store up to 50 kg of grains) or in calabashes. According to farmers, fonio seeds longevity in the traditional storage system is about 10 years.

Nowadays, young farmers are less and less taking an interest in fonio as its production, harvest and processing are tedious. Consequently, the risk to see the crop disappeared in Togo in the forthcoming 20 years rise up on the horizon if nothing is done. It is therefore urgent to develop strategies that will promote its production and ensure the sustainable conservation of its genetic diversity both *ex situ* and *in situ*.

Conclusion

In Togo, a long history of fonio cultivation and tradition coupled with high landraces diversity has led to important amount of indigenous knowledge. For the producers, fonio is more than a staple food crop. Its production and consumption are highly linked to the socio-cultural live of the people. Because of diverse constraints, production of fonio millet is decreasing. For the crop to be promoted there is a need to develop modern harvesting technologies and provide women with adequate husking machine. To complement the *ex situ* conservation of the collected germplasm, on farm conservation strategies should be developed. For this to be sustainable, in-depth studies are needed to define its scientific basis.

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References

Adoukonou-Sagbadja H., Dansi A., Vodouhè R. and Akpagana K. 2003. Collecting fonio (*Digitaria exilis* Stapf, *D. iburua* Stapf) landraces in Togo. Plant Genetic Resources Newsletter (In press).

Berlin B. 1992. Ethnobotanical Classification. Principles of categorization of plants and animals in traditional societies. Princeton, New York, 335 pp.

Bezpaly I. 1984. Les Plantes Cultivées en Afrique Occidentales. Editions MIR, Moscow pp.84–87.

Christinck A., Vom Brocke K., Kshirsagar K.G., Weltzien E. and Bramel-Cox P.J. 2000. Participatory methods for collecting germplasm: experiences with farmers in Rajasthan, India. Plant Gen. Resour. Newslet. 121: 1–9.

Clayton W.D. and Renvoze S.A. 1986. Genera Graminum, Grasses of the World. Kew Bull, Additional Series XIII.

Clément J. and Leblanc J.M. 1984. Collecte IBPGR-ORSTOM de 1977 au Togo. In Prospection des *Digitaria exilis* (Fonio) en Afrique de l'Ouest. Catalogue ORSTOM 1984, pp. 3–7.

Dalziel J.M. 1937. The Useful Plant of West Tropical Africa. An Appendix to The Flora of West Tropical Africa. Hutchinson J. and Dalziel J.M. (eds), Crown Agents, London, 612 pp.

Dansi A., Mignouna H.D., Zoundjihekpon J., Sangare A., Asiedu R. and Quin F.M. 1999. Morphological diversity, cultivar groups and possible descent in the cultivated yams (*Dioscorea cayenensis–Dioscorea rotundata* complex) of Benin Republic. Genet. Resour. Crop Evol. 46: 371–388.

Dumont R. and Vernier P. 2000. Domestication of yams (*Dioscorea cayenensis–rotundata*) within the Bariba ethnic group in Benin. Outlook Agriculture 29: 137–142.

Guarino L. and Friis-Hansen E. 1995. Collecting plant genetic resources and documenting associated indigenous knowledge in the field: a participatory approach. In: Guarino L., Ramanatha Rao V. and Reid R. (eds), Collecting Plant Genetic Diversity, Technical Guidelines. CAB International, Wallengford, UK, pp. 345–366.

Haq N. and Ogbe D.F. 1995. Fonio (*Digitaria exilis* and *Digitaria iburua*). In: Williams J.T. (ed), Cereals and Pseudocereals Chap 5. Chapman & Hall, 2–6 Boundary Row, London SE1 8HN, UK, pp. 225–245.

Henrard J.T. 1950. Monograph of the Genus *Digitaria*. Leaden Univ. Press, Leaden.

Hilu K.W., Mribu K., Liang H. and Mandelbaum C. 1997. Fonio millets: ethnobotany, genetic diversity and evolution. S. Afr. J. Bot. 63(4): 185–190.

Jideani I.A. 1990. Acha – *Digitaria exilis* – the neglected cereal. Agric. Inst. 42(5): 132–43.

Matthews P.J. 1998. Taro in Hawaii: present status and current research. Plant Gen. Resour. Newslett. 116: 26–29.

Mignouna H.D. and Dansi A. 2003. Yam (*Dioscorea* sp.) domestication by the Nago and Fon ethnic groups in Benin. Genet. Resour. Crop Ev. 50(5): 519–528.

Orkwor G.C. 1998. In: Orkwor G.C., Asiedu R. and Ekanayake I.J. (eds), Food Yams, Advances in Research. IITA and NRCRI, Nigeria, pp. 1–12.

Portères R. 1955. Les céréales mineures du genre *Digitaria* en Afrique et Europe. J. Agric. Trop. Bot. Appl. 2 .

Portères R. 1976. African cereals: *Eleucine*, Fonio, Black fonio, Teff, *Brachiaria*, *Paspalum*, *Pennisetum* and African rice. In: Harlan J.R., de Wet J.M.J. and Sternler A.B.L. (eds), Origins of African Plant Domestication. Moulton. The Hauge, pp. 409–452.

Sambatti J.B.M, Martins P.S. and Ando A. 2001. Folk taxonomy and evolutionary dynamics of Cassava: a case study in Ubatuba, Brazil. Econ. Bot. 55(1): 93–105.

Uguru M.I. 1998. Traditional conservation of vegetable cowpea in Nigeria. Genet. Resour. Crop Ev. 45: 135–138.

Van Oosterhout S.A.M.. 1990. A question of cultural context: formal taxonomy versus peasant classifications of *Sorghum bicolor* in Zimbabwe. Mitteilungen aus dem Institut für Allgemeine Botanik, Hamburg 23b: 953–959.

Vietmeyer N.D., Borlaugh N.E., Axtell J., Burton G.W., Harlan J.R. and Rachie K.O. 1996. Fonio (Acha). Lost crop in Africa Chap. 3. BOSTID Publication, 58–75.

Zeven A.C. and de Wet J.M.J. 1982. Dictionary of Cultivated Plants and their Regions of Diversity. Excluding Most Ornamentals Forest Trees and Lower Plants. Centre for Agricultural Publishing and Documentation, Wageningen, 128 pp.

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People and mammals in Mexico: conservation conflicts at a national scale

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Abstract. Contrary to much supposition, recent studies, typically at global and continent-wide scales, have documented a positive relationship between spatial variations in human density and species richness of selected groups of vertebrates. How widely this pattern generalises remains unknown, and particularly how well it extends to analyses at the extent of a country and at reasonably fine spatial resolution, and to regions with well-developed mechanised agricultural infrastructure. Here, we demonstrate that there is a positive relationship between human density and mammal species richness across Mexico, and that this appears to follow from similar patterns between spatial environmental variation (particularly net primary productivity, precipitation and temperature) and both human density and mammal species richness. These results have some potentially important implications for conservation planning in the region, particularly given that optimal complementary sets of areas to represent all mammal species in Mexico tend to lie in areas of disproportionately high human density.

Introduction

The on-going regional and global decline in native biodiversity is, ultimately, associated with growth in the human population and the enterprise that sustains it, particularly that which leads to habitat destruction, fragmentation and degradation (Ehrlich 1995; Hannah et al. 1995; Kerr and Currie 1995; Cincotta et al. 2000; Liu et al. 2001; Fairbanks et al. 2002). Whilst the large 'ecological footprint' of components of this population is important, generating pressures in areas often far removed from where the people responsible reside (Rees 2001; Wackernagel et al. 2002), the extent of the conflicts between people and other species also depends in large part on the degree to which spatially they co-occur. If areas of high human density coincide with those containing a high richness of other species, conservation conflicts are likely to be severe. If, however, there is limited overlap between the two then human development activities may compromise the persistence of other species to a lesser extent.

Evidence as to the relationship between the spatial distribution of people and components of biodiversity is mixed. On the one hand, a number of studies have demonstrated that at local-scales (e.g. areas of the size of a protected area of fine-resolution mapping unit) the abundance and/or occurrence of individual species or groups of species declines with increasing human density (e.g. Hoare and du Toit 1999; Thompson and Jones 1999; Brashares et al. 2001; Harcourt et al. 2001; Parks and Harcourt 2002; Walsh et al. 2003). Unsurprisingly, high human densities and the persistence of many native species, particularly those of large body size, are mutually exclusive. On the other hand, other studies, conducted at more regional scales (e.g. using nations or coarse-resolution mapping units), have documented broad positive relationships between human densities and the native species richness of particular groups of organisms (Hunter and Yonzon 1993; Fjeldså and Rahbek 1998; Balmford et al. 2001; McKinney 2001; Araújo 2003; Luck et al. 2004; Real et. al. 2003). Here, species richness and human density tend to be higher in the same areas, arguably because they have historically responded to the same environmental factors, particularly net primary productivity; high productivity provides a larger resource base enabling more species to persist in an area, and may also have proven attractive for the establishment and enabled the subsequent growth of human populations.

Investigations of the broad relationships between human activity and species richness have principally concerned the Old World (but see Dobson et al. 1997), where the history of human occupation is much longer, and have seldom been undertaken at the within-country scale, nor at a data resolution particularly close to that employed even for broad scale conservation planning efforts (but see Chown et al. 2003). This is significant given recent concerns that existing conservation areas, and those which are high priorities for designation as such, may be located in areas of unusually high human population density (Musters et al. 2000; Harcourt et al. 2001; Parks and Harcourt 2002; Chown et al. 2003). In this paper, we address these gaps, in examining relationships between the spatial variation in the distributions of mammal species richness, human population density, landscape transformation, and conservation areas in Mexico.

The mammals of Mexico make an interesting case study for several reasons. First, the high climatic diversity, and complex topography and geological history, have resulted in Mexico having some of the highest levels of extant species richness and endemism of any country in the world (10% of global biodiversity; Mittermeier et al. 1999). Its mammal fauna ranks second in species richness at the global level (Mittermeier et al. 1999), comprising 525 species of which 30% are endemic to the country (Ceballos et al. 2002). Second, a large number of these species have extremely narrow distributions, 131 of all species occur in areas of less than 114,000 km^2 (Arita et al. 1997). Third, the rest of the mammal fauna shares Mexico with a population of over 98 million people, and includes one of the largest urban settlements (Mexico City) anywhere. Fourth, Mexico has a well-studied history of anthropogenic occupation (Sanders 1979; Bradbury 1982; Butzer and Butzer 1997; Challenger 1998; Grove 2000; Whitmore and Turner 2001).

Methods

Data

Information on mammal distribution was obtained from the National Information System on Mexico's Biodiversity compiled by the Mexican Commission on Biodiversity (CONABIO, http://www.conabio.gob.mx). This database used as a starting point the maps of Hall (1981), at a spatial resolution of a half-degree (measures on average 53.25 km on each side), but updating the information with new taxonomic and distributional data published up to the end of 2000 (Arita et al. 1997; Reid 1997; Wilson and Ruff 1999; Ceballos et al. 2002). Although reserves are almost invariably smaller in extent than entire half-degree grid cells, often substantially so, this resolution can usefully be used to seek out areas in need of conservation attention (Chown et al. 2003; Larsen and Rahbek 2003). For the purpose of this study, the analyses were restricted to land mammals, with introduced and insular species excluded. We also omitted coastal cells with less than 25% land area to avoid confounding the influence of area with other effects. A total of 423 mammal species were analysed within a grid of 705 cells.

For each grid cell we distinguished nine categories: (i) the total number of mammal species (out of a possible 423); (ii) the number of threatened species [subsuming all species categorised as vulnerable, endangered, or critical by IUCN (2000); 41 species]; (iii) the 25% most range restricted species (106 species); (iv) the 25% most range widespread species (106 species); (v) the number of endemic species (restricted to Mexican territory; 112 species), and (vi–ix) the numbers of species in each of four separate body mass categories (1st: 0.002–0.016; 2nd: 0.017–0.040; 3rd: 0.041–0.254, 4th: 0.269–587.52 kg, respectively), based on the quartiles of the body mass distribution (body mass information from Silva and Downing 1995; Reid 1997; Wilson and Ruff 1999; $\sim$106 possible species in each category), and for convenience labelled mass 1 (quartile 1) through to mass 4 (quartile 4).

For each grid cell, values of net primary productivity, precipitation, and temperature were calculated, these three variables having been widely recognized as biologically important influences on levels of species richness (see Currie 1991; O'Brien 1998; Kerr and Currie 1999; Gaston 2000; Morin 2000; van Rensburg et al. 2002). The mean annual monthly values of precipitation (mm yr^{-1}) and temperature (°C) were derived from data from many meteorological stations (n = 5181, Quintas 2000), data on mean annual net primary productivity (g C m^{-2} year^{-1}) were derived from the GPPDI global model (Zheng et al. 2001).

Human population density data were obtained from the most recent Mexican population census (INEGI 2001), comprising the numbers of people in all human settlements (cities, towns and villages). A settlement was classified as lying within a given grid cell if the majority of its area fell within that cell, and the population size of all settlements within that cell were summed. The intersections were carried out using ArcView GIS 3.2a.

The percentage of current land-cover that has been markedly transformed by human activities was determined for each grid cell by summing the areas of five land-cover classes: forest plantations, cultivated lands, urban areas, degraded lands and water bodies. The data were taken from The National Forest Inventory (SEMARNAT 2000), and were based on digital aerial photographs and seasonally standardised Landsat TM (at 1:125,000 scale) satellite imagery captured primarily during 1999–2000.

Data on the size (km^2), geographic limits and shape of 96 protected areas (the vast majority of significant areas) in Mexico, were provided by the National Institute of Ecology (INE, http://www.ine.gob.mx). Most of these protected areas correspond to IUCN categories I, II, IV and IX, these being strict nature reserves, national parks, managed nature reserve/wildlife sanctuaries, and biosphere reserves, respectively. These areas were mapped using ArcView 3.2a.

To evaluate the level of human presence bordering existing designated conservation areas, we delineated a buffer 50 km wide around each of the 96 protected areas and then calculated a mean human population density (individuals.km^{-2}) in these 50-km zones. The 50-km buffer was traced using the buffer facility of ArcView 3.2a.

Analyses

Human population density, rare and threatened species richness, and protected area size were all logarithmically (base 10) transformed, and percentage of land transformation was square root transformed, for analysis.

Spatial structure in the data was explored by determining autocorrelograms for each of the major variables in the analyses. Moran's I was calculated for 15 equal-distance classes of about 213 km in width, and spatial correlograms were produced and tested for significant spatial dependence. Since the study covered a relatively large geographic area, grid cell coordinates were not treated as Cartesian coordinates when measuring distances between them. Instead, distances along great circles were calculated to take into account the curvature of the earth's surface. Bonferroni's correction for multiple comparisons was used in assessing overall correlogram significance.

We report the results of two sets of analyses of the relationship amongst mammal species richness, human population density, environmental and landscape variables, both conducted in SAS (version 8.2). Initially, we conducted analyses assuming an independent errors model using the PROC GLM procedure. Spatial autocorrelation may, however, systematically invalidate the assumption of independent errors, distorting classical tests of association and rendering correlation coefficients, regression slopes and associated significance tests very misleading (Clifford et al. 1989; Cressie

1991; Legendre 1993; Lennon 2000; Legendre et al. 2002). To avoid this, a second set of analyses was conducted using the PROC MIXED procedure to implement spatial correlation models (Littell et al. 1996). Our spatial models assumed an exponential covariance structure as this gave a better fit to the null model than five alternative covariance structures: spherical, gaussian, linear, linear log and power.

As a measure of the pattern of complementarity (*sensu* Williams 2001) exhibited by the mammal fauna in Mexico, we identified a set of optimal solutions to the integer linear programming problem of minimising the number of grid cells such that each species is represented in at least one grid cell in the region (Underhill 1994); this is intended as a basis for exploring the issue of complementarity, and not to imply that such representation would be adequate for many purposes. This was done using the CPLEX optimisation software (ILOG 2001). In the present case, numerous equally optimal solutions exist for this problem, and the specific solution found depends on the order in which variables (cells) are introduced. To avoid repeated selection of the same solutions, each time one was sought an additional restriction was added to the problem that excluded the solution previously found (Rodrigues et al. 2000). This procedure obtains a random set of optimal solutions without replacement. Then, we explored the flexibility (Rodrigues et al. 2000) for minimizing the human population within the complementary networks, by determining whether the complementary cells contained greater human population densities than expected by chance. The human population density for all the optimal set solutions representing all species was calculated and then these values were compared with the mean human population density found for 10,000 sets (each consisting of the same number of cells as the complementary sets that represent each mammal species at least once) of randomly selected grid cells.

Results

Spatial variation

Spatial autocorrelograms for mammal species richness, human population density, and the environmental variables exhibited overall statistical significance and statistical significance at most lag distances (Figure 1). Autocorrelation for overall mammal species richness and the environmental variables declined steeply with increasing lag distances. Initially strong positive values rapidly became negative, but with some up-turn towards the longest lag distances. Autocorrelations for human population density and land transformation showed a much shallower pattern of decline towards longer lag distances, becoming positive again at the longest lag distances, likely reflecting similarly low densities of people and their impacts in the most distantly separated areas of Mexico Figure 2 illustrates the spatial distribution patterns of the main variables across Mexico.

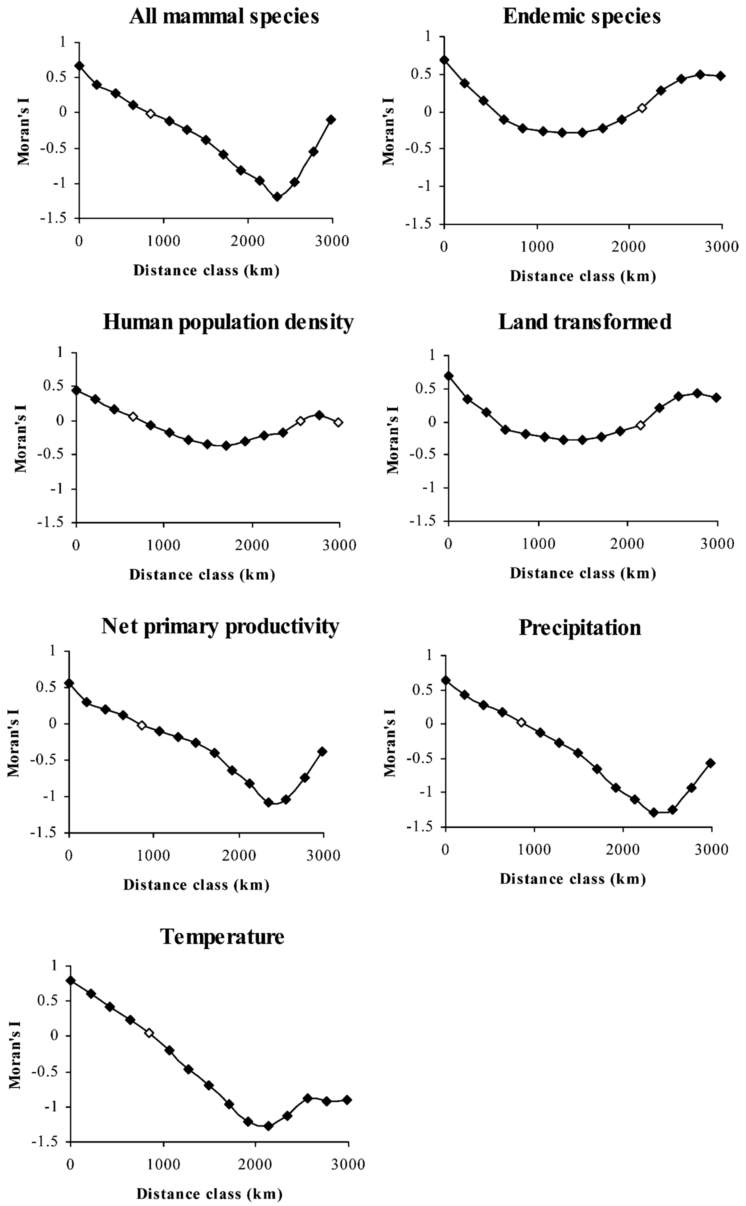

Figure 1. Spatial autocorrelograms of Mammal species and environmental variables across Mexico Distance class values represent maximum distances between pairs of points within each 213 km distance class Sequential Bonferroni correction was applied at $\alpha = 0.001$ to evaluate the statistical significance of each value of Moran's I and the overall significance of each autocorrelogram All autocorrelograms proved statistically significant overall, and filled data points represent statistically significant values.

Mammals are more speciose in the southern part of Mexico, with high richness elsewhere tending to follow the distribution of tropical moist forest. Areas of lowest richness lie in the Baja California Peninsula and the Sonora desert. Endemic and rare species are generally concentrated in areas with intermediate values of overall species richness. The most endemic rich areas lie along the Trans-Mexican Volcanic Belt and the Pacific tropical lowlands of western Mexico, while the most endemic-poor are in the Sonora and

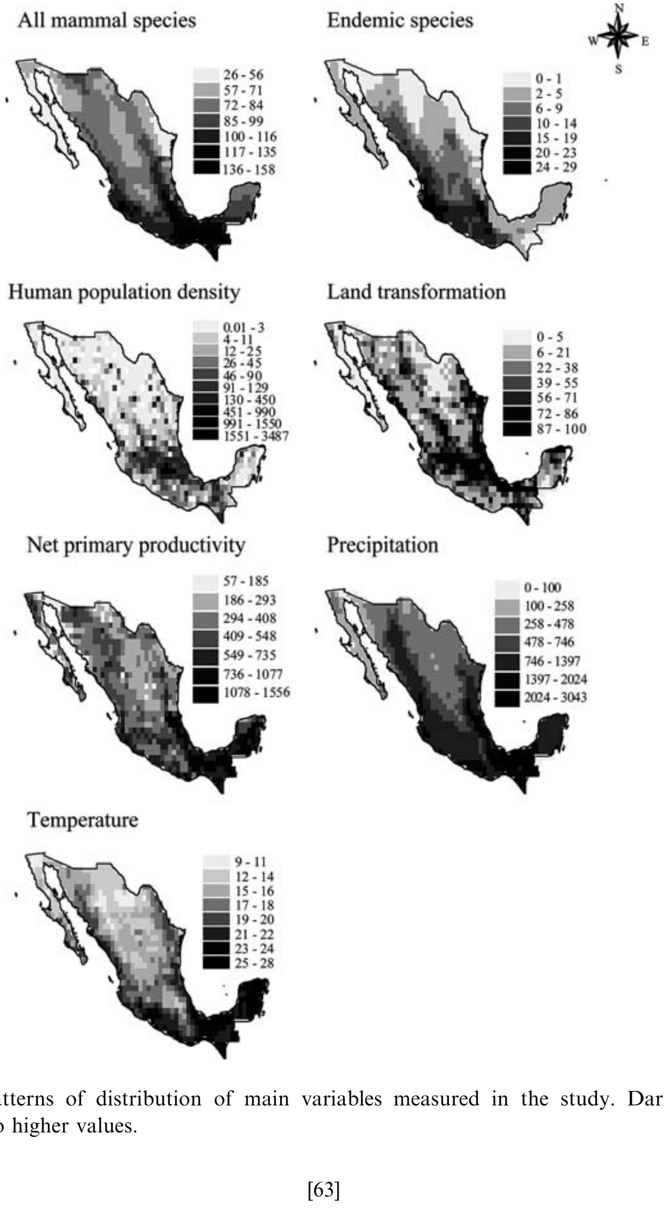

Figure 2. Patterns of distribution of main variables measured in the study. Darker colours correspond to higher values.

Chihuahua deserts and the east slopes of the Sierra Madre Oriental. Rare species are concentrated in the dry deciduous forest on the Pacific coast and montane forest along the Trans-Mexican Volcanic Belt.

The density of the human population across Mexico is highly variable (which is considered to be one of the country's population problems). Whilst the national average density is c 50 persons km^{-2}, there are areas with densities of < 1 persons km^{-2}, and others, particularly in the central Mexican basins, with densities of > 3000 persons km^{-2}. The northern parts of the country, covering big parts of the Sonora and Chihuahua deserts and particularly the Baja California peninsula, have the lowest population densities.

Net primary productivity declines northwards from an average of about 1500 g C m^{-2} $year^{-1}$ on the southern border of Mexico to below 3 g C m^{-2} $year^{-1}$ on the northern border. Precipitation shows similar trends. The driest part of Mexico is the north-west in the interior basins of Chihuahua and Coahuila and, more particularly, in Sonora and Baja California; the Altar and Vizcaino regions (which form part of the Sonora desert) are bone dry and as hot as anywhere on the American continent. Most of the tropical lowlands have mean annual temperatures of over 23 °C and are virtually frost-free. The cold land is typically over 2000 m and includes the volcanic highlands of central Mexico, the southern part of the Sierra Madre Oriental, extensive parts of the Sierra Madre Occidental and the higher ranges of Chiapas and Oaxaca. The intermediate zone lying roughly between 1000 and 2000 m is the most densely settled of the altitudinal zones, with daily temperatures ranging through 10 °C and rarely suffering frost or very high evaporation rates.

Land transformation has been at its most extensive across the central Mexican basins and the highlands and lowlands of the Gulf of Mexico. The most intensively cultivated areas are within the Bajio region, and the states of Tlaxcala, Puebla and Veracruz in which more than three-fourths of the lands are cropland.

Patterns of covariation

Assuming an independent errors model, total mammal species richness across Mexico is positively related to levels of net primary productivity, precipitation and temperature (Table 1, Figure 3). Inclusion of a quadratic term increases the explained variance in each case, but most markedly for precipitation, and there is no evidence that the relationships exhibit a decline phase. This is almost invariably true also of the subsets of mammal species (Table 1; threatened, endemic, rare, common, and in different mass categories). The weakest relationships are typically exhibited by the endemic, rare and common species, when these are analysed separately, suggesting that the relationships for total mammal species richness are dependent on the mix of species with different spatial distributions.

Table 1. Results of testing for bivariate relationships between measures of mammal species richness and human density, and mean annual net primary productivity (NPP), mean annual precipitation (PPT), and mean annual temperature (TP).

	NSM (LR)	SM (LR)	NSM (QR)	SM (QR)
NPP				
All species	$F_{1,704} = 464.0^{***}$, $r^2 = 0.41$	$F_{1,704} = 91.5^{**}$, AIC = 4612.2	$F_{1,704} = 124.4^{***}$, $r^2 = 0.43$	$F_{1,704} = 8.3^{**}$, AIC = 4580.5
Threatened	$F_{1,704} = 412.9^{***}$, $r^2 = 0.37$	$F_{1,704} = 0.01$ns, AIC = –2109.0	$F_{1,704} = 312.8^{***}$, $r^2 = 0.40$	$F_{1,704} = 2.9$ ns, AIC = 2255.3
Endemic	$F_{1,704} = 23.2^{***}$, $r^2 = 0.03$	$F_{1,704} = 7.9^{*}$, AIC = 3074.9	$F_{1,704} = 31.8^{***}$, $r^2 = 0.10$	$F_{1,704} = 8.4^{*}$, AIC = 3038.7
Rare	$F_{1,704} = 123.5^{***}$, $r^2 = 0.15$	$F_{1,704} = 12.8^{*}$, AIC = 2138.0	$F_{1,704} = 21.1^{***}$, $r^2 = 0.17$	$F_{1,704} = 22.8^{*}$, AIC = 2211.0
Common	$F_{1,704} = 8.4^{*}$, $r^2 = 0.18$	$F_{1,704} = 3.4^{*}$, AIC = 4018.0	$F_{1,704} = 19.2^{**}$, $r^2 = 0.20$	$F_{1,704} = 11.5^{*}$, AIC = 4111.0
Mass1	$F_{1,704} = 283.2^{***}$, $r^2 = 0.28$	$F_{1,704} = 50.6^{*}$, AIC = 3425.5	$F_{1,704} = 180.7^{***}$, $r^2 = 0.34$	$F_{1,704} = 2.9\ ^{*}$, AIC = 3423.8
Mass2	$F_{1,704} = 172.9^{***}$, $r^2 = 0.19$	$F_{1,704} = 0.1$ ns, AIC = 3293.8	$F_{1,704} = 118.4^{***}$, $r^2 = 0.25$	$F_{1,704} = 2.4^{*}$, AIC = 3367.9
Mass3	$F_{1,704} = 504.7^{***}$, $r^2 = 0.40$	$F_{1,704} = 0.3$ns, AIC = 2694.1	$F_{1,704} = 266.0^{***}$, $r^2 = 0.43$	$F_{1,704} = 2.8$ ns, AIC = 2449.0
Mass4	$F_{1,704} = 365.5^{***}$, $r^2 = 0.34$	$F_{1,704} = 19.9^{*}$, AIC = 2982.1	$F_{1,704} = 1892.0^{***}$, $r^2 = 0.38$	$F_{1,704} = 12.6^{*}$, AIC = 2784.0
Human population	$F_{1,704} = 129.0^{*}$, $r^2 = 0.20$	$F_{1,704} = 6.5^{**}$, AIC = 1565.7	$F_{1,704} = 1322.0^{**}$, $r^2 = 0.28$	$F_{1,704} = 10.5^{***}$, AIC = 1537.5
PPT				
All species	$F_{1,704} = 295.8^{***}$, $r^2 = 0.29$	$F_{1,704} = 25.8^{*}$, AIC = 3618.4	$F_{1,704} = 579.0^{***}$, $r^2 = 0.62$	$F_{1,704} = 13.5^{**}$, AIC = 4577.0
Threatened	$F_{1,704} = 593.1^{***}$, $r^2 = 0.46$	$F_{1,704} = 1.2$ ns, AIC = -2116.0	$F_{1,704} = 15.05^{***}$, $r^2 = 0.47$	$F_{1,704} = 4.87^{*}$, AIC = 2256.0
Endemic	$F_{1,704} = 75.97^{***}$, $r^2 = 0.11$	$F_{1,704} = 20.4^{*}$, AIC = 3025.1	$F_{1,704} = 147.5^{***}$, $r^2 = 0.29$	$F_{1,704} = 29.7\ ^{**}$, AIC = 3225.2
Rare	$F_{1,704} = 32.38^{***}$, $r^2 = 0.04$	$F_{1,704} = 1.3^{*}$, AIC = 2140.0	$F_{1,704} = 21.95^{***}$, $r^2 = 0.10$	$F_{1,704} = 9.78^{*}$, AIC = 2434.3
Common	$F_{1,704} = 10.1^{*}$, $r^2 = 0.11$	$F_{1,704} = 5.7^{*}$, AIC = 4014.2	$F_{1,704} = 41.14^{*}$, $r^2 = 0.17$	$F_{1,704} = 6.06^{*}$, AIC = 3928.4
Mass1	$F_{1,704} = 671.1^{***}$, $r^2 = 0.49$	$F_{1,704} = 267.0$, AIC = 3442.9	$F_{1,704} = 453.7^{***}$, $r^2 = 0.56$	$F_{1,704} = 33.66^{*}$, AIC = 3413.4
Mass2	$F_{1,704} = 347^{***}$, $r^2 = 0.33$	$F_{1,704} = 0.5$ ns, AIC = 3294.0	$F_{1,704} = 239.1^{***}$, $r^2 = 0.41$	$F_{1,704} = 10.3^{*}$, AIC = 3363.2
Mass3	$F_{1,704} = 907.4^{***}$, $r^2 = 0.56$	$F_{1,704} = 12.4^{*}$, AIC = 2092.6	$F_{1,704} = 484.1^{***}$, $r^2 = 0.58$	$F_{1,704} = 25.68^{*}$, AIC = 2627.3
Mass4	$F_{1,704} = 463.4^{***}$, $r^2 = 0.39$	$F_{1,704} = 4.5^{*}$, AIC = 2980.6	$F_{1,704} = 237.6^{***}$, $r^2 = 0.41$	$F_{1,704} = 6.9^{*}$, AIC = 2784.3
Human population	$F_{1,704} = 219.2^{***}$, $r^2 = 0.24$	$F_{1,704} = 12.1^{*}$, AIC = 1198.8	$F_{1,704} = 165.7^{***}$, $r^2 = 0.32$	$F_{1,704} = 4.6^{*}$, AIC = 1552.5
TP				
All species	$F_{1,704} = 295.8^{***}$, $r^2 = 0.29$	$F_{1,704} = 10.9^{**}$, AIC = 4592.5	$F_{1,704} = 161.1^{***}$, $r^2 = 0.31$	$F_{1,704} = 25.2^{***}$, AIC = 4536.8
Threatened	$F_{1,704} = 593.1^{***}$, $r^2 = 0.46$	$F_{1,704} = 0.4$ ns, AIC = -2125.0	$F_{1,704} = 38.5^{***}$, $r^2 = 0.38$	$F_{1,704} = 3.8^{*}$, AIC = 2228.7
Endemic	$F_{1,704} = 75.97^{***}$, $r^2 = 0.11$	$F_{1,704} = 7.4^{**}$, AIC = 3065.3	$F_{1,704} = 55.2^{***}$, $r^2 = 0.13$	$F_{1,704} = 14.9^{**}$, AIC = 3006.1
Rare	$F_{1,704} = 32.38^{***}$, $r^2 = 0.04$	$F_{1,704} = 0.01$ ns, AIC = 2132.1	$F_{1,704} = 4.9^{*}$, $r^2 = 0.08$	$F_{1,704} = 2.2$ ns, AIC = 2231.9
Common	$F_{1,704} = 10.1^{*}$, $r^2 = 0.11$	$F_{1,704} = 4.9^{*}$, AIC = 3411.5	$F_{1,704} = 35.9^{***}$, $r^2 = 0.10$	$F_{1,704} = 4.9^{*}$, AIC = 3931.7
Mass1	$F_{1,704} = 671.1^{***}$, $r^2 = 0.49$	$F_{1,704} = 4.9^{*}$, AIC = 3411.5	$F_{1,704} = 108.3^{***}$, $r^2 = 0.23$	$F_{1,704} = 6.8^{*}$, AIC = 3388.5
Mass2	$F_{1,704} = 347.0^{***}$, $r^2 = 0.33$	$F_{1,704} = 5.1^{*}$, AIC = 3279.7	$F_{1,704} = 72.7^{***}$, $r^2 = 0.17$	$F_{1,704} = 7.1^{*}$, AIC = 3279.7
Mass3	$F_{1,704} = 907.4^{***}$, $r^2 = 0.56$	$F_{1,704} = 7.4^{*}$, AIC = 2677.3	$F_{1,704} = 207.9^{***}$, $r^2 = 0.37$	$F_{1,704} = 4.42^{*}$, AIC = 2585.1
Mass4	$F_{1,704} = 463.4^{***}$, $r^2 = 0.39$	$F_{1,704} = 4.7^{*}$, AIC = 2969.5	$F_{1,704} = 118.3^{***}$, $r^2 = 0.25$	$F_{1,704} = 5.3^{*}$, AIC = 2985.1
Human population	$F_{1,704} = 219.2^{***}$, $r^2 = 0.24$	$F_{1,704} = 3.9^{*}$, AIC = 1559.4	$F_{1,704} = 98.1^{***}$, $r^2 = 0.22$	$F_{1,704} = 3.3^{*}$, AIC = 1512.8

NSM = Non-spatial model (model fit indicated by r^2), LR = linear regression, QR = quadratic regression, SM = Selected spatial model (model fit indicated by AIC). All relationships were positive. $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$. ns = non significant relationship.

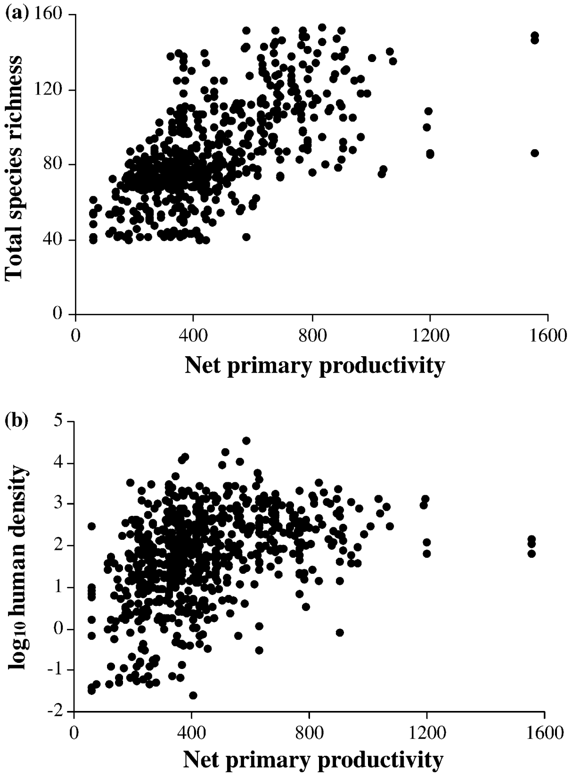

Figure 3. Relationships between net primary productivity and (a) total mammal species richness and (b) $\log_{10}$ human population density.

Controlling for the effects of spatial autocorrelation typically weakens the relationships between mammal species richness and net primary productivity, precipitation or temperature markedly (Table 1). For total species richness these remain statistically significant, but for some combinations of subsets of the mammal assemblage and environmental variables this is not the case. In particular, for threatened species and those of intermediate body mass previously statistically significant relationships are rendered non-significant when controlling for spatial autocorrelation.

As with total mammal species richness, human population density exhibits positive relationships with the environmental variables, whether or not spatial autocorrelation is controlled for (Table 1), although the highest human population densities tend to be associated with somewhat lower levels of net primary productivity than are the highest levels of species richness (Figure 3). In consequence, total mammal species richness and human population density are positively related, using an independent errors model and a model controlling for spatial autocorrelation, with some improvement in model fit with the inclusion of a quadratic term (and no evidence for a decline phase; Table 2,

Table 2. Results of testing for bivariate relationships between measures of mammal species richness and human population density and percentage of land transformed.

	NSM (LR)	SM (LR)	NSM (QR)	SM (QR)
Human population density				
Total richness	$F_{1,704} = 134.4^{***}, r^2 = 0.26$	$F_{1,704} = 57.5^{*}$, AIC = 4602.0	$F_{1,704} = 124.9^{***}, r^2 = 0.27$	$F_{1,704} = 17.7^{*}$, AIC = 4546.0
Threatened	$F_{1,704} = 94.1^{***}, r^2 = 0.12$	$F_{1,704} = 1.8$ ns, AIC = −2127.0	$F_{1,704} = 6.5^{***}, r^2 = 0.20$	$F_{1,704} = 4.1$ ns, AIC = 2222.7
Endemic	$F_{1,704} = 229.3^{***}, r^2 = 0.25$	$F_{1,704} = 4.9^{*}$, AIC = 3065.1	$F_{1,704} = 97.3^{***}, r^2 = 0.28$	$F_{1,704} = 5.3^{*}$, AIC = 3008.4
Rare	$F_{1,704} = 41.5^{***}, r^2 = 0.37$	$F_{1,704} = 8.3^{**}$, AIC = 2122.7	$F_{1,704} = 12.3^{***}, r^2 = 0.39$	$F_{1,704} = 9.2^{***}$, AIC = 2183.2
Common	$F_{1,704} = 75.1^{***}, r^2 = 0.41$	$F_{1,704} = 6.7^{*}$, AIC = 4009.0	$F_{1,704} = 41.9^{***}, r^2 = 0.42$	$F_{1,704} = 3.04^{*}$, AIC = 3900.4
Mass1	$F_{1,704} = 210.1^{***}, r^2 = 0.29$	$F_{1,704} = 2.1$ ns, AIC = 2421.2	$F_{1,704} = 153.8^{***}, r^2 = 0.31$	$F_{1,704} = 4.9^{*}$, AIC = 3391.2
Mass2	$F_{1,704} = 215.9^{***}, r^2 = 0.23$	$F_{1,704} = 16.2^{*}$, AIC = 3383.9	$F_{1,704} = 127.5^{***}, r^2 = 0.27$	$F_{1,704} = 3.6^{*}$, AIC = 3334.8
Mass3	$F_{1,704} = 175.3^{***}, r^2 = 0.19$	$F_{1,704} = 2.0$ ns, AIC = 2683.4	$F_{1,704} = 76.2^{***}, r^2 = 0.21$	$F_{1,704} = 1.78$ ns, AIC = 2589.0
Mass4	$F_{1,704} = 49.9^{***}, r^2 = 0.11$	$F_{1,704} = 0.6$ ns, AIC = 2972.2	$F_{1,704} = 23.5^{***}, r^2 = 0.13$	$F_{1,704} = 2.6$ ns, AIC = 2750.6
Land transformed				
Total richness	$F_{1,704} = 75.7^{***}, r^2 = 0.28$	$F_{1,704} = 21.7^{**}$, AIC = 4403.7	$F_{1,704} = 45.7^{***}, r^2 = 0.29$	$F_{1,704} = 16.3^{***}$, AIC = 4552.1
Threatened	$F_{1,704} = 23.8^{***}, r^2 = 0.03$	$F_{1,704} = 0.3$ ns, AIC = 2124.3	$F_{1,704} = 3.3^{***}, r^2 = 0.10$	$F_{1,704} = 6.5$ ns, AIC = 2228.1
Endemic	$F_{1,704} = 81.3^{***}, r^2 = 0.10$	$F_{1,704} = 16.8^{*}$, AIC = 3066.0	$F_{1,704} = 14.4^{***}, r^2 = 0.11$	$F_{1,704} = 5.9^{*}$, AIC = 3012.3
Rare	$F_{1,704} = 237.8^{***}, r^2 = 0.25$	$F_{1,704} = 6.9^{*}$, AIC = 2132.1	$F_{1,704} = 93.4^{***}, r^2 = 0.30$	$F_{1,704} = 13.5^{*}$, AIC = 1215.1
Common	$F_{1,704} = 131.6^{***}, r^2 = 0.37$	$F_{1,704} = 14.3^{*}$, AIC = 2897.5	$F_{1,704} = 22.8^{***}, r^2 = 0.38$	$F_{1,704} = 4.2^{*}$, AIC = 3930.2
Mass1	$F_{1,704} = 17.7^{***}, r^2 = 0.23$	$F_{1,704} = 7.8^{*}$, AIC = 3423.8	$F_{1,704} = 39.4^{***}, r^2 = 0.25$	$F_{1,704} = 3.7^{*}$, AIC = 3395.3
Mass2	$F_{1,704} = 16.28^{***}, r^2 = 0.17$	$F_{1,704} = 0.2$ ns, AIC = 3285.5	$F_{1,704} = 26.2^{***}, r^2 = 0.20$	$F_{1,704} = 2.5$ ns, AIC = 3341.0
Mass3	$F_{1,704} = 24.4^{***}, r^2 = 0.13$	$F_{1,704} = 5.9^{*}$, AIC = 2679.6	$F_{1,704} = 50.9^{***}, r^2 = 0.14$	$F_{1,704} = 8.7^{**}$, AIC = 2592.9
Mass4	$F_{1,704} = 20.3^{***}, r^2 = 0.02$	$F_{1,704} = 1.1$ ns, AIC = 2974.1	$F_{1,704} = 26.3^{***}, r^2 = 0.10$	$F_{1,704} = 2.6$ ns, AIC = 2757.7

NSM = Nonspatial model (model fit indicated by r^2), LR = linear regression, QR = quadratic regression, SM = Selected spatial model (model fit indicated by AIC). All relationships were positive. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. ns = non significant relationship.

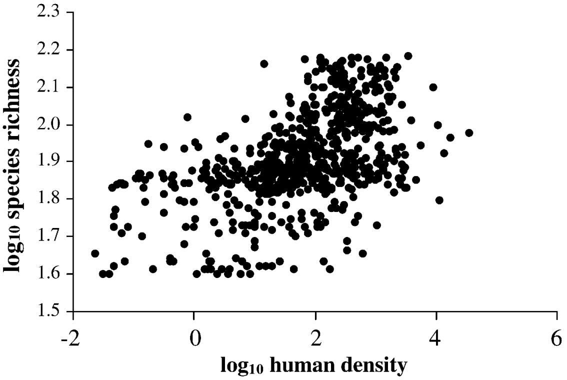

Figure 4. Log–log relationship between total mammal species richness and human population density.

Figure 4). Using an independent errors model, the species richness of subsets of the mammal assemblage is also always significantly positively related to human population density, although in three cases (threatened species and species in two of the mass categories) these relationships lose their statistical significance when controlling for spatial autocorrelation (Table 2).

Patterns of land transformation across Mexico are positively associated with levels of human population density (r^2 = 0.21; AIC = 1517.6, F = 13.29, $p < 0.01$). This is reflected in typically marked positive relationships between the overall numbers of mammal species, the numbers in different subsets of the assemblage, and the level of land transformation (Table 2), with a similar pattern of degradation of these relationships when spatial autocorrelation is controlled for.

Conservation areas

A total of 92 grid cells form part of one or more of each of 100 optimal solutions, each requiring 38 grid cells, to the problem of representing each mammal species in at least one grid cell across Mexico. In the optimal complementarity sets, human population density can vary between 52.9 and 69.4 persons km^{-2}, values significantly higher than expected from a random selection of sites (44.9–46.1 persons km^{-2}, limits of the 95% confidence interval for the 10,000 random draws of 38 cells).

Most existing designated Mexican protected areas are not situated in regions of lower than national average human density (c 50 persons km^{-2}). The size of protected areas is negatively correlated with human population density, such that small-protected areas are more likely than are large protected areas to be located in regions of high human population density (r^2 = − 0.29, $p < 0.001$; Figure 5).

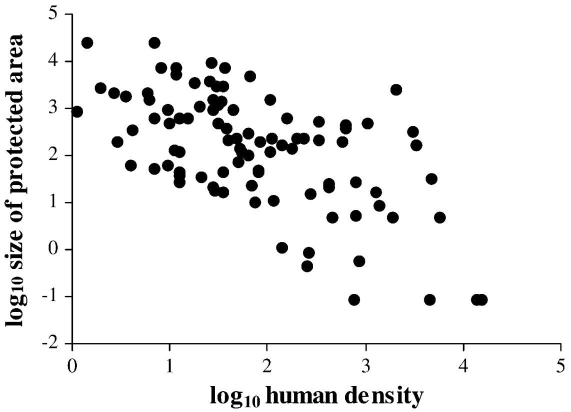

Figure 5. Log_{10} area of 96 Mexican designated protected areas in relation to $\log_{10}$ human population density within a 50 km buffer zone.

Discussion

In keeping with previous analyses at coarser resolutions and/or in other biogeographic regions of the world (see Introduction for references), spatial variation in the species richness of mammals across Mexico is positively correlated with spatial variation in the numbers of people. That is, on average, areas in which there are more mammal species also tend to have more people. The existence of broadly similar relationships of both mammal species richness and human population density with environmental variables supports the argument that the covariation between mammal species richness and human density is a consequence of them responding in similar ways to spatial variation in environmental conditions (Table 1, Figure 3).

It has been argued that positive relationships between numbers of people and patterns of species richness are likely to be more characteristic of regions in which human populations are more dependent on the exploitation of local resources for subsistence agriculture, and therefore more tightly associated with natural patterns of resource provision, than those with a well-developed mechanized agricultural infrastructure (Huston 1993, 2001). However, Mexico has just such a well-developed infrastructure, including extensive areas of intensive agriculture (FAO 2000) and clearly this is not sufficient entirely to disrupt the relationship between human density and mammal species richness at the spatial resolution examined herein. Indeed, the variation about this relationship might be significantly reduced were it possible to improve on the quality of the estimation of the density of humans in different areas.

One explanation for this result is that whilst a well-developed mechanized agricultural infrastructure reduces the immediate dependency of human populations on natural resource provision, and enables production of substantial quantities of foodstuffs from areas where previously this may not have been possible, in the main such an infrastructure is employed in those same areas that historically tended to provide the greatest natural resource provision. If this is so, then the positive relationship between mammal species richness and human density has persisted in Mexico despite the long history of human occupation of the region, the extensive (and sometimes sophisticated) land transformation that accompanied this, and the ebbs and flows in this transformation associated with the rise and fall of a number of major civilisations. Historical demographic research has estimated that before European conquest, the Mexican population may already have exceeded 20 million people and was larger than that of any other comparable American area (Fox 1971). Central Mexico alone may have had a pre-Columbian population of 11 million people (Fox 1971; Zambardino 1980).

Why has the relationship between mammal species richness and human density persisted in the face of such human population pressures, and the associated land transformation? There are two possible reasons. First, there may be sufficient habitat heterogeneity even at a half-degree resolution to enable such persistence (Redford and Dinerstein 1994), with highly disturbed areas residing alongside much less disturbed ones. The complex topography of Mexico would certainly promote such an effect. This is especially true, for example, of the Mexican Mesa Central where highly fertile agricultural lands, large human settlements, and mountains systems lie in close proximity (Butzer and Butzer 1997). In such a circumstance, one might have imagined that small-bodied, and therefore typically less space demanding, species of mammals would be more likely to exhibit a positive species richness-human density relationship, and large-bodied species requiring large home ranges would be less likely to do so. However, there is no evidence for a simple effect of body size on the likelihood of observing such a relationship for the mammals of Mexico, with all body size classes exhibiting a species richness-human density and a species richness-land transformation relationship when treating data points as independent, and only one of the intermediate body size classes exhibiting a species richness-human density relationship and the smallest and an intermediate body size class exhibiting a species richness-land transformation relationship when controlling for spatial autocorrelation (Table 2).

With this first explanation, the species richness-human density relationship has been an inevitable consequence of patterns of human population establishment and growth, from perhaps before these populations had a major influence on patterns of occurrence of other mammal species (see Woodroffe 2000). The relationship has persisted probably because mammal richness has been depressed across much of the breadth of human densities, and not simply at the highest levels. Some of the largest mammals have suffered massive reductions in their geographic ranges in Mexico in recent history (e.g. black bear, *Ursus americanus* and bison, *Bison bison*) and others have undergone regional extinction (e.g. grey wolf, *Canis lupus*). This depression, perhaps particularly at higher human densities, is likely to be more marked than portrayed in the analyses here, as these take no account of the population viability of each species in different areas, nor of possible more recent changes in distributions.

The second possible reason that a positive species richness-human density relationship might have persisted is that extant Mexican mammals have a reasonably high resilience to human activities, with those that did not do so having already been lost. Such filtering effects have been argued to have given rise to, for example, the otherwise counter-intuitive observation that Pacific islands with longer histories of human occupation often tend at present to have fewer threatened species (Pimm et al. 1995). In this connection, it is noteworthy that when accounting for spatial autocorrelation, there is no relationship between the species richness of threatened mammals and human density across Mexico.

The positive relationship between mammal species richness and human population density suggests that the conservation of mammals in Mexico may face greater conflicts than might otherwise be the case. Although patterns of complementarity and species richness need not coincide, this inference is confirmed by considering the distribution of those areas that would be required simply to represent each of the mammal species by at least one spatial occurrence. These have significantly higher human densities than would be expected by chance. Turning to protected areas that have already been designated, underlines this message further. These also lie in areas with disproportionately high human population densities. Moreover, the smaller the protected area the higher the human density in the surrounding lands (Figure 5; see Park and Harcourt 2002 and references therein), suggesting that not only do small protected areas suffer from increased external pressures because of their high perimeter to area ratios, but they may suffer disproportionately because the potential external pressures are much more intense (Harcourt et al. 2001).

In conclusion, the results reported here demonstrate that positive relationships between human density and species richness (i) are not restricted to the Old World but are also exhibited in the New World, where the history of human occupation is much shorter, (ii) are exhibited at a within-country scale, (iii) are exhibited at a finer data resolution than that employed in the majority of previous studies, and (iv) may have significant implications for conservation planning in Mexico.

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References

Araújo M.B. 2003. The coincidence of people and biodiversity in Europe. Global Ecol. Biogeogr. 12: 5–12.

Arita H.T., Figueroa F., Frisch A., Rodríguez P. and Santos-del-Prado K. 1997. Geographic ranges size and the conservation of Mexican mammals. Conserv. Biol. 11: 92–100.

Balmford A., Moore J.L., Brooks T., Burgess N., Hansen L.A., Williams P. and Rahbek C. 2001. Conservation conflicts across Africa. Science 291: 2616–2619.

Bradbury J.P. 1982. Holocene chronostratigraphy of Mexico and Central America. Striae 16: 46–48.

Brashares J.S., Arcese P. and Sam M.K. 2001. Human demography and reserve size predict wildlife extinction in West Africa. Proc. R. Soc. Lond. B 268: 2473–2478.

Butzer K.W. and Butzer E.K. 1997. The 'natural' vegetation of the Mexican Bajío: archival documentation of a 16th Century savanna environment. Quart. Int. 43: 161–172.

Ceballos G., Arroyo-Cabrales J. and Medellín R.A. 2002. The mammals of Mexico: composition, distribution, and conservation status. Occasional Papers, Museum of Texas Tech University 218: 1–27.

Challenger A. 1998. Utilización y conservación de los ecosistemas terrestres de México. Pasado, presente y futuro, CONABIO-IBUNAM, ASM, SC, México.

Chown S.L., van Rensburg B.J., Gaston K.J., Rodrigues A.S.L. and van Jaarsveld A.S. 2003. Species richness, human population size and energy: conservation implications at a national scale. Ecol. Appl. 13: 1223–1241.

Cincotta R.P., Wisnewski J. and Engelman R. 2000. Human population in the biodiversity hotspots. Science 404: 990–992.

Clifford P., Richardson S. and Hemon D. 1989. Assessing the significance of the correlation between two spatial process. Biometrics 45: 123–134.

Cressie N. 1991. Statistics for Spatial Data. Wiley, New York.

Currie D.J. 1991. Energy and large-scale patterns of animal and plant species richness. Am. Nat. 137: 27–49.

Dobson A.P., Rodríguez J.P., Roberts W.M. and Wilcove D.S. 1997. Geographic distribution of endangered species in the United State. Science 275: 550–553.

Ehrlich P.R. 1995. The scale of the human enterprise and biodiversity loss. In: Lawton J.H. and May R.M. (eds), Extinction Rates. Oxford University Press, Oxford, pp. 214–226.

Fairbanks D.H.K., Kshatriya M., van Jaasveld A.S. and Underhill L.G. 2002. Scales and consequences of human land transformation on South African avian diversity and structure. Anim. Conserv. 5: 61–73.

Food and Agriculture Organization of the United Nations (FAO) 2000. FAOSTAT on-line statistical service. Rome: FAO, Available on-line at http://apps.fao.org..

Fjeldså J. and Rahbek C. 1998. Continent-wide conservation priorities and diversification process. In: Mace G.M., Balmford A. and Ginsberg J. (eds), Conservation in a changing world. Cambridge University Press, Cambridge, pp. 139–160.

Fox D.J. 1971. Mexico. In: Blakemore H. and Smith C.T. (eds), Latin America: Geographical perspectives. Methuen, London, pp. 19–71.

Gaston K.J. 2000. Global patterns in biodiversity. Nature 405: 220–227.

Grove D.A. 2000. The Preclassic societies of the central highlands of Mesoamerica. In: Adams R.E.W. and MacLeod M.J. (eds), The Cambridge history of the native peoples of Americas. Cambridge University Press, Cambridge, pp. 122–155.

Hall E.R. 1981. The mammals of North America Vol. 2. Wiley, New York.

Hannah L., Carr J.L. and Lankerani A. 1995. Human disturbance and natural habitat: a biome level analysis of a global data set. Biodiv. Conserv. 4: 128–155.

Harcourt A.H., Parks S.A. and Woodroffe R. 2001. Human density as an influence on species/area relationships: double jeopardy for small African reserves? Biodiv. Conserv. 10: 1011–1026.

Hoare R.E. and du Toit J.T. 1999. Coexistence between people and elephants in African savannas. Conserv. Biol. 13: 633–639.

Hunter M.L. and Yonzon P. 1993. Altitudinal distribution of birds, mammals, people, forest, and parks in Nepal. Conserv. Biol. 2: 420–423.

Huston M.A. 1993. Biological diversity, soils, and economics. Science 262: 176–180.

Huston M. 2001. People and biodiversity in Africa. Science 293: 1591–1592.

ILOG. 2001. CPLEX 7.1. ILOG, Gentilly.

INEGI. 2001. XII censo general de población y vivienda. México, D.F.

IUCN. 2000. 2000 IUCN Red List of the Threatened species. (http://www.redlist.org).

Kerr J.T. and Currie D.J. 1995. Effects of humans activity on global extinction risk. Conserv. Biol. 9: 1528–1538.

Kerr J.T. and Currie D.J. 1999. The relative importance of evolutionary and environmental controls of broad-scale patterns of species richness in North America. Ecoscience 6: 329–337.

Larsen F.W. and Rahbek C. 2003. Influence of scale on conservation priority setting -a test on African mammals. Biodiv. Conserv. 12: 599–614.

Legendre P. 1993. Spatial autocorrelation: trouble or new paradigm? Ecology 74: 1659–1673.

Legendre P., Dale M.R.T., Fortin M.J., Gurevitch J., Hohn M. and Myers D. 2002. The consequences of spatial structure for design and analysis of ecological field surveys. Ecography 25: 601–615.

Lennon J.J. 2000. Red-shifts and red herrings in geographical ecology. Ecography 23: 101–113.

Littell R.C., Milliken G.A., Stroup W.W. and Wolfinger R.D. 1996. SAS system for mixed models. SAS Institute, Cary, N.C.

Liu J., Linderman M., Ouyang Z., An L., Yang J. and Zhang H. 2001. Ecological degradation in protected areas: the case of Wolong Nature Reserve for Giant Pandas. Science 292: 98–101.

Luck G.W., Ricketts T.H., Daily G.C. and Imhoff M. 2004. Alleviating spatial conflicts between people and biodiversity. Proc. Nat. Acad. Sci. USA 101: 182–186.

McKinney M.L. 2001. Effects of human population, area, and time on non-native plant and fish diversity in the United States. Biol. Conserv. 100: 243–252.

Mittermeier R.A., Myers N. and Mittermeier C.G. 1999. Hotspots: earth biologically richness and most endangered terrestrial ecoregions. CEMEX/Conservation International, University of Chicago Press, Chicago.

Morin P.J. 2000. Biodiversity's ups and downs. Nature 406: 463–464.

Musters C.J.M., Degraaf H.J. and Terkeurs W.J. 2000. Can protected areas be expanded in Africa. Science 287: 1759–1760.

O'Brien E.M. 1998. Water-energy dynamics, climate, and prediction of woody plant species richness an interim general model. J. Biogeogr. 25: 379–398.

Parks S.A. and Harcourt A.H. 2002. Reserve size, local human density, and mammalian extinctions in U.S. protected areas. Conserv. Biol. 16: 800–808.

Pimm S.L., Moulton M.P. and Justice L.J. 1995. Bird extinction in the central Pacific. In: Lawton J.H. and May R.M. (eds), Extinction Rates. Oxford University Press, Oxford, pp. 214–226.

Quintas I. 2000. ERIC II, Base de datos climatológica compactada, archivos y programa extractor. Instituto Mexicano de Tecnología del Agua. Morelos, Mexico.

Real R., Barbosa A.M., Porras D., Kin M.C., Marquez A.L., Guerrero J.C., Palomo L.J., Justo E.R. and Vargas J.M. 2003. Relative importance of environment, human activity and spatial situation in determining the distribution of terrestrial mammal diversity in Argentina. J. Biogeogr. 30: 939–947.

Redford K.H. and Dinerstein E. 1994. Biological diversity and agriculture. Science 265: 457–458.

Rees W.E. 2001. Ecological footprint, concept of. In: Levin S.A. (ed.), Encyclopaedia of Biodiversity, Vol 2. Academic Press, San Diego, pp. 229–244.

Reid F.A. 1997. A Field Guide to the Mammals of Central America and Southeast Mexico. Oxford University Press, Oxford.

Rodrigues A.S.L., Orestes Cerdeira J. and Gaston K.J. 2000. Flexibility, efficiency, and accountability: adapting reserve selection algorithms to more complex conservation problems. Ecography 23: 565–574.

Sanders W.T., Parsons J.R. and Santley R.S. 1979. The basin of Mexico: ecological process in the evolution of a civilisation. Academic Press, New York.

SEMARNAT 2000. Inventario Forestal Nacional 2000. México.

Silva M. and Downing J.A. 1995. CRC handbook of mammalian body masses. CRC Press Inc, Boca Raton, Florida.

Thompson K. and Jones A. 1999. Human population density and prediction of local plant extinction in Britain. Conserv. Biol. 13: 185–189.

Underhill L.G. 1994. Optimal and suboptimal reserve selection algorithms. Biol. Conserv. 70: 80–85.

van Rensburg B.J., Chown S.L. and Gaston K.J. 2002. Species richness, environmental correlates, and spatial scale: a test using South African birds. Am. Nat. 159: 566–577.

Wackernagel M., Schulz N.B., Deumling D., Linares A.C., Jenkins M., Kapos V., Monfreda C., Loh J., Myers N., Norgaard R. and Randers J. 2002. Tracking the ecological overshoot of the human economy. Proc. Nat. Acad Sci. USA 99: 9266–9271.

Walsh P.D., Abernethy K.A., Bermejo M., Beyers R., De Wachter P., Akou M.E., Huijbregts B., Mambounga D.I., Toham A.K., Kilbourn A.M., Lahm S.A., Latour S., Maisels F., Mbina C., Mihindou Y., Obiang S.N., Effa E.N., Starkey M.P., Telfer P., Thibault M., Tutin C.E.G., White L.J.T. and Wilkie D.S. 2003. Catastrophic ape decline in western equatorial Africa. Nature 422: 611–614.

Whitmore T.M. and Turner B.L. 2001. Cultivated landscapes of Middle America on the eve of conquest. Oxford University Press, Oxford.

Williams P.H. 2001. Complementarity. In: Levin S.A. (ed.), Encyclopedia of Biodiversity, Vol. 1. Academic Press, San Diego, pp. 813–829.

Wilson D.E. and Ruff S. 1999. The Smithsonian book of North American Mammals. The Smithsonian Institution, Washington.

Woodroffe R. 2000. Predators and people: using human densities to interpret declines of large carnivores. Anim. Conserv. 3: 165–173.

Zambardino R.A. 1980. Mexico's population in the Sixteenth Century: demographic anomaly or mathematical illusion. J. Interdisciplinary Hist. 11: 1–27.

Zheng D.L., Prince S.D. and Wright R. 2001. NPP Multi-Biome: Gridded Estimates for Selected Regions Worldwide, 1989–2001. Data set, Available on-line [http://www.daac.ornl.gov] from the Oak Ridge National Laboratory Distributed Active Archive Center. Oak Ridge, Tennessee.

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Urban domestic gardens (VI): environmental correlates of invertebrate species richness

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Abstract. Domestic gardens associated with residential zones form a major component of undeveloped land in towns and cities. Such gardens may play a vital role in maintaining biodiversity in urban areas, but explanations for the variation in the richness of species assemblages in gardens are lacking. We report the results from a case study of 12 invertebrate groups in 61 domestic gardens in the city of Sheffield, UK. The mean number of species within a taxon, recorded per garden, was no greater than 3, 10, and 20 species in litter, pitfall trap and Malaise trap samples, respectively. Relatively speciose groups exhibited high turnover between gardens, with typically 50% of the group occurring only once. In contrast, several species-poor taxa were virtually ubiquitous. Species richness was analysed by multiple regression and hierarchical *tree* analysis in relation to garden and landscape variables. In general, the two methods of analysis corroborated one another. In total, 22 explanatory variables entered into regression models, although 12 of them only did so once. The amount of variation in species richness explained in models was generally quite high, with the factors involved operating over a range of scales. However, the patterns that emerged were not consistent across taxa. The most important predictors of species richness, of relevance to land use planners, were components of garden vegetation, especially the abundance of trees. Likely reasons for inconsistencies in the relationships are discussed in the context of sampling and species biology.

Introduction

Urbanisation causes wholesale transformation of the local environment, affecting it at a fundamental level by altering habitat, climate, hydrology, and primary production (Sukopp and Starfinger 1999; Kinzig and Grove 2001). An important consequence is change in the composition of species assemblages. Urbanisation generally reduces native species richness across plant and animal taxa (Blair 1996; Denys and Schmidt 1998; Roy et al. 1999; Germaine and Wakeling 2001), although certain groups may be favoured by the creation of novel habitats (e.g. lichens, Gilbert 1990; ground beetles, Eversham et al. 1996) and overall biodiversity may be enhanced by the presence of alien species (Pyšek 1993).

Undeveloped land in towns and cities, generically termed 'green space', supports vegetation and 'unsealed' surfaces, and it can ameliorate the detrimental effects of urbanisation on species assemblages by preserving or creating habitat, and by maintaining corridors for movement through the urban matrix. Domestic gardens associated with residential zones form a major component of urban green space. The few estimates available for UK cities indicate that domestic gardens comprise 19–27% of the entire urban area (Gaston et al. in press b), therefore they may play a critical role in maintaining biodiversity in such regions (e.g. Owen 1991; Miotk 1996; Saville 1997; Owen 2002). With the exception of birds (BTO Garden BirdWatch scheme, Cannon 2000) evidence is limited when trying to explain variation in the richness of garden assemblages. It is either based on long-term data from single gardens (e.g. Allen 1964; Smith 1989; Owen 1991) or on short term data from multiple gardens for a very restricted range of taxa (e.g. Davis 1978; Vickery 1995; Bailey et al. 1998). In order to understand the contributions of different factors related to species richness in urban gardens it is necessary to sample a suite of gardens and taxa simultaneously.

Previous studies in urban environments have demonstrated that the features of habitat patches, such as their size (McGeoch and Chown 1997; Miyashita et al. 1998) and degree of isolation (Soulé et al. 1988; Denys and Schmidt 1998; Fernández-Juricic 2000) are significant factors in determining species richness. Conditions surrounding patches, such as building density, are also influential factors (Jokimäki 1999; Germaine and Wakeling 2001). In the case of urban domestic gardens, it is difficult to predict what the relative roles of 'internal' and 'external' factors may be, since gardens are managed at an individual level, yet they form interconnected tracts of green space. Therefore gardens differ essentially from other components of green space because they constitute much of the urban matrix, rather than existing as isolated patches of habitat.

In this paper we investigate the factors associated with variation in invertebrate species richness in urban domestic gardens, using the city of Sheffield as a case study. This study constitutes part of the Biodiversity of Urban Gardens in Sheffield (BUGS) project, a wider investigation of the resource that domestic gardens provide for biodiversity and ecosystem functioning (Gaston et al. in press b; Smith et al. in press), the factors that influence the levels of biodiversity associated with different gardens (Thompson et al. 2003, 2004), and ways in which features of gardens can be manipulated to enhance biodiversity (Gaston et al. in press a).

Methods

Study site

The city of Sheffield, South Yorkshire, UK (53° 23′ N, 1° 28′ W; OS grid reference SK 38) lies in the centre of England; it is largely surrounded by agricultural land, except where the urban area merges with that of Rotherham to the north-east. The administrative boundaries of the city enclose an area of more than 360 km^2, including farmland and a portion of the Peak District

National Park. The study was carried out in the rear gardens (hereafter called 'gardens') of 61 private, owner-occupied houses in the predominantly urbanised region of the city (about 143 km^2, defined as those 1 km × 1 km cells having more than 25% coverage by residential or industrial zones, as judged by eye from Ordnance Survey 1:25000 scale maps) (Figure 1). The study focussed on rear gardens, which form the major garden component of most properties.

Sixty-one gardens were selected from a pool of 161 householders derived from contacts among ancillary, clerical and academic staff at the University of Sheffield, and from members of the public at lectures or displays. This approach was chosen due to the great difficulty in the alternative of recruiting householders at random who were both sympathetic to research being conducted in their gardens, and able to offer daytime access. Our method also

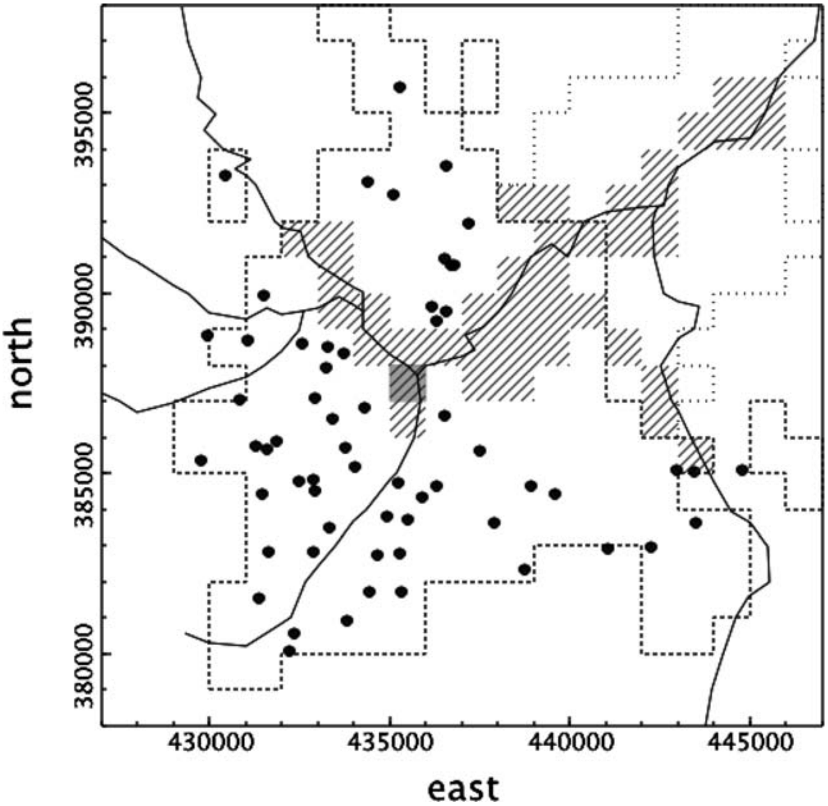

Figure 1. Map of the locations of the 61 study gardens in the predominantly urban area (heavy dashed line) of Sheffield, in relation to zones with > 50% industrial/commercial use (cross-hatching), principal rivers, and the adjoining town of Rotheram to the north-east (light dashed outline). The shaded square indicates 1 km^2 of the central business district, centred on the city hall. Map axes represent distances (m) on the Ordnance Survey National Grid; the map covers 20 km by 20 km.

enabled us to maximise variation in the environmental axes of interest, e.g. house age, garden size, and location across the urban area. Housing was characterised as terraced (two or more adjoining dwellings), semi-detached (one adjoining dwelling), and detached (no adjoining dwellings); they comprised 16, 56, and 28% of the sample, respectively (compared to a random sample of 50, 44, and 6% ($n = 218$) taken from all Sheffield gardens, Gaston et al. in press b). Rear gardens ranged from 32–940 m^2 in area and their associated properties ranged from 5–165 years in age. Altitude was recorded to the nearest 10 m, from Ordnance Survey 1:50,000 scale maps, and gardens ranged between 40 and 250 m above sea level.

Recording garden characteristics

Rear gardens were surveyed between July and September 2000. Principal dimensions were measured to the nearest 0.5 m, and a scale plan was drawn of each garden; this included the side portion on properties occupying corner plots. The plan incorporated boundaries (and their construction), buildings within the garden, and all forms of land use, of which 22 were recognised (Smith et al. ms.). The areas of each type of land use, and the lengths of linear features, were estimated from the plan. Distance to the centre of the nearest 1 km × 1 km cell having less than 25% coverage by residential or industrial zones was measured. Information on garden management and the intentional provision of resources for wildlife (‘wildlife gardening’) was gathered from garden owners using a questionnaire (see Appendix 1 for details).

Recording the garden flora and vegetation

A complete list was made of all vascular plant taxa during the garden survey, and each taxon was allocated to alien or native categories (nomenclature and status followed Stace (1997) where possible, otherwise Wright (1984)). Some plants were allocated to the native taxon (e.g. *Primula vulgaris*, *Aquilegia vulgaris*), even though many garden plants are of hybrid origin. Cultivars were not considered as separate taxa. Although the timing of the survey meant that some strict vernals (e.g. *Anemone blanda*) were missed, the remains of *Hyacinthoides*, *Narcissus* and *Tulipa* spp. were still visible. Measures of vegetation structure were produced by estimating the area covered by a canopy in the following height classes: < 0.5 m, 0.5–1 m, 1–2 m, 2–3 m, and > 3 m. The classes were mutually exclusive, and incorporated tree canopies (including those overhanging from outside the garden) but omitted mown lawn. The number of trees taller than 2 m was also recorded.

Garden measurements using a Geographic Information System (GIS)

The following variables were measured for each property using Ordnance Survey digital 'Land-line Plus' (1:1250) maps, imported to an ArcView GIS (Environmental Systems Research Institute, Inc.): total plot area, house area, and total garden area (calculated as the area of the plot excluding the house). A series of variables for land use surrounding each garden was also created. A circular area of 10,000 m^2 (1 ha, radius c. 56 m), centred on each garden, was believed sufficient to sample the local land uses that might exert an effect on the invertebrates recorded in a garden; this scale of sampling was also adequate in detecting changes in housing density. The variables were: number of houses (where more than half of the area of the house was covered), area of road and pavement, area of buildings, area of gardens (plots minus houses), and area of land not in the former categories. Within a 10,000 m^2 (1 ha) square plot centred on each garden, two other measures of local green space were taken from 1:1250 scale aerial photographs ('Cities Revealed', The GeoInformation Group, Cambridge, UK): the area of the contiguous block of green space in which the survey garden lay, and the total ground area of green space in the quadrat (non-built up, unmetalled ground, including gardens, parks, waste ground, woodland and landscaping).

Human population density was measured using POPSURF data at a 200 m grid cell resolution, based on 1991 UK population census data (Martin and Tate 1997). The value of the cell in which a garden lay was used as a measure of local population density. For three gardens where data were missing, a value was calculated from a bilinear interpolation of the four nearest cells.

Species sampling

The taxa studied in gardens were limited to those that could be identified by the appropriate specialists, or for which reference specimens could be checked.

Leaf-mining insects

This guild of insects was recorded during the inventory of garden plants, in 56 out of the 61 gardens; species were identified from characteristics of the mine, and by rearing adults. Tree species were included by searching foliage up to c. 2 m from the ground.

Pitfall trapping

White, disposable plastic coffee cups, 110 mm high and 70 mm wide at the rim, were used for pitfall traps. They were placed in triplicate in the cultivated borders of each of 60 out of the 61 gardens, as widely spaced as practicable. In one garden without borders, traps were placed along the boundary, which comprised fencing and a hedge. Each trap was half-filled with 50% alcohol, rather than ethylene glycol, due to the risk of being found by pets or children.

When in use, each trap was covered with a ply-board rain shield, positioned 20 mm above the rim of the trap. Traps were opened for the first 2 weeks of each month, June to October inclusive in 2000, resulting in a total of 15 samples (3 locations × 5 months) for each garden.

Litter sampling
Samples of leaf litter and organic debris were collected in triplicate from each of the 61 gardens between the end of July and mid-September 2000. Each sample was taken from a cultivated border, in a circular area of c. 20 cm diameter, to a depth of c. 5 cm, and samples within gardens were collected as far apart as possible. The surface substrate was collected if no litter was present. In one garden without borders, the samples were taken from the base of a boundary hedge. Organisms were extracted from the samples using Tullgren funnels, and collected into 70% ethyl alcohol. Organisms that remained in the dried litter samples, in particular snails, were recovered by hand searching.

Malaise trapping
Single Malaise traps (white roof, black walls) were erected in 16 out of the 60 gardens in order to sample flying insects (although samples also contained substantial numbers of arachnids); traps were placed in gardens where householders were willing to accommodate them, and those gardens spanned the range of property sizes. Malaise traps were located in as standardised a manner as possible in each garden: at the edge of the lawn, with their long axis perpendicular to a border. The traps were operated for the first two weeks of June, July and September 2000 and invertebrates were collected in 70% ethyl alcohol.

Litter, pitfall and Malaise sampling were all selected for their efficiency in gathering standardised data for a wide range of taxa, across a large number of gardens simultaneously. They sampled species richness per unit area (species density; for Malaise traps, based on the area of netting obstructing insect flight paths), although in the cases of pitfall and Malaise traps the area would have varied according to the differential mobilities of the sampled faunas. Nevertheless, the methods remained comparable between gardens because the sampling locations and habitat were similar. With certain exceptions (such as leaf-miners – see above) sampling total garden richness requires considerable resources, can be hard to standardise, and would have been difficult to achieve for the large number of gardens in the survey. However, the scales at which species richness was measured for each group need to be borne in mind when considering the results.

Analyses

We attempted to control the number of independent variables of possible importance by removing closely correlated, and hence redundant, variables.

In each case we retained the variable with the clearer potential biological role, or for which we were most confident of the measurement process. We reduced the number of variables to 32, but a principal components analysis on these failed to reduce the data usefully; nine principal components were required to account for 75% of the variance, and the influences of the original variables on components were typically small (correlation of < 0.3). Although this number of variables was not ideal for model fitting, the aim of the analysis was to identify what, if any, associations occurred between garden environments and species richness, and whether general patterns appeared across different groups of organisms. In addition, the independent variables (excluding positional variables) were checked for evidence of spatial autocorrelation, but there was no consistent pattern for gardens close to each other being more similar than those which were far apart.

The rigour of the analysis was increased by using two modelling approaches and observing how closely the results compared. We used multiple regression and binary recursive partitioning (tree modelling – see below) to provide descriptive models of the relationships between the richness of each group of organisms and the independent variables describing environmental characteristics. The generality of these relationships and the existence of causal mechanisms remain to be explored.

Stepwise multiple regression was used to examine which environmental factors accounted for variation in species richness within each taxonomic group (see Appendix 1 for the list of factors). Five of the independent variables had missing values for a few observations; if these factors failed to enter initial models they were removed in order to maximise degrees of freedom. Data from triplicate samples (pitfall traps and litter samples) were pooled for each garden, and data for all methods were pooled across months. The data for centipedes, millipedes and woodlice, and for spiders, harvestmen and pseudoscorpions were combined, because the number of species per garden was too low to analyse when the taxa were treated individually (Table 1). Similarly, data from litter samples and pitfall traps were amalgamated within a taxon where the number of species was low. The two methods both sampled the ground-dwelling assemblage, and sampling effort within methods was identical across gardens. Whilst none of these data pooling steps was ideal, it was preferable to analyse the data at the most practicable level possible rather than discard significant parts of the sampled taxa.

The values of dependent variables were, when necessary, logarithmically transformed for analyses in order to homogenise variances and normalise residuals. The areas of gardens and their internal land uses, of GIS-derived variables, lengths of internal walls and hedges, and proportions were logarithmically, or arcsine-square root, transformed to linearise the relationship with the dependent variable.

Tree models (Crawley 2002; denoted *tree* for clarity) were used to check the robustness of our inferences from multiple regression. *Tree* models are well suited to situations where explanatory effects may be contingent, and effects are

Table 1. Invertebrate taxa recorded from (a) litter samples (61 gardens), (b) pitfall traps (60 gardens), and (c) Malaise traps (16 gardens).

Taxon	No. of individuals	No. of species	Mean no. of species garden^{-1}	Minimum no. of species garden^{-1}	Maximum no. of species garden^{-1}
(a) *Litter samples*					
Beetles	254	62	2.4	0	8
Slugs	60	4	0.7	0	3
Snails	581	17	2.8	0	8
Spiders	224	20	0.77	0	3
Harvestmen	50	7	0.44	0	2
Pseudoscorpions	16	3	0.23	0	2
Centipedes	89	6	0.80	0	3
Millipedes	249	10	1.3	0	4
Woodlice	3941	8	2.6	0	5
(b) *Pitfall traps*					
Beetles	4329	139	9.4	2	20
Slugs	3416	13	4.9	1	7
Snails	436	13	4.2	0	10
Spiders	842	57	5.1	1	15
Harvestmen	413	14	1.6	0	4
Pseudoscorpions	1	1	0.02	0	1
Centipedes	40	5	1.2	0	3
Millipedes	87	9	1.9	0	6
Woodlice	7903	8	3.4	1	6
(c) *Malaise traps*					
Beetles	672	147	19.9	11	45
Spiders	338	39	6.1	2	11
Harvestmen	56	4	1.0	0	3
Bumblebees	1131	9	6.0	4	8
Sawflies	372	37	7.8	3	17
Craneflies	645	47	10.3	4	17
True bugs	1223	81	13.9	9	20
Solitary bees	80	21	2.8	0	11
Solitary wasps	61	20	2.4	0	10

not simple linear responses. The process involved a sequential binary partitioning of the data with respect to the independent variables. The independent variable explaining the maximum deviance was selected first, and the data were split into two subgroups at a threshold value of this variable, such that the split gave the best reduction of total deviance in the group. This process was then repeated for each of the two subgroups, again selecting from all the independent variables, and continued with each successive subgroup until a group contained too few data to be further partitioned. Here we consider only the most important independent variables in each *tree* model, generally the results of the first two partitions (producing up to four groups, although partitioning sometimes stopped before).

Results

The same nine principal higher taxa were identified from litter samples and pitfall traps, based on 5464 and 17467 specimens, respectively; nine main taxa were identified in Malaise traps, based on 4578 individuals (Table 1). Species richness was generally low, compared to what might have been expected from garden faunal lists (e.g. Owen 1991): the mean number of species, within a taxon, recorded per garden was no greater than 3, 10, and 20 species in litter, pitfall and Malaise samples, respectively. Indeed, the maximum number of species per taxon in a garden never exceeded 8, 20, and 45 in litter, pitfall and Malaise samples, respectively.

The number of species recorded per garden was generally low compared to the species list summed over all gardens (e.g. spiders and beetles in pitfall traps and litter samples, Table 1), indicating high turnover in species composition between gardens. In taxa where more than 19 species were recorded, around a half of those species occurred in just a single garden – for pitfall plus litter (Figure 2): beetles 48%; spiders 42%; and in malaise traps (Figure 3): spiders 62%, craneflies 46%, sawflies 53%, true bugs 43%, solitary bees 57%, and solitary wasps 45%. In contrast, many members of relatively species-poor taxa were widely distributed across gardens, e.g. isopods and molluscs in pitfall and litter samples (Figure 2), and bumblebees in Malaise traps (Figure 3).

Leaf-mining insects (Arthropoda, Insecta: Diptera, Lepidoptera, Coleoptera, Hymenoptera)

Fifty-four leaf-mining species were recorded across 56 gardens, occurring on 104 plant taxa. The leaf-miner species were represented by flies (Diptera, 55.5%), moths (Lepidoptera, 33.3%), sawflies (Hymenoptera, Symphyta: 9.26%), and beetles (Coleoptera, 1.85%).

The number of trees > 2 m high in a garden explained 73% of the total variation in leaf-miner species richness; this was more than 10 times the variation as for other factors (Figure 4, Table 2). The *tree* analysis corroborated the above result: the primary split occurred for canopy vegetation above 2 m high, a measure which reflects well the canopy contributed by trees. The data were separated into groups above and below 47.5 m^2 of canopy > 2 m, with means of 12.1 and 4.2 leaf-mining species, respectively. The latter group was further split along the variable for vegetation > 2 m (means of 5.3 and 2.9 species above and below 10.5 m^2), whilst the former split on the proportion of boundary that abutted green space (means of 13.6 and 7.6 species above and below a threshold of 78%).

Beetles (Arthropoda, Insecta: Coleoptera)

The model for combined pitfall trap and litter sample data (Table 2) indicated that positive relationships with beetle species richness were, most importantly,

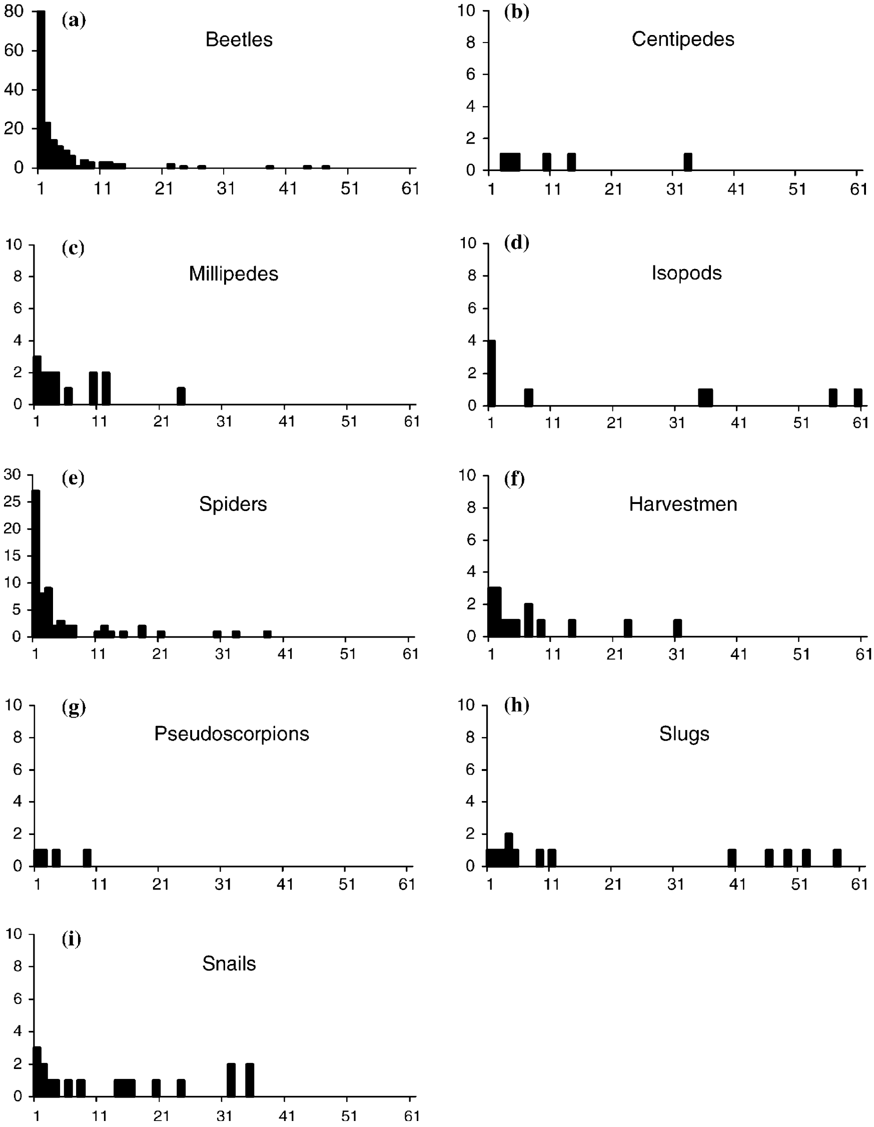

Figure 2. Species occupancy across gardens for taxa sampled by pitfall traps and in litter (combined data), for (a) beetles, (b) centipedes, (c) millipedes, (d) isopods, (e) spiders, (f) harvestmen, (g) pseudoscorpions, (h) slugs, (i) snails. The *x*-axis shows number of gardens, and the *y*-axis shows the number of species. Note that the *y*-axis scale is not constant.

the number of trees, then the presence of composting; house age and garden area were both negatively related to species richness. The significance of trees was supported by the *tree* analysis. This separated observations unevenly along the axis of canopy vegetation >2 m high (closely correlated to the number of

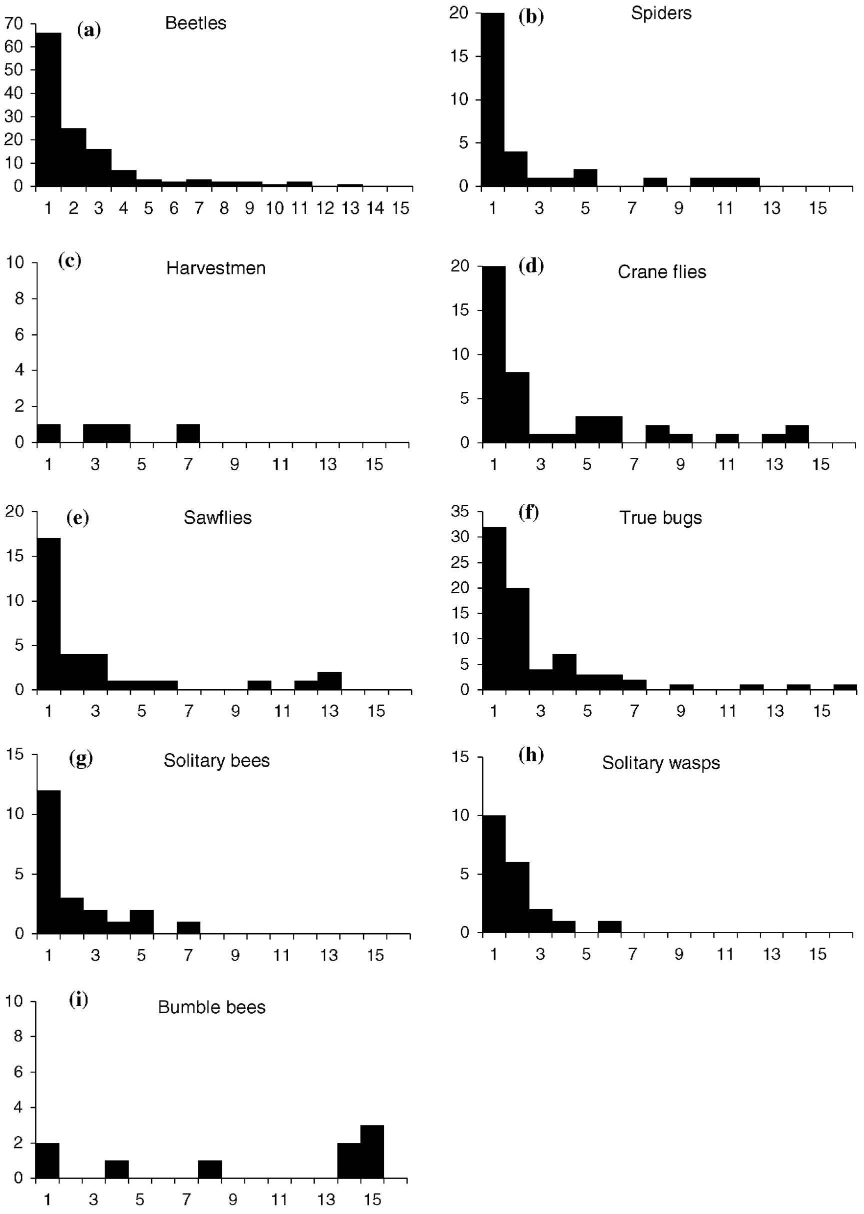

Figure 3. Species occupancy across gardens for taxa sampled by Malaise traps, for (a) beetles, (b) spiders, (c) harvestmen, (d) crane flies, (e) sawflies (f) true bugs, (g) solitary bees, (h) solitary wasps, (i) bumble bees. The x-axis shows number of gardens, and the y-axis shows the number of species. Note that the y-axis scale is not constant.

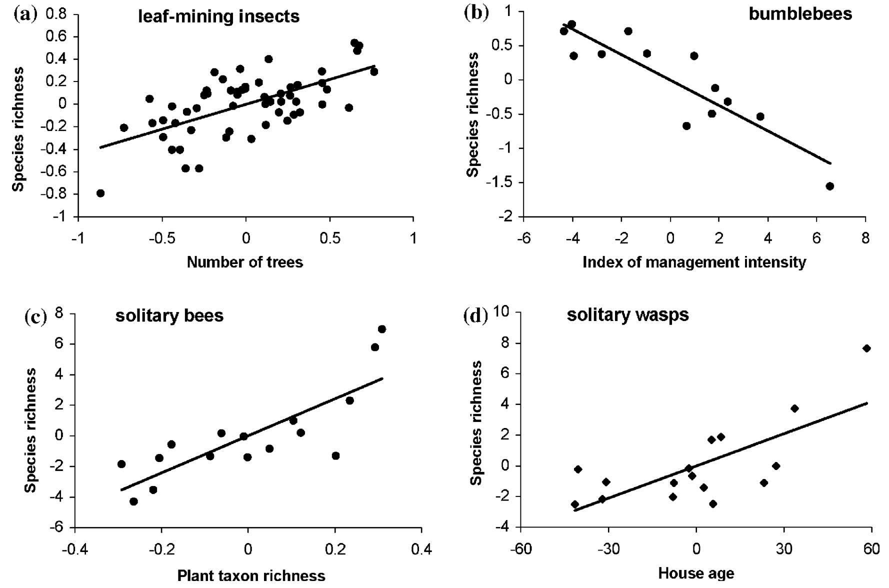

Figure 4. Partial leverage plots (SAS 8.1, SAS Institute Inc., Cary, NC, USA) showing examples of relationships between species richness and internal garden characteristics: (a) leaf-mining insects and number of trees > 2 m high, (b) bumblebees and an index of management intensity, (c) solitary bees and floral taxon richness, and (d) solitary wasps and house age. Plots are derived from stepwise multiple regression models (Table 2) where the *x*-axis represents the residuals of the explanatory variable from a model that regresses that explanatory variable on the remaining explanatory variables. The *y*-axis represents the residuals of the dependent variable calculated from a model with the explanatory variable (of the *x*-axis) omitted.

trees), into a small group below 6.9 m^2 in extent (a terminal node, mean 6.3 beetle species) and a larger one, above (mean 12.3 species). The latter further subdivided into groups with, respectively, means of 20.0 and 11.4 species within and beyond a threshold of 0.86 km to the urban edge.

Considering the data from pitfall traps alone, greater variation in beetle species richness was explained (36%, Table 2). The number of trees > 2 m high in a garden was also the dominant factor, but stronger than in the previous model. Further, the remaining factors of importance were different: negative influence due to the area of hard surfaces within the garden, and a positive effect of the extent of surrounding green space.

A substantial proportion of variation in beetle species richness in Malaise traps (84%) was explained by position on an easterly axis, the presence of composting, and to a lesser extent, the length of a garden's boundary shared by neighbouring gardens (Figure 5, Table 2). The primary, and only, split in the *tree* analysis occurred for local human population density above and below 14.8 people ha^{-1}, for which respective group means were 14.6 and 25 beetle species (i.e. higher richness was associated with gardens in less densely populated locations).

Table 2. A matrix showing the strengths of the effects of independent variables (environmental and housing characteristics) on the species richness' of invertebrate taxa, analysed by stepwise multiple regression (see Methods for details).

Taxon	Leaf-miners	Beetles	Beetles	Beetles	Arachnids	Arachnids	Arachnids	Slugs	Snails	Centipedes millipedes and isopods	Bumblebees	Sawflies	Craneflies	True bugs	Solitary bees	Solitary wasps
Source of data		P, L	P	M	P, L	P	M	P, L	P, L	P, L	M	M	M	M	M	M
Model d.f.	5, 50	4, 55	6, 48	3, 12	1, 58	1, 58	2, 13	6, 47	5, 52	2, 57	3, 9	3, 12	2, 13	1, 14	3, 12	2, 13
Model r^2_{adj}	0.61	0.28	0.36	0.84	0.10	0.09	0.62	0.47	0.42	0.19	0.88	0.70	0.44	0.22	0.63	0.45
Plant taxon richness															3	
Distance east				3												1
Distance north			(−1)									3				
House age		−1						−1								2
Altitude	−1						−3		1	1				−1		
Rural proximity												−1				
Garden area		−1														
Habitat diversity											3					
Structural diversity							2									
Perimeter-area ratio								2								
No. of houses			(1)												2	
Area of gardens									(−1)							
Area of lawn												2				
Area of hard surface			−2		2	2										
Presence of pond													2			
Presence of composting	−1	1		2				1								
Canopy < 2 m															(1)	
Canopy > 2 m										2						

Table 2. Continued.

Taxon	Leaf-miners	Beetles	Beetles	Beetles	Arachnids	Arachnids	Arachnids	Slugs	Snails	Centipedes millipedes and isopods	Bumblebees	Sawflies	Craneflies	True bugs	Solitary bees	Solitary wasps
Source of data		P, L	P	M	P, L	P	M	P, L	P, L	P, L	M	M	M	M	M	M
Model d.f.	5, 50	4, 55	6, 48	3, 12	1, 58	1, 58	2, 13	6, 47	5, 52	2, 57	3, 9	3, 12	2, 13	1, 14	3, 12	2, 13
Model r^2_{adj}	0.61	0.28	0.36	0.84	0.10	0.09	0.62	0.47	0.42	0.19	0.88	0.70	0.44	0.22	0.63	0.45
No. of trees	3	2	3						3							
Length of walls	1							1	2							
Length of gardens on boundary	(1)			1												
Local population density								1					−1			
Area of green space			2								2					
Management index			1						−1		−3					
Wildlife index								2								

Sources of data are: Pitfall traps (P), Malaise traps (M) and Litter samples (L). Negative relationships are indicated by –; for level of significance: 3 = $p < 0.001$, 2 = $p < 0.01$, 1 = $p < 0.05$, (1) = $0.10 > p > 0.05$.

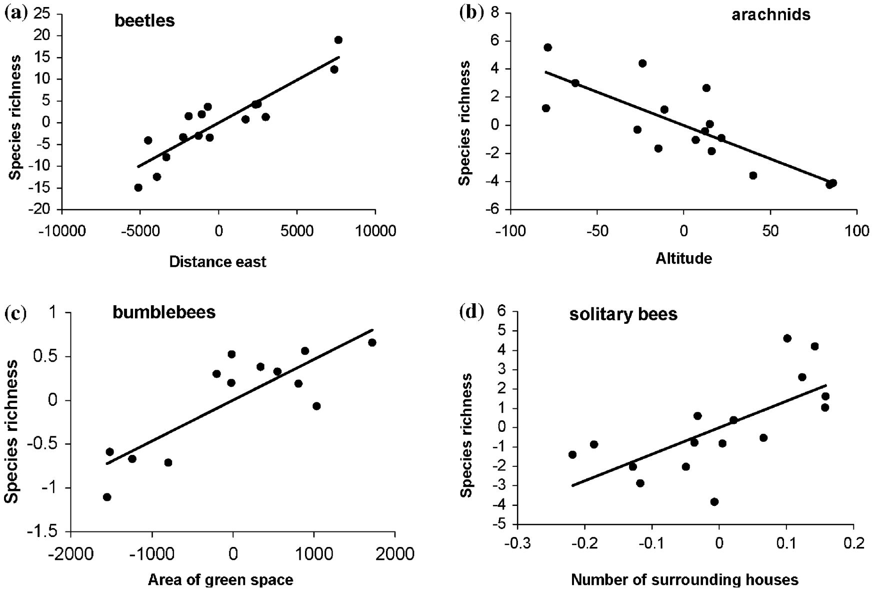

Figure 5. Partial leverage plots (SAS 8.1, SAS Institute Inc., Cary, NC, USA) showing examples of relationships between species richness and features of the environment external to gardens: (a) beetles in Malaise traps and the distance east, (b) arachnids in Malaise traps and altitude, (c) bumblebees and the area of green space in the surrounding 1 ha, and (d) solitary bees and the number of houses in the surrounding 1 ha. Plot axes derived as for Figure 4.

Arachnids (Arthropoda, Arachnida: Aranea, Opiliones, and Pseudoscorpiones)

Little of the variation in arachnid species richness was explained – either for pitfall trap data alone (9%), or for combined pitfall and litter data (10%) – being positively related only to the area of hard surfaces in a garden (Table 2). This was confirmed by the primary split of the *tree* analysis on the same variable, above and below 38.5 m^2 of hard surface, with respective group means of 9.4 and 6.2 arachnid species. The former group split further into subsets with means of 13.2 and 8.3 species below and above 48 m^2 of vegetation under 2 m high. The group associated with relatively less hard surface subdivided into sets with means of 4.9 and 8.0 species below and above 5333 m^2 of gardens in the surrounding 1 ha.

Arachnid species richness in Malaise traps was related positively to the structural diversity of the vegetation and strongly, negatively to altitude (Figure 5, table 2). The *tree* analysis revealed a single, primary split for extent of canopy vegetation more than 2 m high, at 54.0 m^2 . However, the means for the two groups were contrary to what might be expected if arachnid species richness was related to the extent of available canopy habitat: with means of 7.8 species below the split, and only 4.2 above.

Slugs and snails (Mollusca: Gastropoda)

Combined data from pitfall traps and litter samples for slugs showed that species richness was related to factors internal and external to gardens (Table 2). Positive relationships with the perimeter–area ratio of the garden (which is greater in small gardens) and local human population density suggest a general effect of the housing environment. Further, species richness was higher in younger housing. Within gardens, slug species richness was positively related to the presence of composting, the length of walls, and an index of wildlife gardening. Local human population density also featured as the primary split in the *tree* analysis, at virtually the same place as for beetles in Malaise traps (14.5 people ha^{-1}). Species richness was marginally greater at higher population densities: a group mean of 5.4 species compared to 4.4 below the split. Both of these groups then split unevenly on the variable east, and in each case the smaller, more westerly set had slightly higher species richness (lower population group: 5.5 compared to 4.1 species; higher population group: 6.2 compared to 5.0 species).

The length of walls was the only explanatory factor common to slug and snail species richness. However, length of walls accounted for less than half the snail species richness variation as explained by the number of trees. Small positive and negative effects were exerted, respectively, by altitude and the intensity of garden management (Table 2). The *tree* analysis reiterated the significance of number of trees: the relatively small number of gardens which contained more than 17.5 trees possessed nearly double the number of species – 6.2 vs. 3.6. The latter group split further on an easterly axis, with gardens to the west and east having means of 6.2 and 3.3 species, respectively.

Centipedes, millipedes and woodlice (Arthropoda: Chilopoda, Diplopoda and Crustacea (Isopoda))

Little variation was explained in the combined data for centipedes, millipedes and woodlice, the only relationships being positive ones for altitude, and more importantly, the extent of canopy above 2 m (Table 2). The *tree* analysis indicated that species richness was greater in gardens to the west (mean 7.6 species) than to the east (mean 5.6 species); this corroborates the regression analysis, since altitude and distance west are positively correlated ($r = 0.64$, $n = 59$, $p < 0.001$). The westerly gardens then subdivided along a northerly axis, with group means of 6.9 species to the south and 9.1 to the north. The easterly gardens split into sets with means of 6.8 and 5.0 species above and below a threshold garden management index of 11.5, i.e. relatively intensively managed gardens in the east of Sheffield supported marginally more species.

Bumblebees (Arthropoda, Insecta, Hymenoptera: Apidae)

Bumblebee species richness from Malaise traps was strongly positively related to habitat diversity in gardens, and strongly negatively related to the intensity of garden management; the area of surrounding green space was an additional positive correlate (Figures 4 and 5, Table 2). The sole split in the *tree* analysis was for habitat diversity too, with a mean species richness of 7.0 in relatively diverse gardens compared to 5.6 in relatively homogeneous ones.

Sawflies (Arthropoda, Insecta, Hymenoptera: Symphyta)

The distance north was the most important (positive) predictor of sawfly species richness, accounting for 52% of the variation explained by the model. Species richness was also positively related to the area of lawn in a garden, and there was weak evidence for a negative effect the further a garden occurred from the edge of the urban area (Table 2). The *tree* analysis indicated a split above and below an alien floral richness of 50.4 taxa, with means of 11.0 and 5.86 sawfly species for respective groups.

Craneflies (Arthropoda, Insecta, Diptera: Tipulidae, Pediciidae, Limoniidae and Ptychopteridae)

Cranefly species richness was related positively to the presence of ponds, and to a lesser extent, negatively to human population density (Table 2). As for the *tree* analysis for sawflies, cranefly species richness was greater in gardens with more alien plant taxa (14.3 cranefly species above a split of 43.9 plant taxa, and 6.8 species below).

True bugs (Arthropoda, Insecta: Hemiptera, excluding Sternorrhyncha)

A negative effect of altitude was the only factor associated with species richness in true bugs (Table 2), although the sole split in the *tree* analysis was for the number of trees. Below 14.9 trees the group mean was 15.1 species, whereas above the split the mean number of species was only 11.8.

Solitary bees (Arthropoda, Insecta, Hymenoptera: Apoidea)

The species richness of solitary bees was positively related, in order of strength, to the taxon richness of garden plants (Figure 4), the number of surrounding houses (Figure 5), and (marginally) to the extent of canopy vegetation below 2 m high (Table 2). The importance of the garden flora was supported by a single primary split in the *tree* analysis, where above and below a threshold of 50.4 native taxa, gardens had means of 3.8 and 1.0 species, respectively.

Solitary wasps (Arthropoda, Insecta, Hymenoptera: Sphecoidea, Vespoidea)

Solitary wasp species richness was positively related to house age and the distance east (Figure 4, Table 2). However, the tree analysis gave the same result as for solitary bees: a single primary split for native plant richness, with means of 2.3 and 0.4 wasp species above and below 43.9 plant taxa.

Discussion

The results from 16 analyses of 12 invertebrate groups showed that both factors within, and external to, gardens were significantly related to species richness within gardens. In total, 22 explanatory variables entered into stepwise regression models, although 12 of them only did so once. The amount of variation in species richness explained in models was generally reasonably high (Table 2), especially for data based on Malaise traps, where it ranged from 22–88%. However, consistent patterns did not emerge for the effects of factors across taxa, and in some cases relationships existed in opposite directions for different taxa (e.g. the length of walls, and altitude).

The factors external to gardens operated across a range of scales. Beetle and sawfly species richness in Malaise traps were associated with garden position on east-west and north-south axes, respectively, representing spatial correlations occurring over more than 10 km. Such broad influence has been shown for bird assemblages on an urban gradient, independently of the effect of habitat (Cooper 2002). There was evidence for a very general environmental effect of altitude in 5 out of the 16 analyses, although it only possessed a strong (negative) relationship with the species richness of arachnids caught in Malaise traps. Decreasing altitude was given as the cause for butterfly species richness to increase with urbanisation, across the Greater Manchester conurbation, since species-poor uplands bounded the urban area (Hardy and Dennis 1999).

At a more local scale, the quantity of green space in the surrounding 1 ha (including garden habitats) was related to the species richness of beetles in pitfall traps and bumble bees, whilst no variation was explained by the area of gardens alone. The extent of urban cover (i.e. built or sealed surfaces) has been widely cited as having a negative effect upon native species richness: at local scales in butterflies (Blair and Launer 1997; Hardy and Dennis 1999), birds in urban parks (Jokimäki 1999), lizards in residential areas (Germaine and Wakeling 2001), and ground beetles in urban London (Davis 1978). In the present study, effects of other measures of urban cover were also apparent. Local human population density correlated with slug species richness positively and craneflies negatively, although number of houses (in the surrounding 1 ha) was positively associated with solitary bee richness.

It is striking that several important aspects of the garden environment did not appear prominently in the analyses. Overall plant taxon richness, habitat diversity and structural diversity of the vegetation did so only once, and the number of alien or native plant species only in *tree* analyses. Even so, other features of garden vegetation were significant, particularly the number of trees > 2 m high. Tree species supported 35% of the leaf-miners recorded, therefore gardens containing more tree specimens were more likely to harbour suitable hosts. As the number of trees and total garden plant richness are positively correlated, via their relationships with garden size (unpublished data), then trees probably also captured variation in the number of other plant hosts. In this respect, garden area indirectly influences the resources available to certain invertebrate guilds. While the richness of solitary bees was strongly related to plant taxon richness (most likely due to the wider range of floral resources available), this feature of gardens need not necessarily be restricted by size, as planting is under the control of garden owners.

Of the internal garden features related to invertebrate species richness, not all have obvious associations with particular taxa. It is likely that some factors are correlated with other features of real significance. For example, the influence of canopy > 2 m high on centipedes, millipedes and woodlice could be construed as a variety of effects, such as provision of shade and litter. The presence of composting as a factor is readily explicable for beetle richness in Malaise traps, since compost heaps provide specialised microhabitats and resources in gardens (Ødegaard and Tømmerås 2000); but explanations for the relationship between compost heaps and the richness of leaf-mining insects; the richness of arachnids and the area of hard surfaces; between the richness of sawflies and the area of lawn, and between cranefly richness and the presence of ponds, are not at all obvious. The occurrence of such associations, for which mechanisms are difficult to suggest, reinforces the caution necessary in speculating about the causality of both these relationships and also those for which plausible causal links can be postulated. As emphasised initially this is, necessarily, an exploratory analysis documenting the patterns among richness and features of the garden environment, and there remains much work to be done to test the generality and causality in these patterns.

Perhaps the most striking feature of the results is the variation among taxa in the variables with which species richness is associated. There are a number of reasons why this might be the case. It is of course possible that a few of the apparent associations are chance results; many variables are examined, and some of the relationships are weak. We chose not to try to control for the number of comparisons since, firstly, we were more interested in examining the full range of associations and their relative strengths, and secondly, the conceptual and methodological uncertainties with techniques for doing this would have resulted in us making arbitrary judgements about how to apply such corrections (e.g. see Moran 2003). One consequence of this approach is that the weaker results must be viewed with some caution.

However, even among the stronger relationships, there is considerable variation in the factors involved and the direction of the association. The most obvious reason for this is that different factors are important for different groups of organisms. This could be as a result of the spatial scale at which the environment is likely to affect them (and at which we sampled), and of course the biological characteristics of the different taxa.

The autecology of most invertebrates is so poorly resolved that it is rarely known what resources species are using in gardens, and whether they occur as permanent residents, are using gardens for important stages of their life histories, or if they are simply casual or accidental visitors. For example, the high occupancy of gardens by most of the bumblebees recorded suggested that, even if they rarely nest in such habitats (Owen 1991), they are very mobile and readily exploit gardens. The availability of nectar resources and potential nest sites would explain the observed association of bumblebees to the amount of green space surrounding the garden. However, it is not clear why they were related negatively to the index of management intensity within gardens (being mobile, temporary visitors), or positively to land use diversity, which was largely unrelated to their resource requirements. Ironically, ground-active arachnids, centipedes, millipedes and woodlice are easily recognised as garden residents, yet their species richness' were poorly explained by variables describing the environments within the gardens where they were found.

In addition, the scale at which each sampling method operated will interact with the spatial scale at which species are using gardens, potentially contributing further to the variation in explanatory factors. Pitfall trapping and litter sampling were effective at relatively small scales, at the sampling point itself, or in its immediate vicinity. Thus the taxa that such methods sampled – typically woodlice, millipedes, centipedes, and ground-dwelling beetles, arachnids and molluscs – would have been expected to reflect local factors. In contrast, Malaise traps sampled a predominantly aerial fauna (presumably derived from a wider area than the garden itself), so that the recorded taxa should have reflected broader-scale factors. Indeed, for explanatory models of taxa sampled by Malaise traps, the most important relationships were with external garden factors in half of such models; in contrast, for taxa sampled by other methods, the more significant relationships all existed with factors internal to the garden (Table 2).

We believe that this potential combination of factors differing in importance to different taxa, and the differing scales at which they utilise garden environments, probably underpins much of the variation in the variables that feature in the results. However, we would also stress that this applies whether or not the taxon is responding to the variable we measured, or to one or more other factors with which that variable is associated.

A final observation is that this study differed in two important ways from those that have explicitly addressed the effect of urbanisation on species richness: first, it was based largely in residential zones and thus probably captured a smaller range of landscape variation than do studies of urban gradients (e.g. Blair 1996; McGeoch and Chown 1997; Germaine and Wakeling 2001). The latter seek to maximise the range of degree of urbanisation, from truly rural sites or nature reserves to the central business district, so that effects relating to urban cover should be more pronounced. Second, the analysis of habitat or resource fragments, be they host plants (Denys and Schmidt 1998), encapsulated semi-natural vegetation (Soulé et al. 1988; Miyashita et al. 1998; Honnay et al. 1999) or other green space (Jokimäki 1999), has emphasised the roles of isolation and fragment area on species assemblages. These assemblages are considered scarce in the surrounding urban matrix, and therefore governed by extinction and colonisation processes at the scale of the patch. In contrast, urban gardens characteristically form much of the matrix of residential zones, and are connected over large areas. Therefore invertebrates in a particular garden should reflect the species pool outside the boundaries of that garden better than if it was an isolated habitat fragment. For example, in Davis' (1978) study of ground beetles in gardens in London, the effect of distance to the urban edge was lost when the amount of open space in the surrounding 1 km radius was considered. In the present study, there was only evidence for a weak relationship with garden area in one of the five ground-active taxa studied (beetles in pitfall and litter samples, for which the sampling was spatially related to a garden's area); yet this actually showed a negative correlation with garden area. Similarly, proximity to the urban edge was weakly associated with only one taxon – sawflies, in which species richness declined away from the countryside.

In conclusion, the lack of evidence for general correlates of invertebrate species richness in urban gardens reinforces the view that different invertebrate taxa respond to specific resource requirements, both within and around gardens. Urban domestic gardens differ from other types of urban green space because they constitute the urban matrix, rather than being fragments within it. Therefore recommendations to enhance the quality of garden habitats for urban biodiversity may best be focussed upon their configuration in the urban area, to ensure that green space is distributed throughout the urban zone. If specific garden features are to be encouraged for invertebrates, then vegetation – especially tree cover – is likely to provide benefits for the widest range of taxa. Since tree cover is positively associated with garden size (Smith et al. in press), then attention should be given to providing sufficient garden space in new residential developments.

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Appendix 1. Independent variables used in analyses of species richness (see Methods)

One richness of higher plant taxa in garden; 2 richness of alien higher plant taxa in garden; 3 richness of native higher plant taxa in garden; 4 distance east, Ordnance Survey National Grid map coordinate; 5 distance north, Ordnance Survey National Grid map coordinate; 6 age of house calculated in 2000; 7 altitude, m above sea level; 8 rural proximity: distance in km from centre of nearest 1 km cell with $<25\%$ urban land use; 9 habitat diversity: Simpson's diversity index for land uses in each garden; 10 structural diversity: Simpson's diversity index for vegetation canopy cover classes: <0.5 m, 0.5–1 m, 1–2 m, 2–3 m, and >3 m in each garden; 11 area of rear garden in m^2; 12 perimeter–area ratio: ratio of 'exposed' (i.e. excluding perimeter along rear of house) garden perimeter to garden area; 13 area of grass in rear garden (cut + uncut portions); 14 area of non-grass green space in rear garden (grass paths + cultivated border + vegetable patch + neglected/uncultivated); 15 area of hard surfaces in rear garden (hard paths + patios + green house + sheds + garage + decking); 16 presence of ponds in a rear garden (scored 1 or 0); 17 presence of compost bins or heaps in a rear garden (scored 1 or 0); 18 area of vegetation canopy 0–2 m (excluding mown grass); 19 area of vegetation canopy >2 m; 20 no. of trees >2 m tall in rear garden; 21 exposed perimeter length of rear garden (i.e. excluding perimeter along rear of house); 22 length of hedges in rear garden, m; 23 length of walls in rear garden, m; 24 length of garden boundary abutting other gardens, m; 25 human population density (no. 40×10^3 m^{-2}, or 4 ha^{-1}), POPSURF 1991 census data. *Recorded from GIS, for 1 ha circular plot centred on survey garden:* 26 no. of houses (where $>$half of property is included), 27 area of domestic gardens, 28 area of all green space, 29 area of contiguous green space fragment; 30 management intensity index-summation of following values of management variables, data from questionnaire: (a) index of intensity of weeding (weak 1–5 strong), (b) index of intensity of pruning vegetation (weak 1–5 strong); (c) index of intensity of watering borders (weak 1–5 strong), (d) removing dead flower heads (scored 1 or 0), (e) collecting fallen leaves in autumn (scored 1 or 0), (f) use of fertiliser in garden (scored 1 or 0), (g) use of herbicides in garden (scored 1 or 0), (h) use of pesticides in garden (scored 1 or 0); 31 use of slug pellets (scored 1 or 0, used in analyses of molluscs only); 32 wildlife management index-summation of following wildlife gardening variables, data from questionnaire: (a) bird feeding (scored 1 or 0), (b) provision of nest box for birds (scored 1 or 0), (c) other management specifically to attract wildlife (scored 1 or 0).

References

Allen A.A. 1964. The Coleoptera of a suburban garden. Entomol. Rec. J. Variation 76: 261–4.

Bailey S.E.R., North M.C. and Cook L.M. 1998. Slugs and snails and thrushes' anvils: children's surveys of slugs and snails. J. Conchol. Special Publication 2: 171–178.

Blair R.B. 1996. Land use and avian species diversity along an urban gradient. Ecol. Appl. 6: 506–519.

Blair R.B. and Launer A.E. 1997. Butterfly assemblages and human land use: species assemblages along an urban gradient. Biol. Conserv. 80: 113–125.

Cannon A. 2000. Garden BirdWatch Handbook, 2nd ed. British Trust for Ornithology, Thetford.

Cooper D.S. 2002. Geographic associations of breeding bird distribution in an urban open space. Biol. Conserv. 104: 205–210.

Crawley M.J. 2002. Statistical Computing: An Introduction to Data Analysis using S-Plus. John Wiley and sons, Chichester, UK.

Davis B.N.K. 1978. Urbanisation and the diversity of insects. In: Mound L.A. and Waloff N. (eds), Diversity of Insect Faunas. Blackwell Scientific, Oxford, pp. 126–138.

Denys C. and Schmidt H. 1998. Insect communities on experimental mugwort (*Artemisia vulgaris* L.) plots along an urban gradient. Oecologia 113: 269–277.

Eversham B.C., Roy D.B. and Telfer M.G. 1996. Urban, industrial and other manmade sites as analogues of natural habitats for Carabidae. Ann. Zool. Fenn. 33: 149–156.

Fernández-Juricic E. 2000. Avifaunal use of wooded streets in an urban landscape. Conserv. Biol. 14: 513–521.

Gaston K.J., Smith R.M., Thompson K. and Warren P.H. in press a. Urban domestic gardens (II): experimental tests of methods for increasing biodiversity. Biodivers. Conserv. in press.

Gaston K.J., Warren P.H., Thompson K. and Smith R.M. in press b. Urban domestic gardens (IV): the extent of the resource and its associated features. Biodivers. Conserv. in press.

Germaine S.S. and Wakeling B.F. 2001. Lizard species distributions and habitat occupation along an urban gradient in Tucson, Arizona, USA. Biol. Conserv. 97: 229–237.

Gilbert O.L. 1990. The lichen flora of urban wasteland. Lichenologist 22: 87–101.

Hardy P.B. and Dennis R.L.H. 1999. The impact of urban development on butterflies within a city region. Biodivers. Conserv. 8: 1261–1279.

Honnay O., Endels P., Vereecken H. and Hermy M. 1999. The role of patch area and habitat diversity in explaining native plant species richness in disturbed forest patches in northern Belgium. Divers. Distrib. 5: 129–141.

Jokimäki J. 1999. Occurrence of breeding bird species in urban parks: effects of park structure and broad-scale variables. Urban Ecosyst. 3: 21–34.

Kinzig A.P. and Grove J.M. 2001. Urban–suburban ecology. In: Levin S.A. (ed.), Encyclopaedia of Biodiversity, Vol. 5. Academic Press, San Diego, pp. 733–745.

Martin D. and Tate N. 1997. Surpop V2.0: Introduction. http://census.ac.uk/cdu/surpop.htm.

McGeoch M.A. and Chown S.L. 1997. Impact of urbanization on a gall-inhabiting Lepidoptera assemblage: the importance of reserves in urban areas. Biodivers. Conserv. 6: 979–993.

Miotk P. 1996. The naturalized garden- a refuge for animals? – first results Zool. Anz. 235: 101–116.

Miyashita T., Shinkai A. and Chida T. 1998. The effects of forest fragmentation on web spider communities in urban areas. Biol. Conserv. 86: 357–364.

Moran M.D. 2003. Arguments for rejecting the sequential Bonferroni in ecological studies. Oikos 100: 403–405.

Ødegaard F. and Tømmerås B.Å. 2000. Compost heaps – refuges and stepping-stones for alien arthropod species in northern Europe. Divers. Distrib. 6: 45–59.

Owen J. 1991. The Ecology of a Garden: the first fifteen years. Cambridge University Press, Cambridge.

Owen J. 2002. My Romney Marsh garden. Atropos 17: 53–57.

Pyšek P. 1993. Factors affecting the diversity of flora and vegetation in central European settlements. Vegetatio 106: 89–100.

Roy D.B., Hill M.O. and Rothery P. 1999. Effects of urban land cover on the local species pool in Britain. Ecography 22: 507–515.

Saville B. 1997. The Secret Garden: Report of the Lothian Secret Garden Survey. Lothian Wildlife Information Centre, Edinburgh.

Smith C. 1989. Butterflies and moths in suburbia. Nature Cambridgeshire 31: 19–27.

Smith R.M., Gaston K.L., Warren P.H. and Thompson K. in press. Urban domestic gardens (V): relationships between landcover composition, housing and landscape. Landscape Ecology. in press.

Soulé M.E., Bolger D.T., Alberts A.C., Wright J., Sorice M. and Hill S. 1988. Reconstructed dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands. Conserv. Biol. 2: 75–92.

Stace C. 1997. New Flora of the British Isles, 2nd ed. Cambridge University Press, Cambridge.

Sukopp H. and Starfinger U. 1999. Disturbance in urban ecosystems. In: Walker L.R. (ed.), Ecosystems of the World 16. Ecosystems of Disturbed Ground. Elsevier Science, Amsterdam, pp. 397–412.

Thompson K., Austin K.C., Smith R.M., Warren P.H., Angold P.G. and Gaston K.J. 2003. Urban domestic gardens (I): putting small-scale plant diversity in context. J. Veg. Sci. 14: 71–78.

Thompson K., Hodgson J.G., Smith R.M., Warren P.H. and Gaston K.J. 2004. Urban domestic gardens (III): composition and diversity of lawn floras. J. Veg. Sci. 15: 371–376.

Vickery M.L. 1995. Gardens: the neglected habitat. In: Pullin A.S. (ed.), Ecology and conservation of butterflies. Chapman and Hall, London, pp. 123–134.

Wright M. 1984. The Complete Handbook of Garden Plants. Michael Joseph, London.

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Biodiversity conservation in sacred groves of Manipur, northeast India: population structure and regeneration status of woody species

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Abstract. Sacred groves are forest patches conserved by the local people intertwined with their socio-cultural and religious practice. These groves harbour rich biodiversity and play a significant role in the conservation of biodiversity. Population structure and regeneration status of woody species were studied during 2001–2002 in the four sacred groves of Manipur, a state in north east India. A total of 96 woody species was recorded from the four groves, the highest being Konthoujam Lairembi sacred grove (55 species) and lowest in Heingang Marjing sacred grove having 42 species. The density–diameter distribution of woody species in the four groves showed highest stand density and species richness in the lowest girth class (30–60 cm) and decreased in the succeeding girth classes. Overall population structure of the groves based on the number of tree seedlings, saplings and adults, displayed a greater proportion of seedlings followed by saplings and adults while for the selected tree species it varied seasonally and recruitment of species increased during rainy season attaining peak during June. Regeneration status of the four sacred groves based on strength of different age groups in their population showed good regeneration. High occurrence of 'additional species' to the groves may be due to the invasion through dispersal from other areas. Possibly, the prevailing favourable microenvironmental conditions contributed to their establishment and growth in the groves. Absence of seedlings and saplings of some of the species in the groves may be due to their poor seed germination and establishment of seedlings in the forest.

Introduction

Sacred groves are forest patches rich in biodiversity, manifested by a range of traditions and cultural values of the indigenous people who protect the groves with the beliefs in nature worship inherited from their ancestors. They act as reservoirs of much local biodiversity preserving unique flora and fauna. The biological resources make indirect contributions to the welfare and stability of the local environment. Various medicinal plants are found abundantly in sacred groves and they are the vital source of wild cultivars and diverse gene pool. It is because of the local people and their strong socio-religious beliefs and taboos the conservation and protection of the groves is possible. As a result, sacred groves can help in assessing the potential values of forest communities of degraded ecosystem or man made forest.

The major component for the formation of forest communities is the woody species. The nature of forest communities largely depends on the ecological characteristics in sites, species diversity and regeneration status of species. Microenvironmental factors vary with seasonal changes which affect the growth stage i.e. seedling, sapling and young trees of the plant communities that maintain the population structure of any forest. Hence, it becomes an important issue to understand the tree diversity, population structure and regeneration status of forest communities for the maintenance of both natural and control forest. The satisfactory natural regeneration behaviour of the forests largely depends on population structure characterized by the production and germination of seed, establishment of seedlings and saplings in the forest (Rao 1988). Complete absence of seedlings and saplings of tree species in a forest indicates poor regeneration, while presence of sufficient number of young individuals in a given species population indicates successful regeneration (Saxena and Singh 1984). However, the presence of sufficient number of seedlings, saplings and young trees is greatly influenced by interaction of biotic and abiotic factors of the environment (Boring et al. 1981; Aksamit and Irving 1984). While several authors have predicted regeneration status of tree species based on the age and diameter structure of their population (Marks 1974; Bormann and Likens 1979; Veblen et al. 1979; Bhuyan et al. 2003). Various studies on population structure and regeneration status have been carried out by many workers in different forest ecosystems (Pritts and Hancock 1983; Saxena et al. 1984; Khan et al. 1987; Ashton and Hall 1992; Cao et al. 1996; Gunatilleke et al. 2001; Uma Shankar 2001). Tree population structure and its implication for their regeneration has been studied in different forest communities of India e.g. Garhwal (Baduni and Sharma 2001; Bhandari 2003), Himachal Pradesh (Sood and Bhatia 1991), Western Himalayas (Pande et al. 2002), Western Ghats (Parthasarathy 2001) and north eastern region (Yadava et al. 1991; Maram and Khan 1998; Bhuyan et al. 2002, 2003).

Studies on population structure and regeneration pattern of tree species in sacred groves are limited (Khan et al. 1986, 1987; Rao et al. 1990; Barik et al. 1996; Mishra et al. 2003). Though phytosociological and ethnobotanical investigations (Khumbongmayum et al. 2004, in press) have been carried out in sacred groves of Manipur, the studies on population structure and regeneration status are lacking in these groves which harbours rich biodiversity and diverse gene pool of many forest species. Therefore, an attempt has been made to study the population structure and regeneration status of woody species in the four selected sacred groves of Manipur viz., Konthoujam Lairembi, Mahabali, Langol Thongak Lairembi and Heingang Marjing groves.

Study sites

The state of Manipur is situated in the extreme northeastern corner of India and lies between 23°50′–25°42′ N latitudes and 92°58′– 94°45′ E longitudes. It is centrally located on the eastern arm of the Himalaya which separates India from Myanmar. Four sacred groves were selected in Imphal East and Imphal West districts on the basis of size, vegetation and location. The selected sacred groves are situated between 23°50′–25°41′ N latitudes and 93°2′–94°47′ E longitudes and they all have sub-tropical forests as their dominant vegetation. Two groves namely, Konthoujam Lairembi and Mahabali are located in valley and the other two groves, Langol Thongak Lairembi and Heingang Marjing, are located in hills. The four groves represent a rich vegetation of economic and medicinally important plant species which have been conserved and protected imbued with the religious beliefs and taboos of the local people. The Konthoujam Lairembi sacred grove is situated in the Konthoujam village, about 11 km west of the valley area of Imphal city. It lies at the elevation of 711 m, covering an area of ca. 1.41 ha. The Mahabali sacred grove is situated in the midst of Imphal city at 710 m altitude covering ca. 5.05 ha. The Langol Thongak Lairembi sacred grove is located in the Langol hill ranges about 5 km northwest of Imphal city covering ca. 5.05 ha. The altitude ranges from 800 m at the foot hills to 1050 m at the peak. The Heingang Marjing sacred grove is located in the Heingang village, to the north of Imphal city, at the elevation of 834 m covering an area of ca. 7.08 ha. Furthermore, the selected four sacred groves are least disturbed and protected by regulating the human interferences through religious proscription and prescription. Therefore, regeneration process of woody layer mainly depends on forest microclimate which in turn, might be altered due to various physico-chemical variables and seasonal changes.

In all the four sacred groves four layers of vertical stratification were observed. In Konthoujam Lairembi sacred grove, *Ficus benjamina* and *Saprosma* sp. were the dominant species and canopy is closed to each other while *Persea* sp. and *Ficus glomerata* dominate in the Mahabali sacred grove and the canopy of the topstorey layer is sparse. The two sacred groves located in the hill ranges are dominated by the *Pinus kesiya* and canopy coverage is relatively closed.

The climate of the study area is monsoonal with warm moist summer and cool dry winter. During the study period (2001–2002), the mean maximum temperature varied from 22 °C (January) to 30 °C (August) and mean minimum temperature varied from 5 °C (January) to 23 °C (July). The average relative humidity ranged from 58% (March) to 82% (October). The mean monthly rainfall was minimum in December (2.5 mm) and maximum in June (236 mm). The average annual rainfall was 1482 mm.

The soil of the two sacred groves situated in the plains is blackish in colour while it is yellowish red to reddish brown in the other two sacred groves which are located in hilly area. The soil is alluvial in nature and its texture is loamy sand. The soil is acidic with pH ranging from 5.4 to 6.59. The organic carbon content ranged from 4.85% to 5.37% while the total Kjeldhal nitrogen (TKN) ranged from 0.01% to 0.04%. In general the soils are poor in nitrogen.

Methods

Population structure of all the woody species occurring in each sacred grove was studied during 2001–2002 using quadrat method. For this purpose forty quadrats of 10 m × 10 m were laid randomly in each grove. Species were identified and density of all the individuals of seedlings ($\leq$ 20 cm height) and saplings ($<$ 30 cm collar circumference at the base and $>$ 20 cm in height) of all the tree species were determined. While for trees ($\geq$30 cm girth at breast height of 1.37 m), density and basal area of each individual was recorded. Similarity index (community coefficient) of woody species among the four sacred groves was calculated following the formula given by Jaccard (1912).

$$Cj = j/(a + b - j)$$

Where '*j*' is the number of species common to both stands, '*a*' is the number of species in stand A and '*b*' is the number of species in stand B.

Ten important tree species, *Marlea begoniaefolia*, *Eugenia praecox*, *Litsea polyantha*, *Persea* sp., *Heptapleurum hypoleucum*, *Oroxylum indicum*, *Saprosma* sp., *Wendlandia tinctoria*, *Quercus serrata* and *Litsea sebifera* were selected from the four sacred groves for studying detailed population structure. Among the 10 species, two (*Eugenia praecox* and *Litsea polyantha*) were common to the four groves. Population structure of the selected tree species was studied in each grove during December, 2001, May, 2002 and October, 2002 by periodic determination of densities of the individuals belonging to three different categories viz., seedlings, saplings and trees. Relative proportion (%) of the different diameter groups i.e. seedlings, saplings and trees, to the density of a given species or to total density of tree species in a stand was calculated and figures were drawn, with seedling population at the base of the bar.

Regeneration status of species was determined based on population size of seedlings and saplings (Khan et al. 1987; Uma Shankar 2001; Bhuyan et al. 2003): good regeneration, if seedlings $>$ saplings $>$ adults; fair regeneration, if seedlings $>$ or $\leq$ saplings $\leq$ adults; poor regeneration, if the species survives only in sapling stage, but no seedlings (saplings may be $<$, $>$ or $=$ adults). If a species is present only in adult form it is considered as not regenerating. Species is considered as 'new' if the species has no adults but only seedlings or saplings.

Results

Woody species composition

A total of 96 woody species were recorded in the four groves. The Konthoujam Lairembi sacred grove recorded maximum (55) tree species followed by Heingang Marjing sacred grove (42 species) and Mahabali and Langol Thongak Lairembi sacred groves which had 38 species each. The calculated similarity index (community coefficient) of woody species among the sacred groves is given in Table 1. The highest similarity index value (0.35) was recorded between Langol Thongak Lairembi and Heingang Marjing sacred groves and lowest in between Mahabali and Heingang Marjing sacred groves (0.04). Out of the 10 species selected for studying their population structure, two species (*Eugenia praecox* and *Litsea polyantha*) were common to the four groves. *Marlea begoniaefolia* was common in both the groves located in the plains *i.e.* Konthoujam Lairembi and Mahabali sacred groves. *Heptapleurum hypoleucum* and *Saprosma* sp. are exclusive to the Konthoujam Lairembi sacred grove, while *Persea* sp. was exclusive to Mahabali sacred grove. *Wendlandia tinctoria*, *Quercus serrata* and *Litsea sebifera* were common to both the groves located in the hills namely, Langol Thongak Lairembi sacred grove and Heingang Marjing sacred groves. The total density per hectare of all seedlings, saplings and trees taken together ranged from 6353 in the Langol Thongak Lairembi sacred grove to 12192 in the Konthoujam Lairembi sacred grove (Table 2).

Girth class-wise species richness, tree density and basal area

The highest stand density and species richness of the woody species in four groves were recorded in the lowest girth class (30–60 cm). Stand density and species richness consistently decreased with increase in girth from 30–60 cm to >210 cm (Figure 1). In Langol Thongak Lairembi and Heingang Marjing sacred groves no tree was recorded in the girth class 180–210 cm. The highest contribution of stand density per girth class to total density for each grove was recorded in 30–60 cm girth class and maximum stand density (59.05%) was recorded in Langol Thongak Lairembi sacred grove, followed by Konthoujam Lairembi (55.43%), Mahabali (39%) and Heingang Marjing (38.81%). The basal area was maximum (44.63 m^2 ha^{-1}) in the highest girth class (>210 cm) at Mahabali and lowest in Heingang Marjing (1.15 m^2 ha^{-1}). The basal area distribution in different girth classes in two groves located in the plain area showed a similar pattern, and likewise the pattern shown by the two groves in the hills was also similar (Figure 1).

Table 1. Similarity index (community coefficient) of woody species among the four selected sacred groves.

Sacred groves	Mahabali	Langol Thongak Lairembi	Heingang Marjing
Konthoujam Lairembi	0.19	0.13	0.12
Mahabali		0.05	0.04
Langol Thongak Lairembi			0.35

Table 2. Density and regeneration status of woody species in four sacred groves of Manipur.

Species	Konthoujam Lairembi sacred grove				Mahabali sacred grove				Langol Thongak Lairembi sacred grove				Heingang Marjing sacred grove			
	No. of individuals/ha				No. of individuals/ha				No. of individuals/ha				No. of individuals/ha			
	Seedlings	Saplings	Trees	Status	Seedlings	Saplings	Trees	Status	Seedlings	Saplings	Trees	Status	Seedlings	Saplings	Trees	Status
Acacia auriculaeformis A. Curm ex. Benth.	–	–	–	–	–	–	–	–	–	–	–	–	3	#	#	New
Adenanthera pavonina Linn.	#	13	1	New	–	–	–	–	–	–	–	–	–	–	–	–
Albizia lebbeck (L.) Benth.	–	–	–	–	#	8	3	P	–	–	–	–	–	–	–	–
Albizia lucida (Roxb.) Benth.	–	–	–	–	–	–	–	–	35	130	18	F	53	78	5	F
Albizia odoratissima (Linn. f.) Benth	35	93	6	F	–	–	–	–	#	23	5	P	#	5	15	P
Albizia procera (Roxb.) Benth.	–	–	–	–	–	–	–	–	–	–	–	–	#	45	5	P
Albizia stipulata Boivin	–	–	–	–	–	–	–	–	#	8	3	P	#	13	18	P
Alnus nepalensis D. Don	–	–	–	–	–	–	–	–	–	–	–	–	#	3	3	P
Anthocephalus cadamba Roxb.	–	–	–	–	#	10	#	New	–	–	–	–	–	–	–	–
Anthocephalus chinensis (Lamk.) A. Rich. ex Walp.	–	–	–	–	#	#	3	N	–	–	–	–	–	–	–	–
Aphanamixis polystachya (Wall.) Parker	#	#	1	N	–	–	–	–	–	–	–	–	–	–	–	–
Aralia sp.	–	–	–	–	–	–	–	–	#	5	10	P	–	–	–	–
Ardisia sp.	–	–	–	–	–	–	–	–	–	–	–	–	#	5	5	P
Artocarpus heterophyllus Lam.	–	–	–	–	–	–	–	–	#	5	#	New	–	–	–	–
Artocarpus lakoocha Roxb.	313	#	13	F	100	38	8	G	–	–	–	–	–	–	–	–
Bauhinia purpurea Linn.	–	–	–	–	–	–	–	–	#	10	3	P	–	–	–	–
Bauhinia variegata Linn.	#	8	5	P	5	3	#	New	–	–	–	–	–	–	–	–
Bischofia javanica Blume	–	–	–	–	63	#	10	F	–	–	–	–	–	–	–	–
Bombax ceiba Linn.	–	–	–	–	–	–	–	–	#	8	5	P	#	5	#	New
Borassus flabellifer Linn.	–	–	–	–	20	#	#	New	–	–	–	–	–	–	–	–

Caryota urens Linn.	405	50	2	G	218	50	25	G	–	–	–	–	–	–	–	–
Castanopsis hystrix A. DC.	13	45	1	New	#	5	#	New	–	–	–	–	–	–	–	–
Celtis sp.	–	–	–	–	–	–	–	–	–	–	–	–	23	53	#	F
Celtis timorensis Linn.	5	18	3	F	35	38	3	F	10	#	#	New	#	23	#	New
Chukrasia tabularis Andr. Juss.	#	#	3	N	–	–	–	–	–	–	–	–	–	–	–	–
Cinnamomum sp.	28	18	#	New	–	–	–	–	–	–	–	–	–	–	–	–
Citrus maxima Merr	3	5	#	New	23	8	0	New	#	5	#	New	–	–	–	–
Cordia grandis Roxb.	#	#	2	N	–	–	–	–	–	–	–	–	–	–	–	–
Delonix regia (Boj.) Raf.	#	53	2	P	–	–	–	–	–	–	–	–	–	–	–	–
Elaeocarpus sp.	–	–	–	–	–	–	–	–	–	–	–	–	#	10	3	P
Engelhardtia colebrookiana Lindl.	–	–	–	–	–	–	–	–	25	38	#	New	65	143	35	F
Entada scandens Benth	#	#	1	N	–	–	–	–	–	–	–	–	–	–	–	–
Erythrina sp.	5	118	1	New	–	–	–	–	–	–	–	–	–	–	–	–
Eucalyptus citriodora Hook.	–	–	–	–	–	–	–	–	10	10	#	New	#	3	3	P
Eugenia praecox Roxb.	808	100	3	G	435	353	0	New	515	163	10	G	635	230	30	G
Eugenia sp.	#	25	2	P	–	–	–	–	–	–	–	–	–	–	–	–
Ficus benghalensis Linn.	#	#	3	N	–	–	–	–	–	–	–	–	–	–	–	–
Ficus benjamina Linn.	#	#	13	N	–	–	–	–	–	–	–	–	–	–	–	–
Ficus glomerata Roxb.	#	5	6	P	0	13	38	P	–	–	–	–	–	–	–	–
Ficus hispida Linn. f.	18	35	3	F	78	78	115	F	3	38	#	New	#	30	#	New
Ficus religiosa Linn.	–	–	–	–	#	#	3	N	–	–	–	–	–	–	–	–
Ficus semicordata Buch. - Ham. ex J. E. Smith	–	–	–	–	#	15	#	New	#	18	#	New	30	83	18	F
Flacourtia jangomas (Lour.) Raeusch	#	5	#	New	#	5	#	New	–	–	–	–	#	8	8	P
Gardenia companulata Roxb.	#	#	4	N	#	35	98	P	–	–	–	–	–	–	–	–
Gmelina arborea Roxb.	8	18	7	F	–	–	–	–	–	–	–	–	–	–	–	–
Grevillea robusta A. Cum	40	23	#	New	–	–	–	–	–	–	–	–	–	–	–	–
Heptapleurum hypoleucum Kurz	223	78	6	G	–	–	–	–	–	–	–	–	–	–	–	–
*Khajok	–	–	–	–	–	–	–	–	–	–	–	–	#	5	3	P
Holigarna longifolia Roxb.	–	–	–	–	–	–	–	–	–	–	–	–	#	10	13	P
Lagerstroemia flos-regine Retz.	#	38	#	New	#	5	#	New	–	–	–	–	–	–	–	–

Table 2. Continued.

Species	Konthoujam Lairembi sacred grove				Mahabali sacred grove				Langol Thongak Lairembi sacred grove				Heingang Marjing sacred grove			
	No. of individuals/ha				No. of individuals/ha				No. of individuals/ha				No. of individuals/ha			
	Seedlings	Saplings	Trees	Status	Seedlings	Saplings	Trees	Status	Seedlings	Saplings	Trees	Status	Seedlings	Saplings	Trees	Status
Lannea coromandelica (Houtl.) Merr.	5	38	8	G	#	8	#	New	#	10	#	New	–	–	–	–
Lannea grandis A. Rich	#	20	12	P	#	28	8	P	–	–	–	–	–	–	–	–
Ligustrum robustum (Roxb.) Blume	#	68	25	P	–	–	–	–	–	–	–	–	–	–	–	
Litsea citrata Blume	68	43	10	G	68	103	#	New	70	70	8	G	555	375	28	G
Litsea polyantha Juss.	368	385	19	F	368	158	15	G	518	188	15	G	423	150	10	G
Litsea sebifera Thumb.	75	18	#	New	–	–	–	–	345	113	#	New	448	198	15	G
Litsea sp. (1)	#	23	3	P	–	–	–	–	–	–	–	–	–	–	–	–
Litsea sp. (2)	–	–	–	–	#	28	13	P	#	20	#	New	#	40	#	New
Mallotus phillippinensis (Lam.) Muell.- Arg.	68	218	18	G	143	163	10	F	100	130	3	F	158	93	5	G
Mangifera indica Linn.	15	5	16	F	108	48	15	G	–	–	–	–	–	–	–	–
Mangifera sp.	–	–	–	–	–	–	–	–	10	33	3	F	5	8	8	F
Marlea begoniaefolia Roxb.	233	330	11	F	285	115	18	G	–	–	–	–	70	13	#	New
Melia azedarach Linn.	#	3	2	P	70	#	#	New	#	3	3	P	48	3	#	New
Morus nigra Linn.	–	–	–	–	33	40	#	New	#	15	#	New	–	–	–	–
Oroxylum indicum (L.) Vent.	158	173	19	F	–	–	–	–	–	–	–	–	#	15	5	P
Parkia roxburghii G. Don	–	–	–	–	–	–	–	–	#	13	5	P	–	–	–	–
Pasania polystachya (Wall) Schootky	–	–	–	–	–	–	–	–	128	118	48	G	8	88	10	F
Persea sp.	–	–	–	–	2063	480	85	G	–	–	–	–	–	–	–	–
Phyllanthus emblica Linn.	#	10	#	New	#	23	#	New	30	20	3	G	3	15	5	F
Pinus kesiya Royle ex. Gordon	–	–	–	–	–	–	–	–	290	8	690	F	258	133	705	F

Prunus sp.	–	–	–	–	–	–	–	–	–	–	–	–	5	25	8	F
Psidium guajava Linn.	–	–	–	–	48	20	#	New	#	5	#	New	#	3	#	New
Quercus serrata Thumb.	–	–	–	–	–	–	–	–	665	213	40	G	530	425	128	G
Rhus semialata Murray	65	#	3	F	–	–	–	–	500	145	8	G	378	33	#	New
Rubia sp. (1)	13	83	6	F	–	–	–	–	–	–	–	–	–	–	–	–
Rubia sp. (2)	#	#	2	N	–	–	–	–	–	–	–	–	–	–	–	–
Santalum sp.	–	–	–	–	–	–	–	–	#	18	8	P	–	–	–	–
Saprosma sp.	5420	548	54	G	–	–	–	–	–	–	–	–	–	–	–	–
Schima wallichii (D.C.) Korth	#	15	16	P	128	28	#	New	88	115	53	F	108	78	83	F
Spondias pinnata (Linn.f.) Kurz	#	15	1	New	–	–	–	–	–	–	–	–	–	–	–	–
Syzygium cumini (L) Skeels	#	3	#	New	–	–	–	–	–	–	–	–	–	–	–	–
Syzygium jambos (Linn.) Alston	#	#	1	N	–	–	–	–	–	–	–	–	–	–	–	–
Syzygium sp.	–	–	–	–	–	–	–	–	#	13	30	P	–	–	–	–
Tamarindus indica Linn.	3	5	#	New	–	–	–	–	–	–	–	–	–	–	–	–
Terminalia citrina (Gaertn.) Flem.	–	–	–	–	–	–	–	–	38	73	13	F	–	–	–	–
Thevetia neriifolia Juss.ex Steud	#	5	#	New	–	–	–	–	–	–	–	–	–	–	–	–
Toona ciliata M. Roem	–	–	–	–	#	3	#	New	–	–	–	–	#	3	#	New
*Uha	#	13	15	P	–	–	–	–	–	–	–	–	–	–	–	–
Trema orientalis Blume	28	43	6	F	28	53	#	New	#	10	#	New	#	#	5	N
Vangueria spinosa Roxb.	#	48	17	P	30	43	110	F	–	–	–	–	#	8	#	New
Viburnum sp.	–	–	–	–	–	–	–	–	#	#	3	N	–	–	–	–
Wendlandia exerta DC.	–	–	–	–	–	–	–	–	–	–	–	–	#	63	3	P
Wendlandia tinctoria (Roxb.) DC.	–	–	–	–	–	–	–	–	38	153	15	F	168	245	23	F
Xylosma longifolium Clos	388	170	3	G	190	110	23	G	#	5	#	New	230	85	20	G
Zanthoxylum rhetsa (Roxb.) DC.	#	13	4	P	–	–	–	–	–	–	–	–	–	–	–	–
Zizyphus jujuba Lam.	–	–	–	–	8	25	5	F	–	–	–	–	–	–	–	–
	8803	3030	359	12192	4540	2123	600	7263	3415	1943	995	6353	4198	2840	1218	8255

Variance of means of density/ha of the four groves = 6601477.23, Significant at the 0.0005 level.

F – Fair regeneration, G – Good regeneration, P – Poor regeneration and N – No regeneration.

* – Vernacular name, _ absence of species, # – Absence of seedling/sapling/tree.

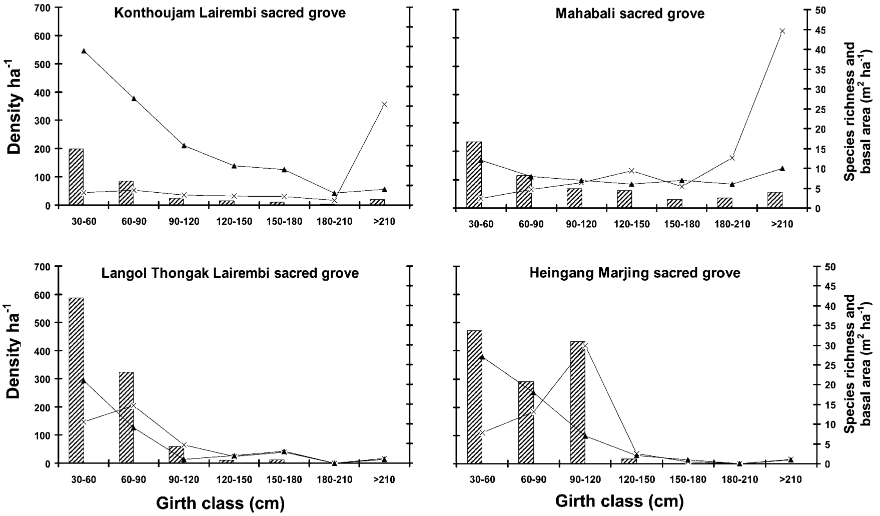

Figure 1. Density ha^{-1} (■), species richness (▲) and basal area (X; m^2 ha^{-1}) of woody species in different girth classes in the four sacred groves.

Population structure of woody species

The population structure of woody species in terms of the proportion of seedlings, saplings and adults in the four groves varied greatly (Figure 2). The relative proportion of seedlings ranged from 72% in Konthoujam Lairembi

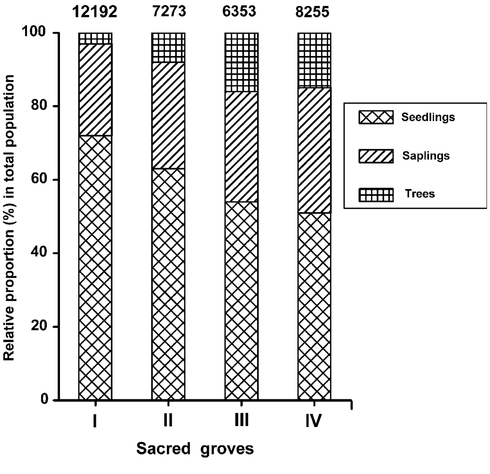

Figure 2. Population structure of all the woody species taken together in the four sacred groves of Manipur in December 2001. Total density of a particular grove is shown at the top of the corresponding bar. I – Konthoujam Lairembi sacred grove; II – Mahabali sacred grove; III – Langol Thongak Lairembi sacred grove and IV – Heingang Marjing sacred grove.

sacred grove to 51% in Heingang Marjing sacred grove. The highest percentage of adults was recorded in Langol Thongak Lairembi sacred grove (16%) and lowest in Konthoujam Lairembi sacred grove (3%).

The population structure of selected tree species in the concerned groves showed that seedlings constituted about 79% of the total density (3640 ha^{-1}) in Konthoujam Lairembi sacred grove, followed by 68% each in Mahabali (total density 1784 ha^{-1}) and Langol Thongak Lairembi (total density 1303 ha^{-1}) and 56% in Heingang Marjing (total density 1586 ha^{-1}). Density–diameter distribution in terms of seedlings, saplings and adults trees of selected tree species (Figure 3a and b) in the four groves indicates the higher proportion of seedlings than the saplings and trees except for *Marlea begoniaefolia* and *Litsea polyantha* in Konthoujam Lairembi sacred grove, *Eugenia praecox* in Mahabali, and *Wendlandia tinctoria* in Langol Thongak Lairembi and Heingang Marjing. *Saprosma* sp. in Konthoujam Lairembi had maximum (89%) seedling population and *Wendlandia tinctoria* in Langol Thongak Lairembi recorded minimum proportion of seedling population (16–34% of the total population).

During May (beginning of the rainy season in Manipur) seedling population of all the selected species in the studied groves was greater as compared to the other seasons except for *Litsea polyantha* in Konthoujam Lairembi and Mahabali sacred groves, *Litsea sebifera* in Langol Thongak Lairembi grove, and *Litsea sebifera* and *Wendlandia tinctoria* in Heingang Marjing which showed maximum seedling population in December. In general, seedling population size decreased substantially after the rainy season.

Sapling population did not show marked seasonal variation in density. Sapling population of *Marlea begoniaefolia* and *Litsea polyantha* in Konthoujam Lairembi and *Wendlandia tinctoria* in Langol Thongak Lairembi and Heingang Marjing groves was higher than the seedling population. Total sapling density per hectare was 645 in Konthoujam Lairembi, 499 in Heingang Marjing, 422 in Mahabali and 331 in Langol Thongak Lairembi sacred grove.

Adult tree population of *Saprosma* sp. and *Eugenia praecox* in Konthoujam Lairembi was very low. No adult individual of *Eugenia praecox* was recorded in the Mahabali sacred grove and the same was true for *Litsea sebifera* in the Langol Thongak Lairembi sacred grove.

Regeneration status of woody species

In Konthoujam Lairembi sacred grove, out of the 55 species, 15% showed good regeneration, 22% fair, 22% poor and 16% were not regenerating, while 14 species (25%) were represented only by seedlings or saplings. The species falling under the last category were regarded as the new arrivals in this grove. In Mahabali grove out of 38 species, 7 (19%) showed good regeneration, while 6 (16%) and 5 (13%) species exhibited fair and poor regeneration, respectively. Two species (5%) showed no regeneration and 18 species (47%) were ‘new’ to

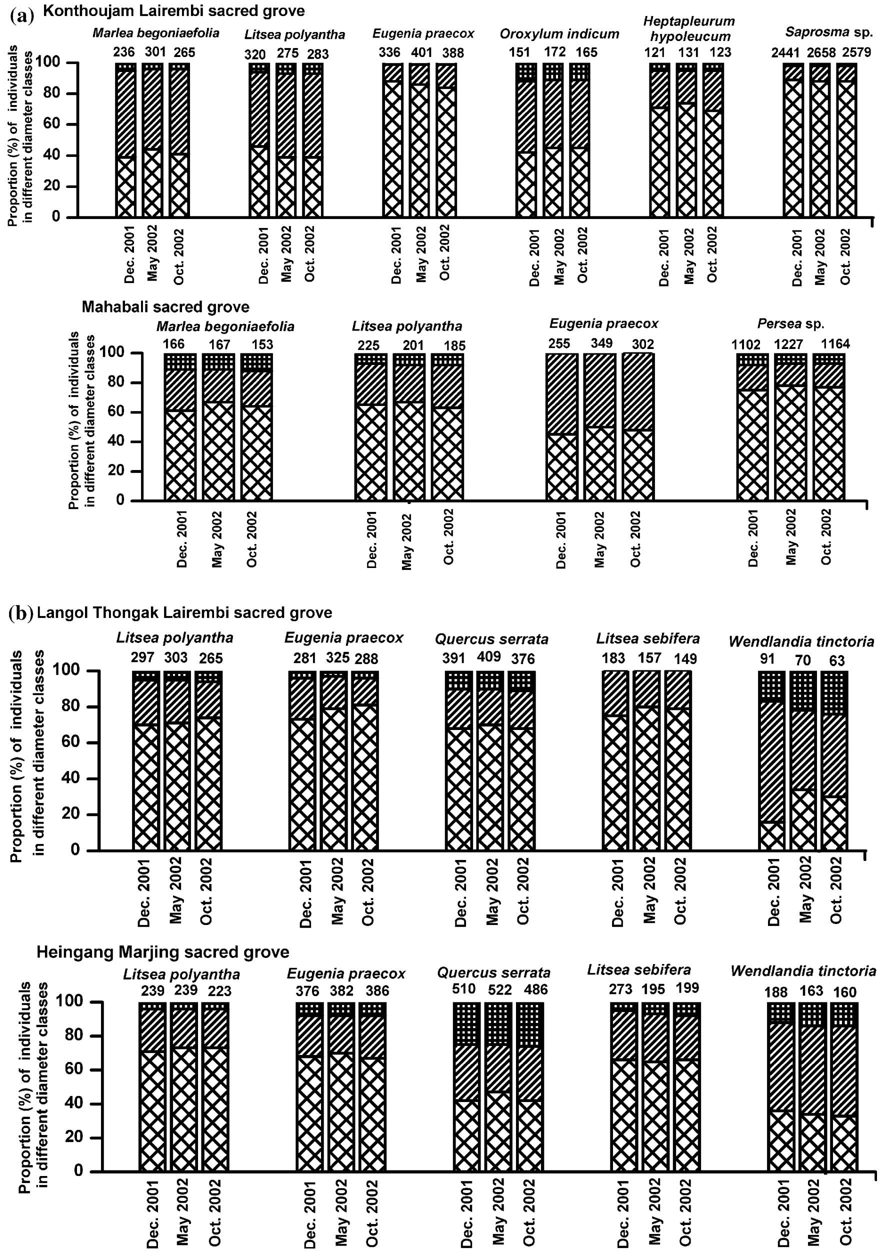

Figure 3. (a) Population structure of the selected woody species in the Konthoujam Lairembi sacred grove and Mahabali sacred grove. Percentages of the total density as seedlings (■), saplings (■) and trees (■) are given. Total density of a particular species is shown at the top of the corresponding bar; (b) Population structure of the selected woody species in the Langol Thongak Lairembi sacred grove and Heingang Marjing sacred grove. Percentages of the total density as seedlings (■), saplings (■) and trees (■) are given. Total density of a particular species is shown at the top of the corresponding bar.

this grove. Among the 38 species in Langol Thongak Lairembi, 9 species (24%) showed poor regeneration, while 7 (18%) species each showed good regeneration (proportion of seedlings > saplings > adults) and fair regeneration (proportion of seedlings > or ≤ saplings ≤ adults). Fourteen species (37%) were newly recruited to the grove, while one species (3%) did not show regeneration. In Heingang Marjing out of 42 species, 7 species (17%) exhibited good regeneration, 11 species (26%) exhibited fair regeneration and 12 species (29%) showed poor regeneration. Eleven species (26%) were categorised as new arrivals, and one species (2%) was found not regenerating (Table 2).

Discussion

Girth class-wise species richness, tree density and basal area

An analysis of population structure of woody species in the groves, based on the girth classes, shows that the abundance of a large number of tree species is stable. It was observed that about 50% of tree species showed reduced abundance in the succeeding girth classes. However, a drastic decrease in abundance was observed with increase in girth beyond a particular stage. The absence of a certain girth class e.g. 180–120 cm in Langol Thongak Lairembi grove and Heingang Marjing groves may indicate an interruption in the regeneration, resulting from the changing microclimatic conditions (Bankoti et al. 1986). The high value of basal area in the highest girth class in the Mahabali sacred grove could be attributed to the presence of *Ficus* species, which had big trees with large basal area. Langol Thongak Lairembi and Heingang Marjing groves recorded the lowest basal area in the highest girth class as compared to the other groves located in the plain area, which may be due to the dominance of *Pinus kesiya* trees having less girth in the groves located in the hilly area. There was a gradual decrease in species diversity and density with increase in girth class which is in conformity with the studies in the Western Ghats, India (Pascal and Pelisseir 1996; Parthasarathy and Karthikeyan 1997), Malaysia (Manokaran and LaFrankie 1990; Newbery et al. 1992), Costa Rica (Lieberman et al. 1985; Nadkarni et al. 1995), New Guinea (Paijmans 1970) and New Caledonia (Jeffre and Veillon 1990). These observations indicate that the groves have the potential of successful regeneration through seeds.

Population structure and regeneration status of woody species

The future community structure and regeneration status of the species could be predicted from the relative proportion of seedlings and saplings in the total populations of various species in the forest. The overall population structure of woody species in the four groves showed that contribution of seedlings to the total population was highest followed by saplings and trees. It shows regeneration of woody species in the four sacred groves is good and the future communities may be sustained. The differences in relative proportion of seedlings, saplings and trees among the four groves may be due to the interactive influence of an array of biotic and abiotic factors. In general, regeneration of species is affected by anthropogenic factors (Khan and Tripathi 1989; Sukumar et al. 1994; Barik et al. 1996) and natural phenomena (Welden et al. 1991).

Variation in the population structure of selected tree species in the four groves may be attributed to the differences in their habitat and prevailing microenvironmental factors. Jones et al. (1994) reported that seedling layer in various forests, differs in composition from their respective overstories. Tall height with relatively close canopy layer of the grove may favour germination of seeds and establishment of the seedlings and saplings. According to Espelta et al. (1995), canopy closure seems to promote seedling germination through changes in the environmental conditions on the forest floor, which might be related to decreasing radiation and water evaporation. The presence of greater number of seedlings may be ascribed to the availability of microsites, which facilitates regeneration through germination of large number of tree seeds. Tripathi and Khan (1990) stated that microsite characteristics of forest floor and microenvironmental conditions under the forest canopy also influence the regeneration of trees by seeds. Many workers have reported that tree species are able to survive and grow at reduced light intensities under the forest canopy (Atzet and Waring 1970; Emmingham and Waring 1977; Minore 1998). On the contrary, many workers have shown that open canopy may favour germination and seedling establishment through increased solar radiation on the forest floor and consequently increase in surface temperature, and reduced competition from the canopy layer (Khan et al. 1987; Srinivas 1992). While the reduction of seedling population in the four groves during the dry winter season may be due to adverse effects of soil moisture stress and unfavourable temperatures on survival of tree seedlings. Similar results have also been reported by several workers (Perira and Kozlowski 1977; Schulte and Marshall 1983; Kumar et al. 1994). Khan et al. (1986) also reported that survival of tree seedlings was lowest during the winter season in tropical deciduous and sub-tropical forests of Meghalaya state in India.

The low sapling population of selected species in the four groves despite the presence of high number of seedlings (except in case of *Marlea begoniaefolia* and *Litsea polyantha* in Konthoujam Lairembi grove and *Wendlandia tinctoria* in Langol Thongak Lairembi and Heingang Marjing groves) may be attributed to the adverse impact of environmental factors prevalent during the sapling growth. The greater populations of saplings of *Marlea begoniaefolia*, *Litsea polyantha* (Konthoujam Lairembi sacred grove) and *Wendlandia tinctoria* (Langol Thongak Lairembi and Heingang Marjing grove) than their seedlings could not be explained, however, it may be due to the poor seed set and seed germination. On the other hand, the species may also suffer high mortality at the seed/seedling stage due to herbivores and thus regeneration of such species may be periodic. The greater number of saplings clearly indicates that these species will persist and may determine the composition of future vegetation of the groves (Swaine and Hall 1988; Jayasingham and Vivekanantharaja 1994). Swaine and Hall (1988) stated that higher number of saplings alone may not represent future composition, because over a period environmental changes could nullify the effect. However, in the absence of catastrophic events the saplings will gradually form future crowns. Presence of species that are represented only by adults e.g. *Eugenia praecox* and *Litsea sebifera* without any seedlings and saplings may be due to their poor seed set, germination and establishment of seedlings in the forest. Species diversity and population structure will be stable or reduced and regeneration potential will be negligible if the number of species represented only by adults becomes higher in any forest.

Woody species represented only by their seedlings and saplings without any adult individuals were high in the four groves which indicate that large number of species were new colonizers in the groves and have managed to reach there due to invasion of ‘new’ species through seed dispersal from other areas. Invasion of new species to the groves may be regarded as a possible factor to the co-existence of the tree species.

The overall population structure of selected woody species reveals that seedling populations dominate tree populations and the fluctuation in population density in various seasons is related to the prevailing environmental factors. Germination of freshly dispersed seeds is high for most of the species during the monsoon season. Therefore, recruitment of all the species increased during the rainy season attaining peak during June, which is the wettest month. Similar observations have been reported in tropical dry forest at Pinkwae, Ghana (Lieberman and Li 1992; Swaine et al. 1990). The four groves showed good regeneration and exhibited high proportion of ‘new’ species facilitated by the dispersal of seed from the nearby forests and receiving favourable micro-environmental conditions for their germination and establishment of seedlings. It may be concluded that tree species richness and stand density decrease gradually with the increase in girth classes in the four groves. Moreover, the four groves reveals good regeneration and exemplify regeneration of tree species is largely depended on the prevailing environmental factors, and if the existing ecological factors are not jeopardized the future maintenance of the tree species in the groves will be sustained. However, differences in regeneration behaviour of various species would determine the structure and dynamics of the groves.

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References

Aksamit S.E. and Irving F.D. 1984. Prescribed burning for lowland black spruce regeneration in Northern Minnesota. Can. J. Forest Res. 14: 107–113.

Ashton P.S. and Hall P. 1992. Comparisons of structure among mixed dipterocarp forests of north-western Borneo. J. Ecol. 80: 459–481.

Atzet T. and Waring R.H. 1970. Selective filtering of light by coniferous forests and minimum light energy requirements for regeneration. Can. J. Bot. 48: 2163–2167.

Baduni N.P. and Sharma C.M. 2001. Population structure and community analysis on different aspects of Sal savanna forest type in outer Garhwal Himalaya. Indian Forester 127(9): 1001–1011.

Bankoti T.N.S., Melkania Uma and Saxena A.K. 1986. Vegetation analysis, an altitudinal gradient in Kumaun Himalaya. Indian J. Ecol. 13: 211–221.

Barik S.K., Rao P., Tripathi R.S. and Pandey H.N. 1996. Dynamics of tree seedling population in a humid subtropical forest of northeast India as related to disturbances. Can. J. Forest Res. 26: 584–589.

Bhandari B.S. 2003. Blue pine (*Pinus wallichiana)* forest stands of Garhwal Himalaya: composition, population structure and diversity. J. Trop. Forest Sci. 15(1): 26–36.

Bhuyan P., Khan M.L. and Tripathi R.S. 2002. Regeneration status and population structure of Rudraksh (*Elaeocarpus ganitrus* Roxb.) in relation to cultural disturbances in tropical wet evergreen forest of Arunachal Pradesh. Curr. Sci. 83(11): 1391–1394.

Bhuyan P., Khan M.L. and Tripathi R.S. 2003. Tree diversity and population structure in undisturbed and human-impacted stands of tropical wet evergreen forest in Arunachal Pradesh, Eastern Himalayas India. Biodivers. Conserv. 12(8): 1753–1773.

Boring L.R., Monk C.D. and Swank W.T. 1981. Early regeneration of a clear cut southern Appalachian forest. Ecology 62: 1244–1253.

Bormann F.H. and Likens G.E. 1979. Pattern and Process in a Forested Ecosystem. Springer-Verlag, New York, USA.

Cao M., Zhang J.H., Feng Z., Deng J. and Deng X. 1996. Tree species composition of a seasonal rain forest in Xishuangbanna, South West China. Trop. Ecol. 37(2): 183–192.

Emmingham W.H. and Waring R.H. 1977. An index of photosynthesis for comparing forest in Western Oregon. Can. J. Forest Res. 7: 165–174.

Espelta J.M., Riba M. and Retana J. 1995. Patterns of seedling recruitment in host – Mediterranean *Quercus ilex* forests influenced by canopy development. J. Veg. Sci. 6: 465–472.

Gunatilleke C.V.S., Weerasekera N., Gunatilake I.A.U.N. and Kathriarachchi H.S. 2001. The role of dipterocarps, their population structures and spatial distributions in the forest dynamics plot a Sinharaja, Sri Lanka. In: Ganeshaiah K.N., Uma Shaanker R. and Bawa K.S. (eds), Tropical Ecosystem: Structure, Diversity, and Human Welfare, Proceedings of the International Conference on Tropical Ecosystems. Oxford & IBH Publishing, New Delhi, pp. 591–594.

Jaccard P. 1912. The distribution of the flora of the alpine zone. New Phytol. 11: 48–50.

Jayasingham T. and Vivekanantharaja S. 1994. Vegetation survey of the Wasgomuvaoya National Park Sri Lanka: analysis of the Wasgomuvaoya forest. Vegetatio 113: 1–8.

Jeffre T. and Veillon J.M. 1990. Etude floristique et structure de deux forests denses humides sur roches ultrabasiques en Nouvelle-Caledonie. Bulletin de la Museum Nationale Histoire Naturalle, Paris 12(B): 243–273.

Jones R.H., Sharitz R.R., Dixon P.M., Segal D.S. and Schneider R.L. 1994. Woody plant regeneration in four floodplain forests. Ecol. Monogr. 64: 345–367.

Khan M.L. and Tripathi R.S. 1989. Effects of stump diameter, stump height and sprout density on the sprout growth of four tree species in burnt and unburnt forest plots. Acta Oecol. 10(4): 303–316.

Khan M.L., Rai J.P.N. and Tripathi R.S. 1986. Regeneration and survival of tree seedlings and sprouts in tropical deciduous and sub-tropical forests of Meghalaya, India. Forest Ecol. Manag. 14: 293–304.

Khan M.L., Rai J.P.N. and Tripathi R.S. 1987. Population structure of some tree species in disturbed and protected sub-tropical forests of north-east India. Acta Oecol–Oec. Appl. 8(3): 247–255.

Khumbongmayum A.D., Khan M.L. and Tripathi R.S. 2004. Sacred groves of Manipur: ideal centres for biodiversity conservation. Curr. Sci. 87(4): 430–433.

Khumbongmayum A.D., Khan M.L. and Tripathi R.S. Sacred groves of Manipur, northeast India: biodiversity value, status and strategies for their conservation. Biodivers. Conserv. (In press).

Kumar R., Singh A.K. and Abbas S.G. 1994. Change in population structure of some dominant tree species of dry Peninsular Sal Forest. Indian Forester 120: 343–348.

Lieberman D. and Li M. 1992. Seedling recruitment patterns in a tropical dry forest in Ghana. J. Veg. Sci. 3: 375–382.

Lieberman D., Lieberman M., Hartshorn G.S. and Peralta R. 1985. Growth rates and age-size relationships of tropical wet forest trees in Costa Rica. J. Trop. Ecol. 1: 97–109.

Manokaran N. and LaFrankie J.V.Jr. 1990. Stand structure of Pasoh Forest reserve, a lowland rain forest in peninsular Malaysia. J. Trop. Forest Sci. 3: 14–24.

Maram Kuba M. and Khan M.L. 1998. Regeneration status of trees in various categories of forests in Manipur. J. Hill Res. 11(2): 178–182.

Marks P.I. 1974. The role of pine cherry (*Prunus pensylvania* L.) in the maintenance of stability in northern hardwood ecosystems. Ecol. Monogr. 44: 73–88.

Mishra B.P., Tripathi R.S., Tripathi O.P. and Pandey H.N. 2003. Effects of disturbance on the regeneration of four dominant and economically important woody species in a broad-leaved subtropical humid forest of Meghalaya, north east India. Curr. Sci. 84(11): 1449–1453.

Minore D. 1998. Effects of light intensity and temperature on the growth of Douglasfir and incense-cedar seedlings. Forest Sci. 34: 215–233.

Nadkarni N.M., Matelson T.J. and Haber W.A. 1995. Structural characteristics and floristic composition of a neotopical cloud forest. Monteverde, Costa Rica. J. Trop. Ecol. 11: 481–495.

Newbery D., McC E.J.F., Campbell Y.F., Lee CF Ridsdale and Still M.J. 1992. Primary lowland dipterocarp forest at Danum valley. Sabah. Malayisa: Structure, relative abundance and family composition. Proc. Trans. Roy. Soc. London 335: 341–356.

Paijmans K. 1970. An analysis of four tropical rain forest sites in New Guinea. J. Ecol. 58: 77–101.

Pande P.K., Negi J.D.S. and Sharma S.C. 2002. Plant species diversity, composition, gradient analysis and regeneration behaviour of some tree species in a moist temperate western Himalayan forest ecosystem. Indian Forester 128(8): 869–886.

Parthasarathy N. 2001. Changes in forest composition and structure in three sites of tropical evergreen forest around Sengaltheri, Western Ghats. Curr. Sci. 80(3): 389–393.

Parthasarathy N. and Karthikeyan R. 1997. Biodiversity and population density of woody species in a tropical evergreen forest in Courtallum reserve, Western Ghats, India. Trop. Ecol. 38(2): 297–306.

Pascal J.P. and Pelissier R. 1996. Structure and floristic composition of tropical evergreen forest in southern India. J. Trop. Ecol. 12: 95–218.

Perira J.S. and Kozlwski T.T. 1977. Water relations and drought resistance of young *Pinus banksiana* and *Pinus resinosa* plantation trees. Can. J. Forest Res. 7: 132–137.

Pritts M.P. and Hancock J.E. 1983. The effect of population structure on growth patterns of the weedy goldenrod *Solidago pauciflos* culose. Can. J. Bot. 61: 1955–1958.

Rao P.B. 1988. Effects of environmental factors on germination and seedling growth in *Querscus floribunda* and *Cupressus torulosa*, tree species of central Himalaya. Ann. Bot. 61: 531–540.

Rao P.B., Barik S.K., Pandey H.N. and Tripathi R.S. 1990. Community composition and tree population structure in a sub-tropical broad-leaved forest along a disturbance gradient. Vegetatio 88: 151–162.

Saxena A.K. and Singh J.S. 1984. Tree population structure of certain Himalayan forest associations and implications concerning their future composition. Vegetatio 58: 61–69.

Saxena A.K., Singh S.P. and Singh J.S. 1984. Population structure of forest of Kumaon Himalaya: implications for management. J. Environ. Manag. 19: 307–324.

Schulte P.J. and Marshall P.E. 1983. Growth and water relations of black locust and Pine seedlings exposed to controlled water-stress. Can. J. Forest Res. 13: 334–338.

Sood V. and Bhatia Monik 1991. Population structure and regeneration status of tree species in forests around Shimla, Himachal Pradesh. Van Vigyan 29(4): 223–229.

Srinivas C. 1992. Plant Biomass, Net Primary Productivity and Nutrient Cycling in Oak *Quercus serrata* Thumb. Forests of Manipur. Ph. D. thesis, Manipur University, Manipur, India.

Sukumar R., Suresh H.S., Dattaraja H.S. and Joshi N.V. 1994. In: Dallmeier F. and Comiskey J.A. (eds), Forest Biodiversity Research-Monitoring and Modeling, Conceptual Background to Old World Case Studies. Parthenon publishing, 1 pp.529–540.

Swaine M.D. and Hall J.B. 1988. The mosaic theory of forest regeneration and the determination of forest composition in Ghana. J. Trop. Ecol. 4: 253–269.

Swaine M.D., Lieberman D. and Hall J.B. 1990. Structure and dynamics in a tropical dry forest in Ghana. Vegetatio 88: 31–51.

Tripathi R.S. and Khan M.L. 1990. Effects of seed weight and microsite characteristics on germination and seedlings fitness in two species of *Quercus* in a subtropical wet hill forest. Oikos 57: 289–296.

Uma Shankar 2001. A case study of high tree diversity in a sal (*Shorea robusta*)- Dominated lowland forest of Eastern Himalaya: Floristic composition, regeneration and conservation. Curr. Sci. 81: 776–786.

Veblen T.T., Ashton D.H. and Schlegel F.J. 1979. Tree regeneration strategies in lowland *Nothofagus* dominated forest in South-Central Chile. J. Biogeogr. 6: 329–340.

Welden C.W., Hewett S.W., Hubbell S.P. and Foster R.B. 1991. Sapling survival, growth and recruitment: relationship to canopy height in a neotropical forest. Ecology 72: 35–50.

Yadava P.S., Singh E.J. and Soreishang K.A.S. 1991. Tree population structure of sub-tropical forests of Manipur, North Eastern India and implications for their regeneration. In: Rajwar G.S. (ed.), Advances in Himalayan ecology. Today and Tomorrows Printers & Publishers, New Delhi, pp. 13–23.

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A numeric index to establish conservation priorities for medicinal plants in the Paravachasca Valley, Córdoba, Argentina

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Abstract. Medicinal plant extraction is a relevant issue in the province of Córdoba, Argentina. A quantitative methodology is proposed for the evaluation of conservation priorities for species used in popular medicine in the Paravachasca Valley, Córdoba. Qualitative attributes were surveyed through the knowledge and perception of local communities. Species are ranked by their index of conservation priority (ICP) values. This index takes into consideration the following data: harvest, abundance, propagation method, origin and commercial demand of species in the area. Among the native species prioritized for conservation are *Minthostachys mollis*, *Hedeoma multiflora*, *Julocroton argenteus*, *Baccharis crispa*, *Trixis divaricata* subsp. *discolor*, *Passiflora caerulea*, *Usnea* spp. and *Equisetum giganteum.*

Introduction

The resurgence of phytotherapy and herbal medicines for health care, has generated an international concern, regarding the increasing threat to medicinal plants as they are permanently removed from their natural habitat (FAO 1996). According to the United Nations Environmental Program (UNEP 1992) the estimated value of pharmaceutical material derived from medicinal plants in the Southern Hemisphere ranges between 35 and 47 billion dollars per year. On the other hand, the social value in the conservation of these resources greatly exceeds the benefits derived from its commercial value as pharmacological products (Mendelsohn and Balick 1995).

The recent increase in the commercialization of medicinal species has lead to a more intensive harvesting of wild plants, ignoring conservation practices consequently, *in situ* conservation was established as priority all across the world (Williams et al. 2000). Many approaches have been taking into account to evaluate conservation issues of medicinal plants, such as, quantitative ecological surveys (Voeks 1996; Caniago and Siebert 1998; Tran et al. 2001) and distribution patterns of rare and endangered species (Kala 2000). Also, geographic information system (GIS) applications and eco-distribution mapping (Rai et al. 2000), as well as, conservation priorities based on indices (Dhar et al. 2000) were achieved. On the other hand, Hall and Bawa (1993), Walker et al. (1995) and Lykke (1998) reported the trends of vegetation changes, taking into account the knowledge and perception of biodiversity by local communities. This latter approach allows setting priorities for species conservation (Hellier et al. 1999); and management practices (Badola 1998; Bolling and Schulte 1999).

According to the World Conservation Union (IUCN), more than 20,000 species of plants are used for medicinal purposes and nearly half of that number are potentially threatened by over-harvesting or by the loss of their habitat. Although one-fourth of the 250,000 species known wide world is found in Latin–America (Elisabetsky and Costa-Campos 1996), information concerning endangered species for that region is scarce (Lucas and Synge 1978; Davies et al. 1986). A partial list of endangered and threatened plant for Argentina, can be found in De la Sota (1977), Cabrera (1977), Noher de Halac et al. (1985), Delucchi and Correa (1992), Planchuelo (2000) and Vischi et al. (2004) but the records about medicinal flora is scarce. In the Province of Córdoba, the available information for medicinal plants are found in Bocco et al. (1997), Nuñez and Cantero (2000), Lagrotteria et al. (1986, 1987a, b), Rodríguez et al. (1992) and Lagrotteria and Affolter (1999). The major users of this resource are diverse industries, such as: 'yerba mate' processors, aperitif beverage distilleries, as well as, laboratories for medicinal, perfumery, cosmetology and aromatherapy products. Dried plants are also marketed in pharmacies, herbalist and dietary product shops that sell the processed plant in several ways and quantities. In addition, the absence of a legal framework regulating germplasm management has generated a reduction in the number of medicinal plant populations, loss of genetic diversity and the degradation of their habitats (López 1996). As Guarino (1995) pointed out there is a close relationship between biological and cultural diversity, therefore the loss of genetic diversity tends to be accompanied by a loss of knowledge in relation to plant uses and properties (Benz et al. 2000). At this point, it is essential to establish rapid methods for assessing the trends of vegetation changes, taking into account the knowledge and perception of biodiversity and the uses of medicinal plants by local communities (Hall and Bawa 1993; Walker et al. 1995; Lykke 1998).

The objective of this paper was to develop an evaluation index to establish priorities in conservation practices, using the available bibliographic information, field surveys and the perception and knowledge of people from local communities in relation to distribution, sources and uses of medicinal plants in the Paravachasca Valley of Córdoba, Argentina.

Materials and methods

Study area

The Paravachasca Valley is part of the Santa Maria Department in the central region of the Province of Córdoba (Figure 1). It is located between 31°30′ and 31°32′ S and between 64°05′ and 64°35′ W, from the eastern slopes of the Sierra Chica to an imaginary line drawn approximately between the populations of Bouwer, La Cruz, Malagueño and Los Molinos river. It extends through foothills in a marginal depression of the hills where the altitude ranges between 300 and 1000 m above sea level. The annual mean temperature is around 16 °C and the annual rainfall in the area ranges from 700 to 900 mm concentrated in summer months (December–March).

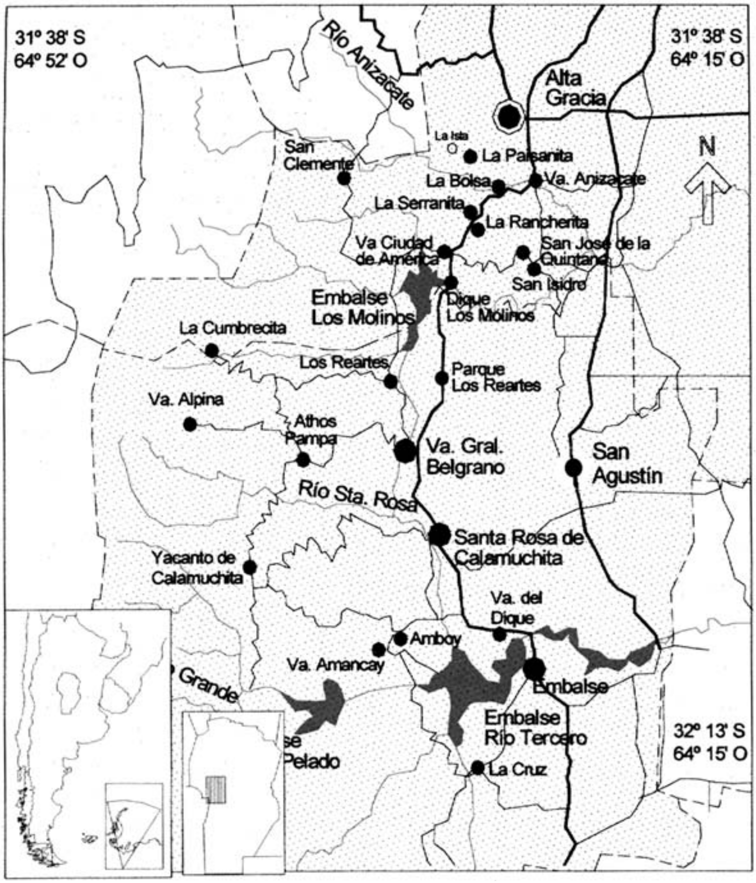

Figure 1. Location of the Paravachasca Valley.

The relicts of natural vegetation belong to the phytogeographic provinces 'Espinal' and 'Chaqueña' (Cabrera 1971, 1976, 1994) this later with the district of 'Bosque Serrano' and 'Romerillal' (Luti et al. 1979). The 'Espinal' is a mixing xerophytes arboreal vegetation with species from the Chaqueña province and grasses from the 'pampas steppe' (Luti et al. 1979) The 'Bosque Serrano' develops between 500 and 1350 m in altitude with several layers of vegetation and the 'Romerillal' develops in open and rocky sectors, spreading up to 1700 m above sea level (Luti et al. 1979; Gorgas and Tassile 2001). Although, the agricultural development has modified most of the flora, relicts arboreal vegetation are still present with trees such *Prosopis alba* and *P. nigra*, *Aspidosperma quebracho-blanco*, *Celtis tala*, *Acacia caven*, *Geoffroea decorticans* together with aromatic shrubs such *Lippia turbinata*, *Minthostachys mollis* and *Aloysia gratissima* (Gorgas and Tassile 2001).

From a social-cultural point of view, tourism is one of the main economic activities of the region, due to the beauty of the landscape and the presence of historic sites of natives Comechingon settlements and Jesuit buildings. The most important urban areas are Alta Gracia (37,284 inhabitants), Despeñaderos (4728 inhabitants), San Agustín (2284 inhabitants), Villa Anisacate (1509 inhabitants) and several others communities with less than 1500 inhabitants.

The population composition in the Paravachasca Valley is heterogeneous. Native peasants, European immigrants and city dwellers coming from the province's capital or other urban districts have settled in the region. The information in this work was obtained from the families of native peasants. The culture of Argentina's native peasants is the product of different dynamic syntheses that developed in the past 500 years. It is characterized by the permanence of European beliefs and practices, both from the Conquistadors' and Colonial times as well as from the past two centuries immigrants, with some fragmented indigenous elements (Idoyaga Molina 2001).

Peasant income come from both seasonal tourism-associated services and beef cattle raising. Collecting and selling herbs provide an extra income (Martínez 2003). Rural and city high schools have educational programs in tourism management and food production.

Data collection

Data sets were developed from questionnaires filled by selected informants about the knowledge, uses and commercial trade of medicinal plants, as well as from an exhaustive literature review and field surveys (Martínez 2003).

The families of 40 students from the three rural high school in the area, that in previous studies (Martínez et al. 2003) proved to be familiar with medicinal flora, were asked to complete a questionnaire about the following: names of plants used as medicinal herb; an estimation of their abundance by meaning of the accessibility to be collected in the area; the quantity of each plant collected from the field; the characteristics of the place from where the plant was collected (field, home gardens); the season and method of harvesting; the parts of the plant used, the method and reason for its use and the amount of trade in a year. Also, a sample of each plant mentioned on the list was requested, as recommended by Bocco et al. (1997). This information was supplemented, following the methodology of Alexiades (1996a, b) and Caniago and Siebert (1998), with field observations and semi-structured interviews of 25 qualified informants (professional collectors, merchants, dealers and owner of herbal shops and pharmacies) from the area. The criteria to select the informants were: no less than 20 years of residence in the study area or region; three or more years of experience in collecting and/or selling herbs; ability to recognize species in the field and experience in the use of medicinal plants. Information concerning the extraction trends, demand and commercial unit (weight or volume) for each species was obtained using a qualitative and quantitative methodology, which recur to consensus reflected by the frequencies of responses in the surveys as proposed by Noher de Halac et al. (1985), Lagrotteria et al. (1987a), Rodríguez et al. (1992) and Nalvarte et al. (1999).

The recognition of the medicinal plants reported in the surveys was done in the field, together with the informant. All plants were identified using the available Floras and the appropriate botanical references. Plant identification was confirmed at genus, species and infraspecific level by a Taxonomist and the specimens collected are deposited in the Herbarium ACOR. The information gathered for each species was recorded in a filing card shown in Table 1.

Determination of the ICP

An ICP was developed to establish conservation priorities of medicinal plants. The index takes into account references information, data from interviews and

Table 1. Example of filling card for species of medicinal interest based on surveys.

Common name
Family and scientific name
Biological categories: *Non cultivated native/Cultivated native/Introduced non cultivated/Introduced cultivated*
Place of collection and herbarium number of voucher specimens.
Medicinal use.
Number of times mentioned.
Code of informants and surveys.
Methods of obtaining the plant: *Purchase or cultivated plot/Family gardens/Field extraction.*
Abundance in the area: *Abundant/Moderately abundant/Not abundant or rare.*
Who collects: *Family members/Local collectors/Tourists or foreigner collectors.*
Why is it collected: *Household use/Product elaboration/Retail sale/Stocking and wholesale.*
Method of collection: *Whole plant including roots or larges branches and sprouts/Only part of the plant without roots, larges branches or sprouts.*
Commercialization categories: *Very high demand/High demad/Moderately demand/Low demand or not negotiable.*

field surveys. It relates biological aspects of the species (propagation or reproduction strategies, origin and distribution of the taxon) with information about abundance (extracted from references, field survey, as well as, the perception of local people expressed as accessibility) and social-economic parameters (extraction methods, plant harvested destination, commercial demand) obtained from interviews. The index was develop using similar attributes as the ones proposed by Dhar et al. (2000) in setting priorities for conservation of medicinal plants for the Indian Himalayas.

The ICP of each species was determined through the sequence and methodology provided in Table 2 and by the following equation:

$$\mathrm{ICP} = (\mathrm{ROA} \times \mathrm{RCD} \times \mathrm{RPV}) * 100/\sum(\mathrm{ROA} \times \mathrm{RCD} \times \mathrm{RPV}),$$

where ROA = Range of origin for the area (Scale of 1–4), RCD = Range of commercial demand (Scale of 1–4), RPV = Range of perceived vulnerability (Scale of 1–18).

Range of origin of the species for the area (ROA)

The species were classified according to their origin or biological categories (Planchuelo et al. 2003) and following the status indicated by Zuloaga et al. (1994), Zuloaga and Morrone (1996a, b, 1999). The attribute of being a non-cultivated native species was considered the most sensitive to the impact of environment changes in the growing area, therefore it was assigned the highest value of the scale (ROA = 4). According to this criterion of vulnerability, values were assigned in decreasing order: cultivated native species (ROA = 3), introduced non-cultivated species (ROA = 2) and introduced cultivated species (ROA = 1).

Range of commercial demand (RCD)

A commercial unit (weight or volume) was identified for each species mentioned in the surveys to herb collectors, retail sellers and herb products shops. Retail sales are small volumes of dried and chopped herbs of about 50–100 g per bag. To classify species according to their demand, the total number of commercial unit traded in a year, for each species, were ranked from highest demand on top to lowest demand on bottom and grouped into four categories of commercial demand (CD). The grouping criteria was based on partition of the complete list of species in four intervals with amplitude calculates as (Max CD – Min CD)/4. Each category of commercial demand was assigned a numerical value, as follows: very high demand (VHD) first group from the top = RCD 4, high demand (HD) second group from the top = RCD 3, medium demand (MD) thirst group from the top = RCD 2, and low demand or not commercial (LD) the last group from the top = RCD 1.

Table 2. Protocol for the development of the ICP for each species.

Range and Scale	Attributes and categories	Category designation	Information source	Definition criteria
$ICP = (ROA \times RPV \times RCD) * 100/\sum(ROA \times RPV \times RCD)$.				
ROA (Scale 1–4)	Origin (Biological categories) Non-cultivated Native (4) Cultivated native (3) Non-cultivated introduced (2) Cultivated introduced (1)		Field survey, botanical identification and bibliography review.	Zuloaga et al. (1994), Zuloaga and Morrone (1996a, b, 1999)
RCD (Scale 1–4)	Demand Very high (4) High (3) Medium (2) Low or not commercial (1)		Surveys to herbalist and retail sellers and herb products shops.	Demand values designated by grouping criteria defined by intervals with amplitude: (CD max – CD min)/4
RPV (Scale 1–18: Combination of categories for each of the three atributes)	Abundance Restricted (Ra) Moderately (Ma) Abundant (Aa)		Literature review, herbarium specimens, field surveys, surveys to collectors, qualified informants and school families.	Ocurrence and biogeographical data (wild species). Presence in homegardens of interviewed people (cultivated species).
	Method of propagation Unique (Up) Multiple (Mp)		Literature review	
	Harvesting Destructive (Dh)	WHI = HEI * WF HEI = CI + HDI + HMI	Surveys with data of Person who collects (CI)	PHI values grouped by the (Max PHI – Min PHI)/3 value.
	Moderate (Mh) Sustainable (Sh)		Harvest destination (HDI) Harvesting method (HMI)	

Range of perceived vulnerability (RPV)

To allocate this range a data matrix was used with three attributes assigned for each species: abundance, form of propagation and harvesting impact.

Two steps were needed to establish the RPV. The first step was to compute the attributes and the second step was to make the data matrix and assign the RPV to each species. The attributes were obtained as follows:

Abundance

Three categories of abundance were considered using the information obtained from 'Flora Fanerogmica Argentina' (Pro Flora 1994–2001), and bibliography such Luti et al. (1979), Cantero et al. (1996), Bocco et al. (1997), Cantero et al. (1998a, b), Nuñez and Cantero (2000) and Gorgas and Tassile (2001). Also, herbarium specimens surveys (ACOR and CORD), data from surveys applied to the families of students and qualified informant and field evaluation were performed. Strategies to evaluated abundance of wild species in the field were taken from Fuentes and Planchuelo (2000) and Planchuelo (2000) and presence/absence information were recorded for cultivated species in each home-gardens.

To assign each species to a corresponding category, a quantification procedure was used. From each source of information a value of 5 (Ra) was assigned when a species was considered rare, restricted or was present in less than 20% of home-gardens. A value of 3 (Ma) was assigned to moderately abundance or when its grows in between 20 and 50% of home-gardens and a value of 1 (Aa) was assigned when was considered abundant or accesible in the area or was recorded as growing in 50% or more of the home-gardens.

With the data extracted from all the sources the average was calculated for each species. The mean value was categorized in the following way: >4 (Ra), $=<4$ >2 (Ma) and $=$ <2 (Aa).

Form of propagation

Information from an exhaustive literature survey as well as field observation were used to established the form of propagation for each species. Following the criterion proposed by Dhar et al. (2000) the species reproductive plasticity was considered in two categories: Unique (Up) when the species, in its natural environment, has only one form of reproduction (seeds in monocots and dicots), and Multiple (Mp) when the species has more that one way of reproduction, for example, seeds and vegetative organs. The species with only one form of reproductive method were considered more vulnerable.

Harvesting impact

Supported by the information obtained from the surveys which consider person who collects, harvest destination and harvesting method, three harvesting impact categories were considered: Destructive (Dh), Moderate (Mh) and

Sustainable (Sh). To obtain the category value the following procedure was developed. At first the harvesting evaluator index (HEI), the weighting factor (WF) and the weighted harvesting index (WHI) were obtained and then with all the data the three harvesting impact categories were established.

The following considerations were done for this index:

Harvesting evaluator index (HEI)

It was calculated with the following equation:

$$\mathrm{HEI} = \mathrm{CI} + \mathrm{HDI} + \mathrm{HMI},$$

where CI = Collector index, HDI = Harvest destination index, HMI = Harvesting method index. Each one of the indexes was calculated as follows

Collector index (CI). This index expresses the destructive impact from each kind of collector generates by harvesting the species considered. It is calculated by an equation with the following components: the numerator is the sum of the different types of collectors mentioned in the surveys, where each one of them is multiplied by a coefficient that varies depending on the impact caused by the harvesting method. The denominator is the sum of the total number of times each type of collector was mentioned in the surveys. The values attributed to each type of collector were based on the information provided in the interviews and in field survey with the collectors using the methodology of Bocco et al. (1997). It was considered that local families (F) harvest plants only when needed, because this was always associated with household use, therefore they were assigned a coefficient of lesser destructive impact, equivalent to 0.5. The collectors (C) harvest plants regularly as a means of income, with the precaution of preserving plants in the field for their reproduction and for future harvests, therefore an intermediate impact coefficient equal to 1, was assigned. The extractions done by tourists or foreigner collectors (T), do not follow any preservation concepts, consequently they received the highest impact coefficient number of 1.5. The CI is expressed as follows:

$$\mathrm{CI} = (0.5 * \mathrm{F} + \mathrm{C} + 1.5 * \mathrm{T})/(\mathrm{F} + \mathrm{C} + \mathrm{T})$$

Harvest destination index (HDI). The HDI expresses the importance of the different destinations of the harvested plants. The following destinations were considered: minimum household use (HU), product elaboration for families uses, not for sale (PE), retail sale (RS) and stocking and wholesale (WS). The numerator of the equation is the sum of each one of the destinations, which have been multiplied by a coefficient. The coefficients range in value from 1, for the destinations which require the highest amount of plants, consequently have the highest destructive impact (WS); 0.5 for those of intermediate amount of plant and lesser impact (PE and RS) and 0 for those of low or null impact (HU) because the amount of plants involve is very small. The denominator is the sum of the total number of times that each of the components was mentioned in the surveys. The HDI is expressed as follows:

$$\mathrm{HDI} = (0.5 * \mathrm{RS} + 0.5 * \mathrm{PE} + \mathrm{WS})/(\mathrm{HU} + \mathrm{RS} + \mathrm{PE} + \mathrm{WS})$$

Harvesting method index (HMI). The HMI assesses the impact of plant harvesting methods. If harvesting takes place in a natural vegetation area and the method consists of pulling out the whole plant including its root or by cutting large branches and sprouts which prevents plant regeneration (IR), the coefficient assigned was equal to 1. In case harvesting is also from natural field but takes only small part of the plant, leaving the roots, the large branches and the sprouts intact (WR), the assigned coefficient was 0.5. If the species were obtained from a home garden or a cultivated plot (GC), the assigned coefficient was 0. The HMI is expressed as follows:

$$\mathrm{HMI} = \mathrm{IR} + 0.5 * \mathrm{WR}/(\mathrm{IR} + \mathrm{WR} + \mathrm{GC})$$

Considering all of the individual index components, the resulting equation for the HEI is:

$$\begin{aligned}\mathrm{HEI} =& [(0.5 * \mathrm{F} + \mathrm{T} + 1.5 * \mathrm{C})/(\mathrm{F} + \mathrm{T} + \mathrm{C})] \\ &+ [(0.5 * \mathrm{RS} + 0.5 * \mathrm{PE} + \mathrm{WS})/(\mathrm{HU} + \mathrm{RS} + \mathrm{PE} + \mathrm{WS})] \\ &+ [\mathrm{IR} + 0.5 * \mathrm{WR}/(\mathrm{IR} + \mathrm{WR} + \mathrm{GC})]\end{aligned}$$

Weighting factor (WF)

A WF to account for the relationship between the number of times of different destinations for each species were mentioned in the surveys and the total number of destinations for all the species cited, was developed as follows:

$$\mathrm{WF} = (\mathrm{HU} + \mathrm{RS} + \mathrm{PE} + \mathrm{WS}) * 100/\sum(\mathrm{HU} + \mathrm{RS} + \mathrm{PE} + \mathrm{WS}),$$

where HU = Household use, PE = Product elaboration, RS = Retail sale, WS = Stocking and wholesale.

Weighted harvesting index (WHI)

The WHI evaluated the impact of harvesting of each species in relation to the impact of the total number of species considered in the study. It is expressed by the following equation:

$$\mathrm{WHI} = \mathrm{HEI} \times \mathrm{WF},$$

where HEI = Harvesting evaluator index, WF = Weighting factor. Three harvesting impact categories were determined. The WHI values were ranked (highest to lowest) and grouped into three harvesting categories: destructive (Dh), moderate (Mh) and sustainable (Sh). The grouping criteria was based on partition of the complete list of species in three intervals with amplitude calculated as (Max WHI – Min WHI)/3.

The second step to assign the RPV to each species was to organize the data matrix by combining the different categories for the three harvesting attributes (Dh, Mh, Sh), abundance (Aa, Ma, Ra) and propagation methods (Mp, Up). The RPV was assigned as a number, from 18 (higher sensitivity) to 1 (less sensitivity), as is shown in Table 3.

Results

Figure 2 shows the percentages of lichens and pteridophytes and flowering plants for the 84 species mentioned in the surveys, grouped according to their taxonomic group, habit and biological categories. It can be observed that pteridophytes and lichens are less than 5% and the major groups are flowering plants from which herbaceous species represented 42%, shrubs represented 38% and trees 15% of total species mentioned. In relation to the biological categories, all pteridophytes and lichens are native non-cultivated, also to this category belongs a high percentage of shrubs and herbaceous flowering plants. The cultivated natives are represented only by trees and shrubs, the cultivated introduced are present in more than 5% in all groups of flowering plants and the non cultivated introduced are about 10% of the herbs and 2% of the shrubs.

Table 4 shows the RPV, the RCD and the ROA of each species, ordered in decreasing ICP values and grouped according to their habit. In general, considering all habits, native non-cultivated species had the highest values of RPV.

Table 3. Structure of the matrix for the RPV.

RPV	Harvesting	Abundance	Propagation
18	Dh	Ra	Up
17	Dh	Ra	Mp
16	Dh	Ma	Up
15	Dh	Ma	Mp
14	Dh	Aa	Up
13	Dh	Aa	Mp
12	Mh	Ra	Up
11	Mh	Ra	Mp
10	Mh	Ma	Up
9	Mh	Ma	Mp
8	Mh	Aa	Up
7	Mh	Aa	Mp
6	Sh	Ra	Up
5	Sh	Ra	Mp
4	Sh	Ma	Up
3	Sh	Ma	Mp
2	Sh	Aa	Up
1	Sh	Aa	Mp

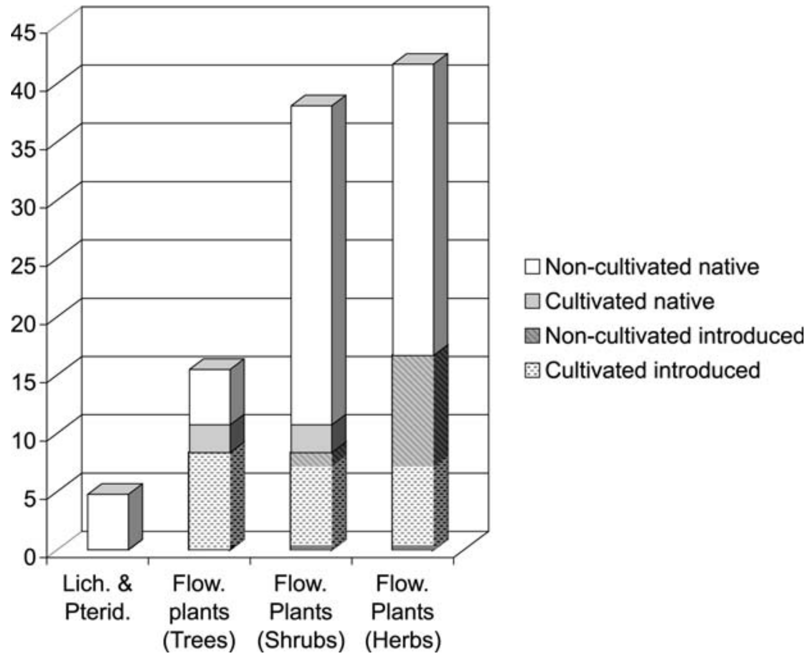

Figure 2. Percentages of species classified by taxonomic group and habit and grouping in four biological categories. Lich. = lichens; Pterid. = pteridophytes; Flow. Plants = flowering plants.

Table 4. Medicinal plants grouped according to habits and ordering in decreasing values of the ICP.

Species	RPV	RDC	ROA	ICP
Trees				
Geoffroea decorticans (Gillies ex Hook. and Arn.) Burkart	10	2	4	1.92
Celtis tala Gillies ex Planch.	6	1	4	0.58
Bauhinia forficata subsp. *pruinosa* (Vogel) Fortunato and Wunderlin	4	2	3	0.58
Tilia spp.	7	3	1	0.50
Jodina rhombifolia(Hook. and Arn.) Reissek	3	1	4	0.29
Acacia caven (Molina) Molina	3	1	4	0.29
Schinus areira L.	3	1	3	0.22
Eriobotrya japonica (Thunb.) Lindl.	3	3	1	0.22
Eucalyptus cinerea F. Muell. ex Bentham	7	1	1	0.17
Fraxinus spp.	6	1	1	0.14
Morus alba L.	5	1	1	0.12
Morus nigra L.	5	1	1	0.12
Salix babilonica L.	1	1	1	0.02
Shrubs				
Minthostachys mollis Griseb.	14	4	4	5.38
Julocroton argenteus (L.) Didr.	18	3	4	5.19

Table 4. Continued.

Species	RPV	RDC	ROA	ICP
Baccharis crispa Spreng.	16	3	4	4.61
Trixis divaricata subsp. *discolor* (D. Don) Katinas	16	3	4	4.61
Aloysia gratissima (Gillies and Hook.) Tronc.	14	3	4	4.04
Lippia turbinata Griseb.	14	3	4	4.04
Baccharis articulata (Lam.) Pers.	14	3	4	4.04
Phacelia pinnatifida Griseb. ex Wedd.	10	3	4	2.88
Jungia polita Griseb.	10	3	4	2.88
Croton serpyllifolius Baill.	10	2	4	1.92
Aloysia polystachya (Griseb.) Moldenke	8	3	3	1.73
Achryrocline satureioides (Lam.) DC.	14	1	4	1.35
Dolichandra cynanchoides Cham.	4	3	4	1.15
Ligaria coneifolia (Ruiz and Pav.) Tiegh	6	2	4	1.15
Aloysia citriodora Palau	7	2	3	1.01
Buddleja cordobensis Griseb.	10	1	4	0.96
Sphaeralcea cordobensis Krapov.	3	3	4	0.86
Ephedra spp. (*E. triandra* Tul. emend. J.H. Hunz./*E. ochreata* Miers)	6	1	4	0.58
Colletia spinosissima J.F. Gmel.	4	1	4	0.38
Croton hirtus L' Hér.	4	1	4	0.38
Heimia salicifolia (Kunth) Link	4	1	4	0.38
Margyricarpus pinnatus (Lam.) Kuntze	4	1	4	0.38
Porlieria microphylla (Baill.) Descole, O'Donell and Lourteig	2	1	4	0.19
Gnaphalium gaudichaudianum DC.	2	1	4	0.19
Schinus longifolia (Lindl.) Speg.	2	1	4	0.19
Pyracantha coccinea M. Roem.	4	1	2	0.19
Aloe spp. (*Aloe saponaria* (Aiton) Haw./*Aloe* sp.)	7	1	1	0.17
Ruta chalepensis L.	7	1	1	0.17
Punica granatum L.	2	2	1	0.10
Salvia officinalis L.	3	1	1	0.07
Laurus nobilis L.	3	1	1	0.07
Rosmarinus officinalis L.	1	1	1	0.02
Herbs				
Hedeoma multiflora Benth.	18	3	4	5.19
Passiflora caerulea L.	16	3	4	4.61
Scoparia montevidensis (Spreng.) R.E. Fr.	14	2	4	2.69
Solanum sisymbriifolium Lam.	9	3	4	2.59
Cuphea glutinosa Cham. and Schltdl.	8	2	4	1.54
Gaillardia megapotamica var. *scabiosoides* (Arn. ex DC.) Baker	8	2	4	1.54
Chenopodium ambrosioides L.	15	1	4	1.44
Guilleminea densa (Willd. ex Roem. and Schult.) Moq.	7	2	4	1.35
Plantago major L.	7	2	4	1.35
Tagetes minuta L.	7	2	4	1.35
Urtica urens L.	11	2	2	1.06
Mentha spp. (*Mentha spicata*/*Mentha* × *piperita v. citrata* (Ehrh.) Briq.)	13	3	1	0.94
Marrubium vulgare L.	9	2	2	0.86
Euphorbia serpens Kunth	4	2	4	0.77
Xanthium spinosum var. *spinosum* L.	4	2	4	0.77
Foeniculum vulgare Mill.	6	2	2	0.58
Coronopus didymus (L.) Sm.	3	2	4	0.58

Table 4. Continued.

Species	RPV	RDC	ROA	ICP
Pluchea sagittalis (Lam.) Cabrera	6	1	4	0.58
Malva spp. *(M. parviflora* L./*M. sylvestris* L.)	7	3	1	0.50
Argemone subfusiformis G.B. Ownbey	4	1	4	0.38
Verbena litoralis Kunth	4	1	4	0.38
Conyza bonariensis (L.) Cronquist	4	1	4	0.38
Parthenium hysterophorus L.	3	1	4	0.29
Amaranthus quitensis Kunth	1	2	4	0.19
Mimulus glabratus Kunth	2	1	4	0.19
Capsella bursa-pastoris (L.) Medik	3	1	2	0.14
Chenopodium album L.	3	1	2	0.14
Taraxacum officinale Weber ex F.H. Wigg.	1	2	2	0.10
Ambrosia tenuifolia Spreng.	1	1	4	0.10
Melissa officinalis L.	2	1	2	0.10
Mentha rotundifolia (L.) Huds.	2	1	2	0.10
Thymus vulgaris L.	3	1	1	0.07
Ocimum basilicum L.	3	1	1	0.07
Artemisia spp. (A. *absinthium*/*A. verlotiorum* Lamotte)	1	1	1	0.02
Origanum vulgare L.	1	1	1	0.02
Horsetails, ferns and lichens				
Usnea spp. (*U. amblyoclada*/*U. subflorida*	14	3	4	4.04
Equisetum giganteum L.	14	3	4	4.04
Anemia tomentosa var. *tomentosa* (Savigny) Sw.	10	2	4	1.92
Adiantum spp.(A. *raddianum* C. Presl/*A. thalictroides* Willd. ex Schltdl.)	6	1	4	0.58

Trees have the lowest ICP, being the highest value 1.92 for *Geoffroea decorticans*.

Considering the values of ICP (in brackets) of the species surveyed we point out the priorities for conservation as follows: For natives plants (ROA 4), the highest priorities in conservation practices must be for the following shrubs: *Minthostachys mollis* (5.38), *Julocroton argenteus* (5.19), *Baccharis crispa* (4.61), *Trixis divaricata* subsp. *discolor* (4.61), *Aloysia gratissima* (4.04), *Lippia turbinata* (4.04) and *Baccahris articulata* (4.04) and for two herbs, *Hedeoma multiflora* (5.19) and *Passiflora caerulea* (4.61), one lichen *Usnea* spp. (4.04) and one pteridophyte (horsetails) *Equisetum giganteum* (4.04). Also some attention in conservation practices needs to be given to all others natives species which ICP values are between 5 and 2. For native cultivated species (ROA 3), the highest priorities in conservation practices should be for the sub shrubs *Aloysia polystachya* (1.73) and *Aloysia citriodora* (1.01). For introduced non cultivated species (ROA 2) and introduced cultivated species (ROA 1) the ICP values are in general too low to be considered priorities for conservation practices. For those categories the species with highest ICP values are: *Urtica urens* (1.06), *Marrubium vulgare* (0.86), *Foeniculum vulgare* (0.58) for ROA2 and *Mentha* spp. (0.94) and *Malva* spp. (0.50) for ROA 1.

Discussion and conclusions

We established a methodology to assign conservation priorities to medicinal plants. Our results show that the major group of plants used in folk medicine are non-cultivated native species while Dhar et al. (2000) showed that wild-cultivated forms which accounted for more than 52% of the 'use value index' (UVI). Another difference is that they limited the study to species used by the pharmaceutical industry and we evaluated also other destinations of the collected plants such household use, product elaboration for peasant families, retail sale and stocking and wholesale. In this case, the harvest destination index, no treated by the others authors, is a good indicator of the destructive impact of collecting natives plants in the field, because introduced medicinal species are mainly cultivated and obtained directly from home-gardens.

This work is the first quantitative approach which includes, through ICP, the most important steps to develop a list of endangered or threatened plants such the one proposed by Cunningham (1997). Althought there are many local floras, checklists, monographic reviews and ecological studies that provide information about abundance of natives species for Córdoba, there are few documents treating the risk of extinction (Noher de Halac et al. 1985; Vischi et al. 2004) as in this paper. Lucas and Synge (1978) indicated a lack of field studies to included species from Argentina in the IUCN Plant Red Data Book (Lucas and Synge 1978) and in fact there is not a National Red Data Book for Argentina (Davies et al. 1986).

Some agreement were observed between our list of species with high ICPs such as *Minthostachys mollis*, *Hedeoma multiflora*, *Lippia turbinata*, *Equisetum giganteum* and *Baccharis crispa* and the species mentioned to be protected, due to their extraction and use levels, in the provincial district of Rio Cuarto (Southern Córdoba) by Bocco et al. (1997). Also, *Aloysia gratissima* and *Lippia turbinata* are included in the list of 20 endangered native medicinal species mentioned for other areas of the Province of Córdoba by Lagrotteria et al. (1987a) and Lagrotteria and Affolter (1999). Moreover *Minthostachys mollis*, is considered a threatened medicinal species by a private organization such as Wildlife Argentine Foundation and *Equisetum giganteum* was settled as an endangered species by De la Sota (1977).

We pointed out a number of medicinal plants that could be threatened with extinction in the short or medium term such as *Julocroton argenteus*, *Trixis divaricata* subsp. *discolor* and *Phacelia pinnatifida* which were not mentioned by other authors (Lagrotteria et al. 1987a; Bocco 1996; Lagrotteria and Affolter 1999).

Recently, new studies and activities related to adjustment, spreading and assessment of germplasm of some species prioritized for conservation in this work have been documented for *Minthostachys mollis* (Ojeda et al. 1998, 2001; Ojeda 2004), *Achyrocline satureioides* (Nóbile et al. 1999), *Hedeoma multiflora* (Martínez and Fernández 1998) and *Passiflora caerulea* (Martínez

2003; Mediondo et al. 2003). However, there is a need for additional research in medicinal plant ecology. The list of species and priorities introduced here will allow to orientate and define the type of ecological research, as well as the contribution to perform local conservation activities.

Finally, this study set the bases for new approaches to development others indexes based on information from people participation and ethnographical studies promoting environmental conservation activities (Martin 2000) such as community herbariums, botanical gardens and local germplasm banks (Cubero 1990). This research may result effective, not only for conservation of native species, but also to preserve local conservation practices (Gómez Ocampo 1981; Benz et al. 2000). The native species treated in this research are good representatives of the flora of Córdoba and the central region of Argentina, therefore, the IPC values and range of vulnerability for each species can be applied for a larger area in order to make recommendation at provincial and national level for environmental preservation practices.

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References

Alexiades M.N. 1996a. Standard techniques for collecting and preparing herbarium species. In: Alexiades M.N. (ed.), Selected Guidelines for Ethnobotanical Research: A Field Manual. New York Botanical Garden, Bronx, New York, pp. 99–126.

Alexiades M.N. 1996b. Protocol for conducting ethnobotanical research in the tropics. In: Alexiades M.N. (ed.), Selected Guidelines for Ethnobotanical Research: A Field Manual. New York Botanical Garden, Bronx, New York, pp. 5–18.

Badola R. 1998. Attitudes of local people towards conservation and alternatives to forest resources: a case study from the lower Himalayas. Biodiv. Conserv. 7: 1245–1259.

Benz B., Cevallos J., Santana F., Rosales J. and Graf S. 2000. Losing knowledge about plant use in the Sierra de Manantlan Biosphere Reserve, Mexico. Economic Bot. 54((2): 183–191.

Bocco M.E., Vischi N. and Montani N. 1997. Relevamiento de las plantas medicinales espontneas del Departamento Río Cuarto (Córdoba, Argentina). Parodiana 10: 11–18.

Bolling M. and Schulte A. 1999. Environmental change and pastoral perceptions: degradation and indigenous knowledge in two African pastoral communities. Human Ecol. 27(3): 493–514.

Cabrera A.L. 1971. Fitogeografía de la República Argentina. Boletín Soc. Arg. Botánica. 14(1–2): 1–42.

Cabrera A.L. 1976. Regiones Fitogeogrficas Argentinas. Enciclopedia Argentina de Agricultura y Jardinería. Tomo II. Acme, Buenos Aires, 85 pp.

Cabrera A.L. 1977. Threatened and endangered species in Argentina. In: Prance G. and Elias T. (eds), Extinction is Forever. Threatened and Endangered Species of plants in the Americas and their significance in ecosystems today and in the future. The New York Botanical Garden, Bronx, New York, 437pp.

Cabrera A.L. 1983. Flora de la Provincia de Jujuy. Coleccin Científica del INTA.

Cabrera A.L. 1994. Regiones Fitogeográficas Argentinas. Enciclopedia Argentina de Agricultura y Jardinería. Tomo II (1) Acme, Buenos Aires, 85pp.

Caniago I. and Siebert S. 1998. Medicinal plant ecology, knowledge and conservation in Alimantan, Indonesia. Economic Bot. 52: 229–250.

Cantero J.J., Cantero A. and Cisneros J.M. 1996. La vegetacion de los paisajes hidrohalomficos del centro de Argentina. UNRC, 296pp.

Cantero J.J., Cantero A. and Cisneros J.M. 1998a. Habitat structure and vegetation relationships in central Argentina saltmarsh landscapes. Plant Ecol. 137: 79–100.

Cantero J.J., Cisneros J.M., Zobel M. and Cantero A. 1998b. Environmental relationships of vegetation patterns in salt marshes of central Argentina. Folia Geobot. 33: 133–145.

Cubero J.I. 1990. Tcnicas de conservación de recursos genéticos vegetales de interés económico en riesgo de extinción. In: Hernndez Bermejo J.E., Clemente M. and Heywood V. (eds), en: Botanic Gardens. Koeltz Sc. Books, pp. 17–26.

Cunningham A.B. 1997. The 'Top 50' listing and the medicinal plants action plan. Med. Plant Conserv. 3: 5–7.

Davies S.D., Droop S.J.M., Gregerson P., Henson L., Leon C.J., Villa-Lobos J.L., Synge H. and Zantovska J. 1986. Plants in Danger. What do we know? International Union for Conservation of Nature and Natural Resources, UK, 461 pp.

De la Sota E.R. 1977. The problems of threatened and endangered plant species and plant communities in Argentina. pp. 240–244. In: Prance G. and Elias T. (eds), Extinction is Forever. Threatened and Endangered Species of Plants in the Americas and their Significance in Ecosystems Today and in the Future. The New York Botanical Garden, Bronx, New York, 437 pp.

Delucchi G. and Correa R.F. 1992. Las especies vegetales amenazadas de la Provincia de Buenos Aires. In: López, H.L. andTonni E.P. (eds), Situación ambiental de la Provincia de Buenos Aires. Recursos y rasgos naturales en la evaluación ambiental, Vol. 2, no. (14). CIC. Provincia de Buenos Aires, pp. 1–39.

Dhar U., Rawal R.S. and Upreti J. 2000. Setting priorities for conservation of medicinal plants – a case study in the Indian Himalaya. Biol. Conserv. 95: 57–65.

Elisabetsky E. and Costa-Campos L. 1996. Medicinal plant genetic resources and international cooperation: the Brazilian perspective. J. Ethnopharmacol. 51: 111–120.

FAO 1996. Informe sobre el estado de los recursos fitogenticos en el mundo. Rome.

Fuentes E. and Planchuelo A.M. 2000. Wild lupins as pioneers of riverside sand banks. In: van Santen E., Wink M., Weissmann S. and Remer P. (eds), Lupin, an Ancient Crop for the New Millenium. Canterbury, New Zealand, pp. 316–319.

Gómez Ocampo C. 1981. Conservación de recursos genéticos (22). In: Ramos J.L. (ed.), Tratado del Medio Natural, Vol. 2. Universidad Politécnica de Madrid, Madrid, pp. 97–124.

Gorgas J.A. and Tassile J.L. 2001. Regiones naturales de la Provincia de Crdoba. Agencia Córdoba Ambiente, Gobierno de la Provincia de Córdoba.

Guarino I. 1995. Secondary sources on cultures and indigenous knowledge. In: Guarino I., Rao R.V. and Reid R. (eds), Collecting Plant Genetic Diversity: Technical Guideliness. CAB International, UK.

Gupta A., Vats S.K. and Brij Lal 1998. How cheap can a medicinal plant species be? Current Sci. 74: 555–556.

Hall P. and Bawa K. 1993. Methods to assess the impact of extraction of non-timber forest products on plant populations. Economic Bot. 47: 234–247.

Hellier A., Newton A.C. and Ochoa Gaona S. 1999. Use of indigenous knowledge for rapidly assessing trends in biodiversity: a case study from Chiapas, Mexico. Biodiv. Conserv. 8: 869–889.

Idoyaga Molina A. 2001. Lo sagrado en las terapias de las medicinas tradicionales del NOA y Cuyo. Scripta Ethnol. XXIII: 9–75.

Kala Ch P. 2000. Status and conservation of rare and endangered medicinal plants in the Indian trans-Himalaya. Biol. Conserv. 93: 371–379.

Kossmann I. 1999. Recursos genéticos y derechos comunitarios. Raíces 21(X): 4–9.

Lagrotteria M. and Affolter M. 1999. Sustainable production and harvest of medicinal and aromatic herbs in the Sierras de Córdoba Region, Argentina. In: Nazarea V.D. (ed.), Ethnoecology. Situated Knowledge/Located lives. The University of Arizona Press, Tucson, USA, 299 pp.

Lagrotteria M., Toya M.A. and Montenegro R.A. 1986. Demanda comercializacin de plantas medicinales y aromáticas. Subsec. Gest. Amb. Sec. Min. y Coord., Gobierno de la Provincia de Córdoba.

Lagrotteria M., Di Feo M., Toya M.A. and Montenegro R.A. 1987a. Situación de plantas medicinales aromáticas en la provincia de Córdoba. Anales de Saipa 8: 111–125.

Lagrotteria M., Toya M.A. and Montenegro R.A. 1987b. Manejo comercialización de plantas medicinales y aromáticas. Subsec. Gest. Amb. Sec. Min. y Coord. Gobierno de la Provincia de Córdoba.

López M.A. 1996. Algunos aspectos económicos del cultivo de plantas espontáneas utilizadas en medicina popular. Anales de Saipa 14: 269–287.

Lucas G. and Synge H. 1978. The IUCN Plant Red Data Book. Comprising Red Data Sheets on 250 Selected Plants Threatened on a World Scale. International Union For Conservation of Nature and Natural Resources, Switzerland.

Luti R., de Solís M.A., Galera F.M., de Ferreira N., Berzal M., Nores M., Herrera M.A. and Barrera J.C. 1979. Vegetación. In: Vasqués J.B., Miatello R. and Proqué M.E. (eds), Geografía Física de la Provincia de Córdoba Ed. Boldt, Córdoba.

Lykke A.M. 1998. Assessment of species composition change in savanna vegetation by means of woody plants' size class distributions and local information. Biodiv. Conserv. 7: 1261–1275.

Martín G. 2000. Etnobotánica. Manual de Conservación. Serie 'Pueblos y Plantas'. WWF-UK. UNESCO y Royal Botanic Gardens, Kew, Reino Unido. Ed. Nordan Comunidad, Montevideo, Uruguay, 240 pp.

Martínez E. and Fernández E.A. 1998. Ensayo de enraizamiento de esquejes jóvenes de peperina de las lomas (*Hedeoma multiflora* Bentham). Resúmenes del XII Congreso Nacional de Recursos Naturales Aromáticos y Medicinales, Córdoba, pp.45.

Martínez G.J. 2003. Estudio etnobotánico de las plantas vinculadas con la medicina tradicional de los campesinos de Paravachasca y Calamuchita, Provincia de Córdoba. Aportes para su conservación, Tesis de Maestría, Facultad de Ciencias Agropecuarias, Universidad Nacional de Córdoba, 248 pp.

Martínez G.J., Planchuelo A.M., Ojeda M.S. and Villalba P. 2003. Aporte de las etnociencias a la regionalización de la curricula de las escuelas rurales: una propuesta de valoración del conocimiento etnobotánico local en Paravachasca y Calamuchita. Provincia de Córdoba- Revista de Educación en Biología 6(2): 19–28.

Mediondo G.M., Amela Garca M.T. and Hoc P.S. 2003. Germinación de *Passiflora caerulea* (Passifloraceae). Boletín de la Sociedad Argentina de Botánica Supplemento 38: 187.

Mendelsohn R. and Balick M.J. 1995. The value of undiscovered pharmaceuticals in tropical forests. Economic Bot. 49: 223–228.

Miasek M.A. and Long Ch. R. 1985. Endangered Plant Species of the World and their Endangered Habitats: A Compilation of the Literature. Revised and Enlarged Edition, The New York Botanical Garden Library, Bronx, New York, 153 pp.

Nalvarte W.A., de Jong W. and Domínguez G. 1999. Plantas amazónicas de uso medicinal. Diagnóstico de un sector económico con un potencial de realización. CIFOR Universidad Nacional Agraria La Molina, Lima Perú.

Nóbile R., Serdiuk I. and Rolando R. 1999. Adaptación de *Achyrocline tomentosa* Rusby 'marcela' al cultivo. Resúmenes del IV Encuentro Nacional de Plantas Medicinales, Córdoba, pp. 14

Noher de Halac R.I., Castro M. and Frank E. 1985. Encuesta de datos sobre los recursos de fauna y flora de la provincia de Córdoba. Secretaría de Gestión, Ambiental, Gobierno de Córdoba, Argentina.

Nuñez C. and Cantero J.J. 2000. Las plantas medicinales del Sur de la Provincia de Córdoba. Editorial de la Fundación de la Universidad Nacional de Río Cuarto, 145 pp.

Ojeda M. 2004. Caracterizacóin de poblaciones y avances en la domesticación de peperina *Minthostachys mollis* (Kunth.) Griseb. Tesis doctoral, Facultad de Ciencias Agropecuarias, Universidad Nacional de Córdoba, 134 pp.

Ojeda M., Coirini R., Cosiansi J., Zapata R. and Zygadlo J. 2001. Evaluation of variability in natural populations of peperina (*Minthostachys mollis* (Kunth.) Griseb.), an aromatic species from Argentina. Plant Genet. Resour. Newslet. 126: 27–30.

Ojeda M., Sanchez M., Bielkiewicz E. and Capelleti L. 1998. Determinación del porcentaje de germinación de distintas poblaciones de peperina *Minthostachys mollis*. Resúmenes XII Congreso Nacional de Recursos Naturales Aromáticos y Medicinales, Córdoba, pp. 45

Parodi L.R. 1980. Enciclopedia Argentina de Agricultura y Jardinera. 3rd ed. ed. actualizada por M.J. Dimitri. Ed. Acme. Acme. Buenos Aires.

Planchuelo A.M. 2000. Endangered species of wild lupins in South America. In: van Santen E., Wink M., Weissmann S. and Remer P. (eds), Lupin, an Ancient Crop for the New Millenium, pp. 320–323.

Planchuelo A.M., Carreras M.E. and Fuentes E. 2003. Las plantas nativas como recursos ornamentales: Conceptos y generalidades. In: Mascarini L. and Vilella y F.E. Wright. (eds), Floricultura en la Argentina. Investigacin y Tecnología de Producción. Facultad de Agronomía, Buenos Aires, pp. 303–313.

Pro Flora, CONICET 1994–2001. Flora Fanerogámica Argentina. Fasc. 1–79. CONICET, Buenos Aires.

Rai L.K., Pasad P. and Sharma E. 2000. Conservation threats to some important medicinal plants of the Sikkim Himalaya. Biol. Conserv. 93: 27–33.

Rodríguez A., García S. and Ruesta M. 1992. Caracterización y cuantificación de la oferta y la demanda de plantas aromáticas y medicinales. Provincia de Córdoba. Anales de Saipa 9(10): 93–195.

Tran V.O., Quyen D., Dinh Bich L., Jones B., Wunder J. and Russell-Smith J. 2001. A survey of medicinal plants in Ba Vi National Park, Vietnam: methodology and implications for conservation and sustainable use. Biol. Conserv. 97: 295–304.

UNEP. 1992. Programa de Naciones Unidas para el Medio Ambiente. Saving our planet: challenges and hopes. UNEP, Nairobi, Kenia.

Vischi N., Natale E. and Villamil C. 2004. Six endemic plant species from central Argentina: an evaluation of their conservation status. Biodiv. Conserv. 13: 997–1008.

Voeks R.A. 1996. Tropical forest healers and habitat preference. Economic Bot. 50: 381–400.

Walker D., Sinclair F. and Thapa D. 1995. Incorporation of indigenous knowledge and perspectives in agroforestry development. Agrofor. Syst. 30: 235–248.

Williams V., Balkwill K. and Witkowski E.T.F. 2000. Unraveling the commercial market for medicinal plants and plant parts on the Witwatersrand, South Africa. Economic Bot. 54(3): 310–327.

Zuloaga F.O., Nicora E.G., de Agrasar Z.E., Morrone O., Pensiero y J. and Cialdella A.M. 1994. Catálogo de la Familia Poaceae en la República Argentina. Monogr. Syst. Bot. Missouri Bot. Gard. St. Louis, Missouri.

Zuloaga F.O. and Morrone O. 1996a. Catálogo de las Plantas Vasculares de la República Argentina. I. Monogr. Syst. Bot. Missouri Bot. Gard. St. Louis, Missouri.

Zuloaga F.O. and Morrone O. 1996b. Catálogo de las Plantas Vasculares de la República Argentina. II. Monogr. Syst. Bot. Missouri Bot. Gard. St. Louis, Missouri.

Zuloaga F.O. and Morrone O. 1999. Catálogo de las Plantas Vasculares de la República Argentina. III Monogr. Syst. Bot. Missouri Bot. Gard. St. Louis, Missouri.

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Subsistence hunting and conservation issues in the game reserve of Gile, Mozambique

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Abstract. Ethnozoological research was conducted to gather information on the hunting activities and their relevance for the subsistence of local people in 8 villages around the game reserve of Gile, Mozambique. Two series of data were gathered by questionnaires to: (a) 510 householders from eight villages located in the outskirts of the Reserve; (b) 10 hunters from the village of Gile, the main centre of the study area. Several hunting techniques were recorded: spears, nets, traps (including gin-traps) and wildfires, while the use of guns did not appear relevant. The importance of subsistence hunting for local people was underlined by the high percentage of respondents who declared that they usually conduct this activity and sell bushmeat. The proportion of hunters per village was related to the village size but not to its geographical location of villages and the household composition. A positive relationship existed between the proportion of hunters, crop production and fishing activities, indicating that hunting is part of an integrated system of subsistence activities. Most animals harvested were mammals (89.5%, of which 46.7% were ungulates) and most were captured within the Reserve (96%). A higher percentage of animals was sold (56%), representing a relevant income source for the villagers. Small animals were mainly captured by traps during solitary hunting, medium-sized animals in collective net hunting; larger prey were captured by gin-traps adopted by both solitary and collective hunting. In the diet of the local people wild animals represented a higher protein source than domestic animals.

Introduction

In tropical Africa the meat of wild animals represents an important part of the staple diet of hundreds of thousands of people, as well as a remarkable source of income for rural hunters (Bellamy 1993; Carpaneto 1994; Carpaneto and Fusari 2000; Colell et al. 1994; Fa et al. 1995; Fa and García Yuste 2001; FitzGibbon et al. 1995; Kock 1995; Lahm 1993; Wilkie et al. 1992; Ziegler 1996). Recent data reveal that bushmeat harvests are unsustainable in several African countries (Alvard et al. 1997; Fa and Peres 2001; Fa and García Yuste 2001; Barnes 2002; Bennett et al. 2003; Ling et al. 2003; Robinson and Bennet 2003). This situation is particularly severe especially where rural people hunt within poorly managed protected areas.

In this paper, we studied the impact of hunting in the game reserve of Gile (GRG), Zambezia Province, Mozambique. This Reserve, first established on 1932, suffered since 1982 from a decrease in management and lack of financial resources, owing to civil war. The result was a drastic decline in staff, including rangers, and patrol activities. This situation and the accompanying rapid worsening of human life conditions, encouraged an increased exploitation of natural resources in the protected area (Chande et al. 1997; Carpaneto, 2001). The understanding of how local dwellers exploit indigenous resources was considered essential to develop an appropriate conservation strategy and to ensure a food supply for local population. In this optic, the aim of the present work was to assess the extent of subsistence hunting activities in the surroundings of the protected area and their relevance for rural livelihood.

The present paper is the first study on bushmeat exploitation in Mozambique and represents an important contribution to the knowledge of this growing activity that is going to evolve from subsistence to market. Mozambique is one of the poorest countries of Africa and it is not surprising that people will take advantage of any opportunity to earn money. After the devastation of 16 years of civil war, Mozambique is undergoing a rapid transformation and also susbsistence activities may change into a trade opportunity. Despite the Mozambique's wildlife was decimated during the war, poaching continues to occur throughout the country and is becoming an easy source of income. The quantitative data emerging from the present research may provide wildlife managers and conservation officers a tool for assessing the extent of bushmeat trade in the country. Through a quantitative description of bushmeat harvest, the present paper attempts to look at the correlations between hunting and other activities of the villagers, so that predicting models of wildlife exploitation in changing rural economies could be developed in the future.

Study area

Geographic location and local people

The GRG is located in the north-eastern part of Zambezia Province. It represents, together with the Niassa game reserve and the Quirimbas National Park, one of the most important protected areas in Mozambique north of the Zambezi River (Figure 1). Originally, the Reserve extended over an area of approximately 5000 km^2, and was mainly created to protect black rhinos and elephants, but also for professional and sport hunting to other large game, such as antelopes and buffaloes. Despite the intended protection regime, the black rhino was eradicated from the area by 1973 (Dutton et al. 1973), and elephants were reduced to very low densities (Martines and Ntumi 2002). In 1960, the GRG was reduced to its actual size of 2100 km^2, because a large buffer zone, in the northern part of the Reserve, was abandoned owing to the impossibility of governmental authorities to manage the area. The GRG is included in the Districts of Gile (154,988 inhabitants, population density 15.4/km^2) and Pebane (150,538 inhabitants, population density 15.8/km^2). Both districts experience high rates of population growth: Gile (4.9%) and Pebane (3.3%), which led to an estimated 202,668 and 189,883 inhabitants in 2010 respectively (INE 1997).

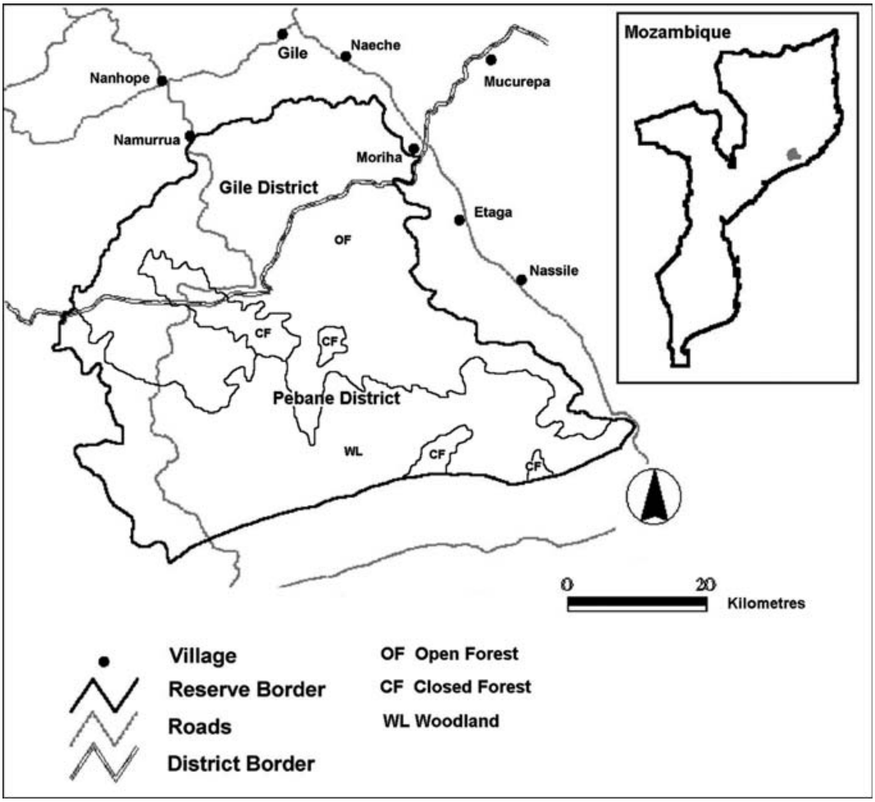

Figure 1. Location of the study area: the game reserve of Gile, Zambezia, Mozambique.

Most people in the northern sector of the Zambezia Province belong to the Lomwé tribe, one of the 20 ethnic groups recognized in Mozambique. Other ethnic groups in the area are the Chuabo, the larger group within the province, and the Macua, mainly settled along the coast. Both the Lomwé and Chuabo are essentially Catholics; however, because of the strong influence of the Swahili culture, most people living on the coast (both Lomwé and Macua) are Muslims.

Most households in Gile District and in the interior of Pebane District depend on subsistence agriculture (Galego and Rasul 2001). Local farmers practise slash-and-burn agriculture producing cassava, maize, rice, sweet potatoes, groundnuts and beans as staple foods. Sunflower, sesame, and cashew nuts (*Anacardium occidentale*) are important cash crops. Nonetheless, their annual production is limited: an average household produces around 60 kg of sunflower, 39 kg sesame and 168 kg cashew nuts, of which 25%, 38% and 79% are respectively sold, and the remainder consumed or used to pay labour (Galego and Rasul 2001). During the study period, crop traders from Nampula, a town north of the study area, bought sunflower, sesame and cashew nuts for 0.20–0.40 USD per kg. Hence, an average household would earn about 49 USD per year from cash crops. In the area, the only off-farm profit opportunities available to most households, apart from trading bushmeat, are informal, e.g. sale of traditional drinks or temporary labour in neighbours' fields. Animal husbandry, even if limited by diseases, represented an important protein source. An average household owned 7.7 pigeons, 3.3 goats, 2.5 pigs, 6.4 chickens, 2.6 ducks, 2.7 guineafowl, and 3 rabbits (Galego and Rasul 2001). Cattle is very scarce due to poor pasture, occurrence of tsetse fly, and lack of knowledge of cattle rearing by local people. Hence, subsistence patterns and livelihood strategies are largely based on the exploitation of several non-timber forest products (NTFPs), among which bushmeat is essential (IUCN 1998; Carpaneto 2001; Fusari 2002; Galego 2002).

Climate, landscape and vegetation

The study area is 100–200 m above sea level and lies within Walter's tropical summer-rainfall climatic zone (see White 1983), with a distinct wet period between November and April and a dry period through the other 6 months (May–October). Annual rainfall is around 800–1000 mm. The maximum average temperature is 35.7 °C, at the onset of the rainy season, and a minimum is 13.5 °C during the dry season. The landscape is characterized by a gently sloping plain and several granite outcrops (inselbergs) that emerge from woodland. The area has a complex river system with three major watercourses and numerous small permanent or seasonal streams.

A mosaic of deciduous woodland (miombo) and savannah patches characterizes the vegetation within the Reserve. The miombo, classified as closed forest, open forest and woodland according to different canopy cover (DNFFB 1995; Trollope and Trollope 2002; Martines and Ntumi 2002), is dominated by *Brachystegia spiciformis*, *B. boehmii*, *Julbernardia globiflora* and *Pterocarpus angolensis*. Other common trees are: *Afzelia quanzensis*, *Albizia versicolor*, *Annona senegalensis*, *Burkea africana*, *Millettia stuhlmannii*, *Strychnos* spp., and *Swartzia madagascariensis*. Savannah patches consist of edaphic grasslands (dambos) that cover seasonally waterlogged depressions and which harbour some rich and diverse herbaceous communities with *Stipa* sp., *Schizachyrium jeffreysii*, *Eragrostis* spp., and sedges (Cyperaceae). Human activities have modified the landscape around villages, because slash-and-burn practice for field cleaning and fuel wood exploitation have reduced conspicuously the tree vegetation.

Hunting methods

AK-47 machineguns were still common in the area as a legacy from the long civil war. However, their use has decreased due to the high cost and/or scarcity of cartridges, as well as the low numbers of large mammals. Trapping is thus the commonest hunting technique. Neck and leg snares (*mranko* or *muraho*) are frequently used and hand-made from natural fibres. They allow the capture of small antelopes, hares, small and medium mammals but also game birds. Another trap (*nicolope*) consists of a trunk hanging on a wire and placed along the track of an animal, to catch small to medium size mammals and game birds. Pitfall traps (*intchepe*) are not common in the study area, but are used occasionally and prepared by arming the bottom of large holes dug in the ground with several iron-tip spears (*nevaka*). Gin-traps (*rapito* or *langa*), introduced by the Portuguese colonists, are widespread and intensively used in the study area. These iron-made traps with a jaw-edge, manufactured locally with the leaf springs of old vehicles, allow the capture of mammals of varying size from hares to large ungulates. Netting is conducted by groups ranging from three/five hunters to entire households, including women and children. Nets are still made from natural fibres, although some are made of synthetic materials; lengths vary from 15 m to 35 m, height is normally 1.5 m (Carpaneto 2001).

Fire is used to directly kill small animals that live on the ground (small rodents, elephant shrews and reptiles such as monitors and tortoises), or to detect their dens. Burning is also used to clear ground from grass and bushy vegetation and facilitate both trapping and netting. Hunting with fire was essentially practised at the end of the dry season (September–November), because of high temperatures and drought which facilitate burning, but also on account of the large amount of fuel biomass represented by leaf litter and standing grass. Extended and repeated fires occur annually, with serious effects on the vegetation at GRG (Trollope and Trollope 2002; van Aarde 2002), despite the important ecological role of fire in miombo environments (Chidumayo 1997).

Methods

The first data set was collected during a 5 month period between June and October 2001, in eight villages close to the GRG: the nearest Namurrua (0.5 km), the more distant Mucurepa (20 km). Six villages are located within the Gile District: Gile (Gile administrative department, population = 13,198); Moriha, Mucurepa and Naeche (Naeche administrative department, population = 3319); Namurrua and Nanhope (Nanhope administrative department, population = 7492). The other two villages were in Pebane District: Etaga (Mihecue administrative department, population = 4227); and Nassile (Namanipe administrative department, population = 2805). It is important to note that there were no human settlements within the GRG (demographic data are from INE 1997).

Although the study was designed to apply a questionnaire per household and 100 questionnaires per each village (800 in total), only 510 questionnaires were completed (64%). This was because many householders refused to respond because they were worried by questions regarding hunting, which they conducted illicitly. The sample represents ca. 5% of the 9700 estimated households in the studied administrative departments.

Questionnaires were used to collect data related to hunting activities: (1) age of the householder; (2) household composition; (3) the five most hunted animals; (4) use of each species (personal consumption and/or sale); (5) eventual market price of each species. We asked respondents to use vernacular names of animals in Elomwé language to avoid taxonomic misinterpretation (Carpaneto 2001). When possible, remains or entire animal carcasses were examined. However, some records were difficult to assign to species level, so these were classed according to order, family or subfamily. Such difficulties are because, for some taxonomic groups, villagers used the same vernacular name to indicate different species, or because some taxonomic groups were of difficult identification (small rodents and elephant shrews).

We evaluated the proportion of householders who declared that they harvested game, by using multiple regression analyses, considering as possible predictors the following groups of variables: (a) distance of each village from the Reserve border, the distance of each village from Gile (the main human settlement of the study area), the distance of each village from the nearest village (these two variables were considered a measure of remoteness); (b) the size of each village classified according to an ordinal scale (score from 1 to 8; the exact numbers of inhabitants were not available), (c) household composition, i.e. the average number of household's members, proportions of males, females and children; (d) proportion of respondents who declared that they produce from a maximum of 5 to a minimum of 2 crops.

To assess the level of game harvesting in the area, further quantitative data were gathered by interviewing 10 collaborative hunters during 4 months (April–July 2002). For each hunter, a questionnaire was completed approximately every 10 days to monitor their hunting activities by gathering the following information: (1) animals captured; (2) weapon used for each quarry; (3) hunting period for each quarry (day/night); (4) hunting location for each quarry (inside/outside the Reserve); (5) use of each quarry (personal consumption and/or sale); and (6) eventual market price of each quarry. This sample was not included in the previous one, and the data were analysed separately.

Means are reported with ± 1 S.D. Regression analyses were performed with the least square methods and percentages were normalized with an arcsine transformation.

Results

A total of 510 questionnaires were completed in the eight study villages, an average of 64.5 per village. All respondents were males, with an average age of 39.4 ± 3.3. Average number of members per household was five. For the 10 hunters of Gile, whose activities were monitored during a 4 month period, the average age was 38.3 ± 16.1 and the number of household members was 5.9 ± 3.2.

Hunting activity

Subsistence hunting (*ossaia*) proved to be an important activity for Lomwé people. During the study period, 416 respondents (81.6%) declared that they harvested game. The highest hunting activity was recorded in the village of Mucurepa (100%), Nassile (98.3%) and Moriha (89.9%), the lowest in Nanhope (72.6%) (Table 1). There were highly significant differences among villages in the number of respondents who declared that they harvested game (Goodness of fit test, $\chi^2 = 26.55$, $p < 0.01$, d.f. = 7). However, the geographical location of villages and their distance from the Reserve did not influence the extent of hunting activities in the study area. Instead, the village dimension proved to be a significant predictor of the proportion of hunters in each village ($R^2 = 0.726$, $F_{1,6} = 15.928$, $p = 0.007$). In particular, there was a negative relationship between village size and proportion of hunters: the smaller the village, the larger the proportion of hunters recorded (Figure 2). Household size and composition, did not correlate with proportion of hunters. However, the percentage of respondents who produced 5 crops was a significant predictor ($R^2 = 0.522$, $F_{1,6} = 6.562$, $p = 0.43$), indicating a positive relationship between hunting and crop production as non-alternative livelihood strategies (Figure 3).

We used data from a previous study in the area (Fusari 2002), considering possible relationships between hunting activities and two further important livelihood strategies for local populations: trade of cultivated products and fish exploitation. The following correlations (Spearman coefficient) were observed: (1) a significant positive correlation between hunters and respondents who

Table 1. Householders who harvested game in eight villages of the study area. N = householders interviewed; H = householders who declared that they harvested game; T = householders who declared that they have sold bushmeat; D = Distance from Reserve border (km); G = Distance from Gile village (km).

Villages	N	H	%	T	% of N	% of H	D (km)	G (km)
Etaga	90	71	78.9	31	34.4	43.7	10	40
Gile	51	41	80.4	38	74.5	92.7	12	–
Moriha	49	44	89.8	31	63.3	70.5	1	24
Mucurepa	24	24	100	24	100	100	20	25
Naeche	87	68	78.2	38	43.7	55.9	5	7
Namurrua	88	65	73.9	29	33.0	44.6	0.5	31
Nanhope	62	45	72.6	31	50.0	68.9	11	18
Nassile	59	58	98.3	43	72.9	74.1	7	48
Total	510	416	81.6	265	52.0	63.7		

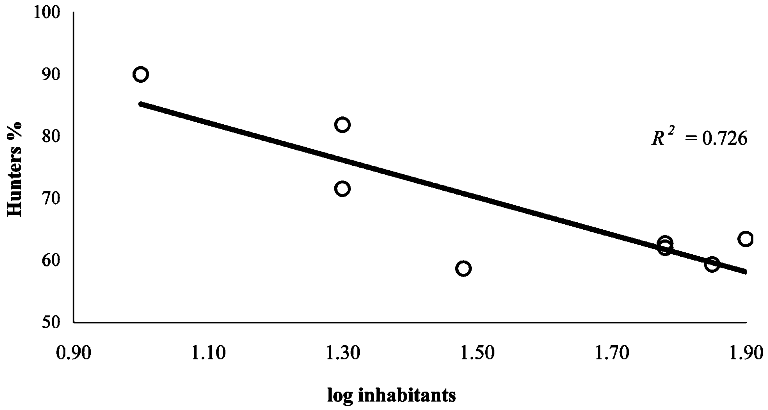

Figure 2. Relation between the percentage of hunters and village size.

harvest freshwater fish ($r_s = 0.762$, $p < 0.05$); (2) a significant positive correlation between bushmeat sellers and respondents who harvest freshwater fish ($r_s = 0.738$, $p < 0.05$). No significant correlation was detected between hunting activities (including bushmeat trade) and crop trade.

Species hunted

Householders reported that the most commonly harvested species are: (1) common duiker (*Sylvicapra grimmia*), declared by 299 hunters (74%); (2) larger cane rat (*Thryonomys swinderianus*), 272 hunters (67.3%); (3) two species

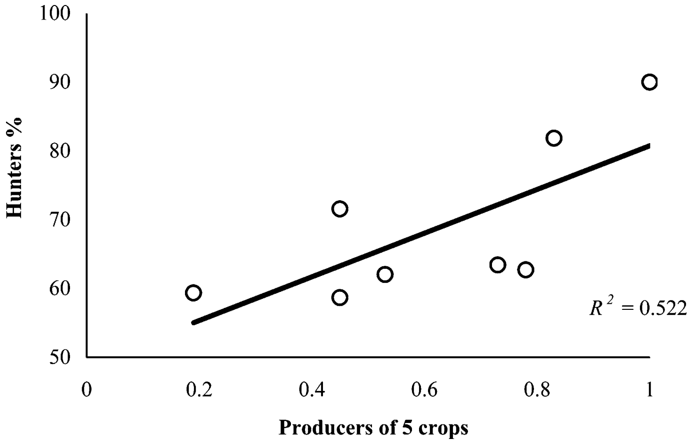

Figure 3. Relation between the percentage of hunters and crop producers.

of hares (*Lepus saxatilis* and *Pronolagus crassicaudatus*), 268 hunters (52.5%); (4) giant pouched rat (*Cricetomys gambianus*), 190 hunters (37.3%); (5) banded mongoose (*Mungos mungo*), 120 hunters (23.5%). Another 15 species or taxonomic groups of vertebrates (11 mammals, 2 birds and 2 reptiles) were hunted (Table 2). Highly significant differences were recorded among villages in the number of respondents who declared that they hunted a given species (common duiker, $\chi^2 = 80.83, p < 0.01$, d.f. = 7; larger cane rat, $\chi^2 = 42.80, p < 0.01$, d.f. = 7; hares, $\chi^2 = 103.39$, $p < 0.01$, d.f. = 7; giant pouched rat $\chi^2 = 57.47$, $p < 0.01$, d.f. = 7; banded mongoose, $\chi^2 = 47.25$, $p < 0.01$, d.f. = 7), as reported in Figure 4. The proportion of householders declaring to exploit any species was not related to the geographical location of the village or to its size.

The off-take of the 10 hunters from Gile consisted of 257 animals, 25.7 ± 6.1 per hunter (range 21). A total of 230 mammals (89.5%), 19 reptiles (7.5%), and 8 birds (3%) were hunted. Almost half of captures were ungulates (46.7%) (Table 3). Duikers and suni represented by far the most captured species (21%); in particular, the common duiker was the main prey (12.8% of total). Large rodents (larger cane rat and giant pouched rat) were the second most harvested category (11.3%), followed by the yellow baboon *Papio cynocephalus* (10.2%), hares (7.8%), and southern reedbuck *Redunca arundinum* (7.4%). Each hunter monthly harvested 6.4 ± 1.5 animals (range 5.2) of which 63% have a biomass higher than 5 kg, and 37% were antelopes.

The bushmeat trade

In the study area, to elude surveillance of the governmental authorities, hunters conducted a hidden bushmeat trade. Bushmeat was sold at village level, simply informing other villagers of game availability. No important trade of bushmeat to the major centres of Nampula and Quelimane was detected. Some 265 householders declared to have sold bushmeat (52% of respondents, 63.7% of hunters). The highest percentage of sellers was recorded in Mucurepa (100%) and Gile (74.5%, 92.7%), whereas the lowest percentage was recorded in Etaga (34.4%, 43.7%) (Table 1). Differences recorded among villages were highly significant ($\chi^2 = 57.05, p < 0.01$, d.f. = 7). The distance between villages was significantly positively correlated with the percentage of bushmeat sellers ($R^2 = 0.661$, $F_{1,6} = 11.692$, $p = 0.14$) (Figure 5). Both village size and household composition were not significant predictors. Instead, percentage of respondents who cultivated five crops was correlated with bushmeat trade in each village ($R^2 = 0.510$, $F_{1,6} = 6.247$, $p = 0.47$) (Figure 6). Respondents reported five species or groups of species most commonly commercialised: larger cane rat (34.3% of hunters) for an average price of 0.73 ± 0.43 USD per specimen; hares (29.3%), for an average price of 0.78 ± 0.07 USD per specimen; common duiker (19.4%) for an average price of 0.75 ± 0.1 USD per kg; giant pouched rat (18.9%) for an average price of 0.46 ± 0.12 USD per

Table 2. The most common prey items in eight villages of the study area (% = percentage of hunters who declared that they harvested each item).

Scientific name	Common name	Etaga	Gile	Moriha	Mucurepa	Naeche	Namurrua	Nanhope	Nassile	Total	%
Mammals											
Sylvicapra grimmia	Common duiker	58	33	27	24	65	30	18	45	300	72.1
Thryonomys swinderianus	Larger cane rat	38	22	20	21	43	55	24	49	272	65.4
Leporidae spp.	Hares	47	25	39	11	11	50	37	48	268	64.4
Cricetomys gambianus	Giant pouched rat	37	15	27	19	19	11	25	37	190	45.7
Mungos mungo	Banded mongoose	23	15	20	7	9	2	17	27	120	28.8
Rodentia spp.	Small rodents	25	14	23	3	1	7	20	13	106	25.5
Redunca arundinum	Southern reedbuck	24	7	3	14	37	4	1	9	99	23.8
Macroscelidea spp.	Elephant shrews	9	21	17	–	3	22	8	6	86	20.7
Potamochoerus larvatus	Bush pig	21	3	2	1	13	4	2	6	52	12.5
Papio cynocephalus	Yellow baboon	9	3	6	6	9	2	1	6	42	10.1
Otolemur crassicaudatus	Greater galago	5	2	7	–	4	1	4	9	32	7.7
Hippotragus niger	Sable antelope	12	–	1	5	–	–	–	–	18	4.3
Tragelaphus scriptus	Bushbuck	5	4	–	–	2	1	–	4	16	3.8
Phacochoerus africanus	Common warthog	13	–	–	–	1	1	–	1	16	3.8
*Genetta*sp.	Genet	–	–	1	2	–	–	–	–	–	–
Civettictis civetta	African civet	2	–	1	2	3	–	–	2	10	2.4
Birds											
Numida meleagris	Helmeted guineafowl	11	3	11	–	4	3	5	6	43	10.3
Francolinus spp.	Francolins	6	2	1	–	–	1	2	2	14	3.4
Reptiles											
Varanus spp.	Monitors	8	4	5	–	4	4	6	23	54	13.0
Kinixys belliana	Bell's hinged tortoise	3	5	2	7	4	5	1	16	43	10.3

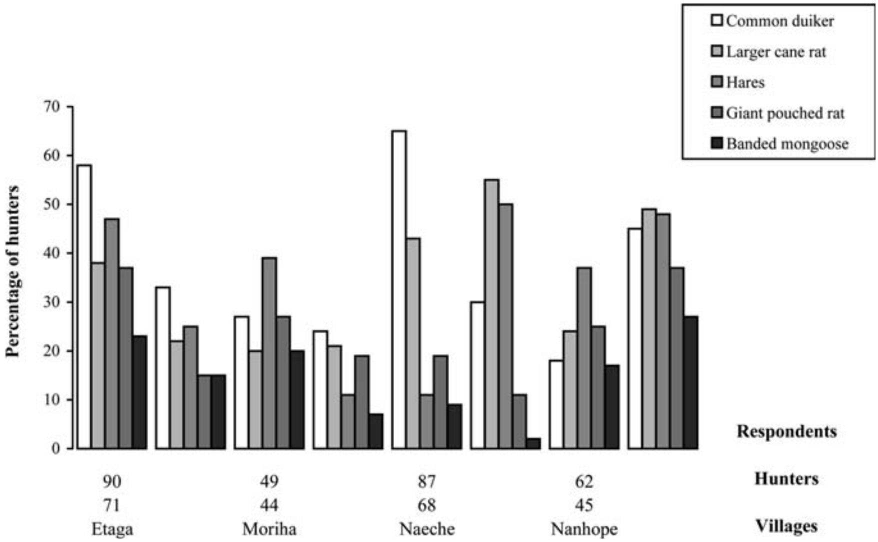

Figure 4. Differences between villages in the percentage of hunters who declared that they exploit a given species.

specimen; southern reedbuck (5.7%) for an average price of 0.97 ± 0.18 USD per kg (Table 4). For a comparison, during our surveys, the price for poultry was 1.3 USD per specimen.

According to the data gathered from 10 hunters of Gile, most quarry was sold (56%), whereas the remainder (44%) was consumed. An average hunter earned circa 29 USD from selling bushmeat over the four month study period. This income was relevant if we consider that the income of an average household per year from crop trade was 49 USD.

Hunting methods

Animals were captured/killed using five different methods: nets (40%, used by 8 hunters); traps (25%, 4 hunters); gin-traps (20%, 5 hunters); spears (12%, 9 hunters), and guns (2.3%, 1 hunter). Two hunters used simultaneously 4 methods, three hunters used 3 methods, four hunters used 2 methods and one hunter use only 1 method (traps). Only one hunter used a lent gun during a single beat. Spears and gin-traps were usually bought from local artisans whereas nets and snares were self-made. The proportion of animals captured during the day (53%) and the night (47%) was very similar. Most animals (96%) was captured within the Reserve.

Netting and trapping activities (including gin-traps) were conducted in groups that varied between 10 and 30 people. Off-take from netting and trapping was shared out among the group members following a complicated

Table 3. The off-take of 10 hunters from the village of Gile during the study period (April–July 2002).

Scientifc name	Common name	*H*1	*H*2	*H*3	*H*4	*H*5	*H*6	*H*7	*H*8	*H*9	*H*10	Total	%
Reptiles													
Kinixys belliana	Bell's hinged tortoise	–	1	1	2	–	–	–	1	–	–	5	1.9
Varanus albogularis	White-throated monitor	–	4	2	3	2	3	–	-	–	–	14	5.4
Birds													
*Francolinus*sp.	Francolins	–	-	–	1	–	2	–	-	–	-	3	1.2
Numida meleagris	Helmeted guineafowl	–	-	–	3	–	2	–	-	–	-	5	1.9
Mammals													
Papio cynocephalus	Yellow baboon	2	6	6	–	2	–	3	2	1	4	26	10.1
Otolemur crassicaudatus	Greater galago	–	-	–	2	2	–	-	–	1	2	7	2.7
Petrodromus tetradactylus	Bush pig	–	-	–	1	–	-	–	-	–	-	1	0.4
Leporidae spp.	Hares	–	2	1	3	2	5	1	2	1	3	20	7.8
Paraxerus cepapi/palliatus	Squirrels	–	2	–	2	1	3	–	-	–	-	8	3.1
Anomalurus derbianus	Lord Derby's anomalure	–	1	–	1	–	1	–	-	–	-	3	1.2
Thryonomys swinderianus	Larger cane rat	2	–	1	4	–	3	1	1	2	2	16	6.2
Cricetomys gambianus	Giant pouched rat	1	1	–	3	2	4	–	1	–	1	13	5.1
Muridae spp.	Wild rats and mice	–	-	–	1	–	-	–	-	–	1	2	0.8
Mungos mungo	Banded mongoose	–	-	–		–	-	1	–	-	1	2	0.8
Atilax paludinosus	Marsh mongoose	–	-	–	1	–	2	–	-	–	-	3	1.2
*Genetta*sp.	Genet	–	-	–	1	–	-	–	-	–	-	1	0.4
Civettictis civetta	African civet	1	–	-	2	–	3	–	-	–	2	8	3.1
Phacocherus africanus	Common warthog	–	-	–	-	–	-	2	2	–	1	5	1.9
Potamochoerus larvatus	Bush pig	4	–	1	–	-	–	4	4	3	4	20	7.8
Tragelaphus strepsiceros	Greater kudu	–	-	–	-	–	-	1	–	1	–	2	0.8
Sylvicapra grimmia	Common duiker	2	6	6	–	4	1	3	3	3	5	33	12.8
Cephalophus natalensis	Natal duiker	1	–	-	–	-	–	-	3	1	3	8	3.1
Neotragus moschatus	Suni	2	2	2	2	1	–	-	2	–	2	13	5.1
Redunca arundinum	Southern reedbuck	3	3	2	–	3	–	2	1	1	4	19	7.4
Kobus ellipsiprymnus	Waterbuck	3	–	-	–	-	–	4	2	1	1	11	4.3
Alcelaphus lichtensteinii	Hartebeest	1	–	-	–	-	–	1	–	-	–	2	0.8
Hippotragus niger	Sable antelope	2	–	-	–	-	–	4	1	–	-	7	2.7
Total		24	28	22	32	19	29	27	25	15	36	257	100

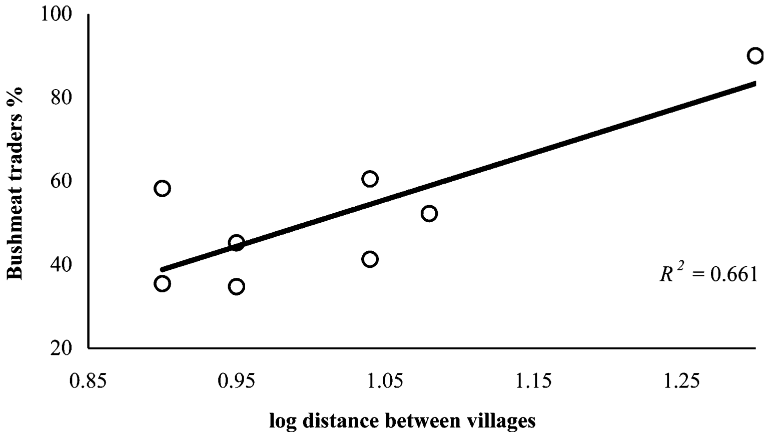

Figure 5. Relation between the percentage of bushmeat traders and the distances between villages.

system of traditional rules (see: Carpaneto 2001, for ethnological details). An average group of 20 hunters captured 24.1 ± 6.7 animals, of which 15 ± 5.8 animals were caught by nets and traps, and 10.6 ± 5.5 by gin-traps. The off-take of an average hunter operating in a group was 4.3 ± 3.8 animals of which: 0.7 ± 0.3 animals captured with nets and various traps; 0.5 ± 0.3 animals captured with gin-traps; 3.8 ± 3.7 animals with spears. On the other hand, an average hunter who only operated by himself captured 29.3 ± 2.5 animals over the same period, using mainly snares and sometimes a spear. Highly significant differences between hunters were recorded in the average

Figure 6. Relation between the percentage of bushmeat traders and crop producers.

Table 4. The most commercialized prey items and their average price in USD (±S.D.).

Taxon	Common name	Etaga	Gile	Moriha	Naeche	Namurrua	Nanhope	Nassile	Total	%	Price USD
Thryonomys swinderianus	Larger cane rat	20	16	13	31	16	13	34	143	34.4	0.73 ± 0.43 each
Leporidae spp.	Hares	19	17	19	–	18	19	30	122	29.3	0.78 ± 0.07 each
Sylvicapra grimmia	Common duiker	6	24	11	8	11	–	21	81	19.5	0.75 ± 0.1 per kg
Cricetomys gambianus	Giant pouched rat	11	9	10	11	3	12	23	79	19.0	0.46 ± 0.12 each
Redunca arundinum	Southern reedbuck	–	7	–	17	–	–	–	24	5.8	0.97 ± 0.18 per kg

number of animals captured (One-way ANOVA, $F_{9,107} = 30.9$, $p < 0.01$). Numerically, the average off-take of a solitary hunter was more than six times the off-take of a group-operating hunter. Nevertheless, collective hunting allowed the capture of larger animals, e.g. large ungulates, whereas solitary hunters obtained mostly small animals, such as rodents, hares, small antelopes, birds and tortoises. A biomass comparison between the booty of solitary and collective hunting, based on the animal weight reported by several authors (Skinner and Smithers 1990; Kingdon 1997; Bothma 2002) showed that the prey body mass was always higher from the latter (Table 5). However, in the study area hunters operated either in-group or alone. We did not consider in the previous analyses the off-take obtained with the gun (2.3% of total) because only one hunter (who was not the owner of the weapon) used it during only one hunting beat. Moreover, no one of the 510 householders reported to use guns, highlighting its scarce relevance as hunting tool.

Discussion

In many African countries, bushmeat is largely traded and represents a primary source of income for rural people (Juste et al. 1995). In recent years, there was a progressive and important transition from subsistence to commercial hunting, essentially because of the increase in human population density, the modernisation of hunting techniques and a greater accessibility to remote forest areas (Wilkie and Carpenter 1999; Fa and García Yuste 2001). In this context, the present study underlines the importance of subsistence hunting and bushmeat trade for villagers settled around GRG. This protected area is threatened by the increasing rural population, the persistent lack of management and a better accessibility to the forested area, due to the construction and/or rehabilitation of roads for logging and mining.

Results of the regression analyses showed that the proportion of householders who declared to have harvested game is not correlated to the geographical location of the village but is inversely correlated with village size. These results can be explained as follows: (1) the distance from the Reserve border did not prevent hunting because of the importance given to this activity; (2) hunting expeditions are arranged by villagers who spend several days within the Reserve

Table 5. Number and percentage of animals captured over four months during solitary and collective hunting, in relation to their body mass (animal mass was obtained from Skinner and Smithers 1990; Kingdon 1997; Bothma 2002).

Body mass	Solitary hunting	Collective hunting	Total
Less than 5 kg	53 (60.2%)	42 (24.9%)	95 (36.9%)
Between 5 and 30 kg	17 (19.3%)	79 (46.7%)	96 (37.4%)
More than 30 kg	18 (20.5%)	48 (28.4%)	66 (25.7%)
Total	88 (100%)	169 (100%)	257 (100%)

hunting and smoking bushmeat; (3) large villages offer alternative livelihood strategies such as trade and labour, whereas small villages are more dependent on natural resources including bushmeat; (4) the depletion of game around large villages induced a decrease in hunting activity because it became unprofitable. However, the proportion of hunters in each village was positively correlated to crop production. Such a result led us to consider that: (1) hunting is not an alternative to agricultural production because crops, such as starch foods and vegetables, cannot replace meat protein; (2) an increase in crop production may facilitate the purchase of hunting equipments (cartridges, gin-traps and nets). Most villagers interviewed (78.5%) hunted and fished, revealing the importance of these activities that appeared to be not alternative but complementary.

The species most commonly harvested by householders were all mammals and included antelopes, hares, large rodents and carnivores (mongooses). The geographical location of villages and their size were not correlated with proportions hunted of each species, which can be ascribed to the different hunting techniques adopted. Within his four month booty, an average hunter secured 2.9 wild ungulates (antelopes and wild pigs), the equivalent of 50% of domestic ungulates (goats and pigs) kept by an average householder. Thus, wild meat was the main animal protein source for local people during the study period.

According to data gathered from all householders and ten Gile hunters, the four most captured species were also the most traded. The remoteness of a village was associated with a more intensive bushmeat trade: small and remote villages did not offer alternative activities to generate money. A further explanation is given by the surplus of game hunters harvested from these less inhabited areas. The bushmeat trade was positively correlated with crop production, once more underlying that hunting and agricultural development were not alternative strategies for subsistence in the study area. The profits obtained by the ten hunters of Gile during four months (circa 29 USD) revealed that bushmeat trade was probably the most relevant income source for local people, exceeding the revenue derived from crop trade on annual basis (circa 49 USD). The use of firearms has declined mainly because of the high cost of cartridges and maintenance. Hunters almost exclusively used nets and traps (including gin-traps) either alone or in a group. Lone hunters captured a higher proportion of small animals but les medium-sized animals, in contrast to hunters who operated in group, while the proportion of larger animals was similar. In fact, small animals were mainly captured by traps adopted in great number during solitary hunting; many medium-sized animals were captured in collective net hunting; larger mammals were captured by gin traps used during both solitary and collective hunting. Hence, local hunters adopted both strategies, to increase diversity of preys and their body mass range. According to the ten hunters from Gile, 96% of the animals was captured within the Reserve, revealing the importance of the protected area as a source of bushmeat for rural people, but at the same time, underlining the threat represented by subsistence hunting for wildlife conservation.

Conclusions

The patterns of wildlife exploitation derived from the present research are likely valid for all the rural communities close to and within miombo woodland ecosystems in Zambezia. Hunting is an important livelihood strategy for people and bushmeat represents the major animal protein supply, owing to scarcity of domestic animals. Local hunters adopt essentially trapping techniques and collective net hunting. Gin-traps are largely used and destructive, but the use of fire-weapons declined. The results indicate that smaller the village, higher is the proportion of hunters. Hence, patrolling activities for poaching control should be mainly conducted in small villages. As hunting activity is not dependent on the distance between villages and the Reserve borders, all the householders within a radius of 20 km need to be considered as possible harvesters of faunal resources within protected areas. Moreover, our data show that hunting activities and bushmeat trade are not alternative to agriculture practices as livelihood strategies. The results indicate that a mere increase of crop production in the study area (pursued by many conservation projects as a strategy to diminish the impact of subsistence hunting) would not produce an effective decrease of bushmeat exploitation. Wildlife represents the most relevant protein source for the villagers and also an important income for local bushmeat traders. An average bushmeat trader can earn a relevant income, larger than crop trader, because the off-farm profit opportunities are practically inexistent. To prevent wildlife exploitation other ways should be explored, e.g. to assess the potentiality of local pastures for cattle grazing out of the protected areas, and to develop projects for improving the people's knowledge of cattle rearing. All these considerations should be taken into account by the reserve authorities of Zambezia's protected areas and NGOs, for planning future projects of sustainable development.

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References

Alvard M.S., Robinson J.G., Redford K.H. and Kaplans H. 1997. The sustainability of subsistence hunting in the Tropics. Conserv. Biol. 11: 977–982.

Barnes R.F.W. 2002. The bushmeat boom and bust in west and central Africa. Oryx 36: 236–242.

Bellamy R. 1993. Ethnobiology in Tropical Forests. Royal Geographical Society, London, UK.

Bennett E.L., Milner-Gulland E.J., Bakarr M., Eves E.H, Robinson G.J. and Wilkie D.S. 2003. Hunting the world's wildlife to extinction. Oryx 36: 328–329.

Bothma J.P. 2002. Game Ranch Management. Van Schaik Publishers, Pretoria, RSA.

Carpaneto G.M. 1994. Parc National d'Odzala: ethnozoologie, faune et ecotourisme. Rapport Final. Republique du Congo - Ministère des Eaux et Forêts, AGRECO/CTFT, Bruxelles, Belgium.

Carpaneto G.M. 2001. The Sustainable Exploitation of Wildlife in the National Reserve of Gile ("Reserva do Gilé", Zambezia, Mozambique). Final Report. Movimondo, Rome, Italy.

Carpaneto G.M. and Fusari A. 2000. Subsistence hunting and bushmeat exploitation in central-western Tanzania. Biodivers. Conserv. 9: 1571–1585.

Chande B., Zolho R., Chidiamassamba C., Longamane F. and Cumbane R. 1997. Reconhecimento bio-ecològico da Reserva do Gilé. Ministério para a Coordenação da Acção Ambiental-MICOA, Maputo, Mozambique.

Chidumayo E.N. 1997. Miombo Ecology and Management: an Introduction. Intermediate Technology Publications, London, UK.

Colell M., Maté C. and Fa J.E. 1994. Hunting among Moka Bubis in Bioko: dynamics of faunal exploitation at the village level. Biodivers. Conserv. 3: 939–950.

DNFFB 1995. Mapa Florestal da Provincia da Zambézia. Direção National de Floresta e Fauna Bravia, Maputo, Mozambique.

Dutton T.P., Dutton E.A.R. and Balsinhas A. 1973. Preliminary Ecological Reconnaissance of the "Reserva Especial do Gilé" and the Adjoining "Regime de Vigilancia", District of Zambezia. Report for the Servicio de Veterinaria de Moçambique, Maputo.

Fa J.E., Juste J., Del Val J.P. and Castroviejo J. 1995. Impact of market hunting on mammal species in Equatorial Guinea. Conserv. Biol. 9: 1107–1115.

Fa J.E. and García Yuste J.E. 2001. Commercial bushmeat hunting in the Monte Mitra forests, Equatorial Guinea: extent and impact. Anim. Biodivers. Conserv. 24(1): 31–52.

Fa J.E. and Peres C. 2001. Hunting in tropical forests. In: Reynolds J.D., Mace G.M., Redford K.H. and Robinson J.G. (eds), Conservation of Exploited Species. Cambridge University Press, Cambridge, UK, pp. 203–241.

Fitz Gibbon C.D., Mogaka H. and Fanshawe J.H. 1995. Subsistence hunting in Arabuko-Sokoke Forest, Kenya, and its effects on mammal populations. Conserv. Biol. 9: 1116–1126.

Fusari A. 2002. Utilization of the Indigenous Resources by Dwelling People in the National Reserve of Gile (Zambezia Province-Mozambique). Final Report. Movimondo, Rome, Italy.

Galego J.L. 2002. Caterpillars, Traps and Bees: Livelihood Dependence on Wild Resources in the National Reserve of Gile. Final Report. Movimondo, Rome, Italy.

Galego J.L. and Rasul I. 2001. Baseline Survey (Food Security Programme in the Districts of Ile and Gile, Zambezia Province-Mozambique). Final Report. Movimondo, Rome, Italy.

INE 1997. II Receseamento Geral da População e Habitação. Instituto Nacional de Estatística, Maputo, Mozambique.

IUCN 1998. Mozambique Bush Meat Trade Study Report. IUCN Mozambique's Consultancy for the TRAFFIC East/Southern Africa (TESA). IUCN, Maputo, Mozambique.

Juste J., Fa J.E., Del Val J. and Castroviejo J. 1995. Market dynamics of bushmeat species in Equatorial Guinea. J. Appl. Ecol. 32: 454–467.

Kingdon J. 1997. The Kingdon Field Guide of African Mammals. Academic Press, London, UK.

Kock R.A. 1995. Wildlife utilization: use it or lose it - a Kenyan perspective. Biodivers. Conserv. 4: 241–256.

Lahm S.A. 1993. Utilization of forest resources and local variation of wildlife populations in Northeastern Gabon. In: Hladik C.M., Linares O.F., Pagezy H., Semple A. and Hadley M. (eds), Tropical Forests, People and Food. UNESCO, Paris, France, pp. 213–226.

Ling S., Kümpel N. and Albrechtsen L. 2003. No new recipes for bushmeat. Oryx 36: 330.

Marks S.A. 1994. Local hunters and wildlife surveys: a design to enhance participation. Afr. J. Ecol. 32: 233–254.

Martines A. and Ntumi C. 2002. Plant Diversity, Vegetation Ecological Status, Spatial and Temporal Movements of Elephants and Economic Value of Natural Resources in the National Reserve of Gile, Zambezia Province-Mozambique. Final Report. Movimondo, Rome, Italy.

Robinson G.J. and Bennett E.L. 2003. Will alleviating poverty solve the bushmeat crisis? Oryx 36: 332.

Skinner J.D. and Smithers R.H.N. 1990. The Mammals of the Southern African Subregion. University of Pretoria Press, Pretoria, RSA.

Trollope W.S.W. and Trollope L.A. 2002. Fire Management Program for the National Reserve of Gile in Zambezia Province, Mozambique. Final Report. Movimondo, Rome, Italy.

van Aarde R.J. 2002. The Potential for Game Farming and the Rehabilitation of Wildlife Resources in the National Reserve of Gile (“Reserva do Gilé”, Zambezia, Mozambique). Final Report. Movimondo, Rome, Italy.

White F. 1983. The Vegetation of Africa. UNESCO, Paris, France.

Wilkie D.S., Sidle J.G. and Boundzanga G.C. 1992. Mechanized logging, market hunting and a bank loan in Congo. Conserv. Biol. 6: 1–11.

Wilkie D.S. and Carpenter J.F. 1999. Bushmeat hunting in the Congo Basin: an assessment of impacts and options for mitigation. Biodivers. Conserv. 8: 927–955.

Ziegler S. 1996. An initial study of hunting in the Upper Niger National Park. Wildlife Nat. 4: 13–28.

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The catch and trade of seahorses in Vietnam

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Abstract. Catch monitoring and surveys were used to assess the seahorse trade in Vietnam. Despite low daily catch rates, potentially 6.5 t of dried seahorses (~2.2 million seahorses) were taken annually as bycatch by trawlers operating out of five coastal provinces of Vietnam. Individual seahorse catches were collated by a few local buyers, who supplied wholesalers in three major markets: Ho Chi Minh City, Hai Phong City and Da Nang. Domestic consumption was small and most seahorses were exported, generally through unofficial and unregulated channels across the northern border into Guangxi province of China. Overall, the seahorse trade was of low economic value to Vietnam, but may constitute an important source of income to upper level buyers and exporters. Most fishers and buyers surveyed reported that seahorse catch had declined over time. This paper should help in meeting the new CITES requirements – through implementation of an Appendix II listing in 2004 – that all international trade in seahorses must be monitored and managed for sustainability.

Introduction

Seahorses (genus *Hippocampus*) are rarely subject to fisheries management or monitoring, despite an international trade that consumes millions of these fishes, dried for use in traditional medicine (TM) and as curios, and live for display in aquaria (Vincent 1996). Seahorses are caught, directly or indirectly, in fisheries around the world, ranging from small-scale hand collectors to by-catch in commercial shrimp trawlers (Vincent 1996). The trade, therefore, is often diffuse and difficult to track, involving many participants over many regions. Moreover, these fisheries are often considered small-scale, both in terms of catch volumes and economic value, and are rarely of concern to traditional fisheries management bodies. Seahorses are also emblematic of many other species threatened by small-scale fisheries for markets such as traditional medicines, aquarium species, and luxury foods (Wood 1985; Lau and Parry-Jones 1999; Sadovy and Vincent 2002; Pajaro et al. 2004). The high value placed on some of these species, and the fact that value may increase with rarity, provides increased incentives for over-exploitation (Sadovy and

Vincent 2002). These fisheries may also generate high economic value for low volume and contribute much needed income for local communities in developing nations (Pajaro et al. 1997; Sadovy and Vincent 2002).

Official statistics and trade surveys have highlighted an increased pressure on global seahorse populations. The global trade in seahorses increased from the 1980s, in part due to increased demand created by economic growth in Asia, and in part due to increased supply of seahorses from bycatch in the world's growing trawl fisheries (Vincent 1996). Surveys of fishers have suggested that seahorse populations have declined during this time in at least some areas of the world (Vincent 1996). In addition, these fishes are threatened by degradation of their sensitive coral, seagrass and mangrove habitats (Hodgson 1999). In May 2004, in recognition of threats to their conservation status, seahorses were added to Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). Signatories to the convention are now compelled to monitor international trade and source countries will need to ensure that exports are non-detrimental to the long-term persistence of wild populations.

Vietnam is reportedly a supplier of dried seahorses, although little is known about the nature and size of the trade, or the status of its seahorse populations. Unregulated (by)catch and export of seahorses was previously reported for Vietnam, though such data rarely showed up in official Customs records of the main dried seahorses importing nations (Vincent 1996). Past surveys suggested most of the trade went unrecorded across the northern border into China (Vincent 1996). A large, and often unregulated, trade of other wildlife across the Vietnam border into China, particularly to the province of Guangxi, has been documented (Li Wenjun et al. 1996; Li Yiming and Li Dianmo 1998).

There are seven species of seahorses known from Vietnam's waters, based on the recently revised morphological and genetic taxonomy of Vietnamese seahorses (Lourie et al. 1999a), which may still not be definitive. As a genus, seahorses live among seagrasses (*Thalassia* spp.) and corals and in estuaries along the coast of Vietnam (Dao Xuan Loc and Hoang Phi 1991). All seahorse species were marketable but here the focus is on the three species that were most widely encountered in trade; *Hippocampus spinosissimus, H. trimaculatus* and *H. kuda*. The species now identified as *H. spinosissimus* was previously and incorrectly called *H. histrix* in most publications (e.g. Truong Si Ky and Ton Nu My Nga 1995; Do Huu Hoang et al. 1998). The Red Data Book lists four seahorse species as Vulnerable in Vietnam [*Hippocampus histrix* (may be *H. spinosissimus), H. kelloggi, H. kuda* and *H. trimaculatus*] (Ministry of Science, Technology, and Environment 1992).

We here report on the structure, potential magnitude and significance of the Vietnamese catch and trade of seahorses, in order to guide directions for management, particularly in light of the new CITES requirements.

Methods

Information on the Vietnam seahorse fishery was collected from three sources; (1) biological measurements of a sample of seahorses landed at Cua Be estuary (Khanh Hoa province), (2) informal fishery and trade surveys and (3) catch monitoring. Results from these sources were combined to give an overall picture of the Vietnam seahorse fishery from landings through domestic trade to exports.

Biological measurements

A sample of seahorses, landed as bycatch at Cua Be (located within the larger city of Nha Trang, Khanh Hoa province), were measured (wet) to obtain biological information (Figure 1). The data for *H. spinosissimus* and *H. trimaculatus* were derived from the period June 1995 to May 1996 and thus represented an annual sampling. So few *H. kuda* were landed as bycatch that we extended our measurements from June 1995 to March 1998. Seahorse

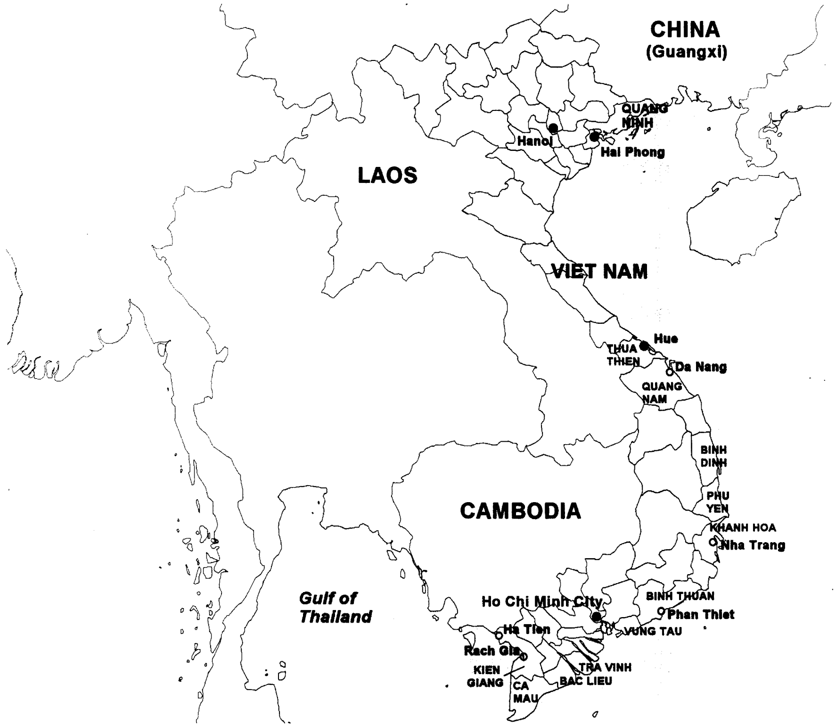

Figure 1. Map of Vietnam showing study locations and sites mentioned in text.

standard length (SL), the total length from the snout tip to where the opercular ridge and mid-line meet to the tail tip, was measured with calipers (Lourie et al. 1999b). Weight (Wt) was measured for freshly caught seahorses.

Fishery and trade surveys

Between 1995 and 1999, two Vietnamese biologists conducted semi-structured, informal interviews with 206 fishers and 95 buyers in a total of 10 provinces (Figure 1), asking about the seahorse species caught, catch locations, trade routes, volumes caught (traded), prices and temporal trends in supply. Additional information was obtained from interviews with fisheries scientists and casual surveys of traditional medicine and marine products shops. Data were supplemented with reports from trade interviews and Customs data from other countries.

Surveys were used to produce (a) a qualitative description of the seahorse fishery and trade, (b) quantitative estimates of trade volumes and prices and (c) a description of the perceived temporal trend in seahorse landings. The informal nature of the surveys made it difficult to collect quantitative data rigorously, as not all respondents were asked, or chose to respond, to all questions. Where quantitative data are presented, sample sizes indicating the number of respondents are provided. No attempt was made to address possible sources of error or bias in survey responses, such that data provide only a preliminary description of the Vietnam seahorse trade.

Catch monitoring

The diffuse and unregulated nature of the Vietnam fishery complicated our survey with many small, unregistered vessels operating out of many ports along the coastline of Vietnam. For this study we focused on the bottom trawl 'fishery', consisting of a widespread fleet of differing vessel and net size, but with reportedly common fishing areas, depths, times and target species. At the time of survey, most vessels encountered were engaged in bottom trawling (Do Huu Hoang pers. obs.).

From initial trade and fishery interviews, four main ports for seahorse landings (in four provinces) were identified for direct bycatch monitoring; Phan Thiet (Binh Thuan), Rach Gia (Kien Giang), Ganh Hao (Bac Lieu) and Song Doc (Ca Mau) (Figure 1). Ports were surveyed from 2 to 4 occasions (see Table 1 for exact years for each port) between 1995 and 1999. On each visit, the researchers visited as many trawlers as possible, while vessels were unloading their catch after returning to port. Researchers recorded the number of seahorses taken as bycatch and retained by fishers.

Recorded landings and reported trip durations were used to calculate catch per unit effort (CPUE) (seahorses day^{-1} boat^{-1}). Mean catch per unit effort

Table 1. Catch per unit effort (CPUE) ± standard error (seahorses day^{-1} boat^{-1}), number of boats monitored (n) and reported total provincial fleet size for four provinces in southern Vietnam.

Year	Binh Thuan			Ca Mau			Bac Lieu			Kien Giang		
	CPUE	*n*	Fleet	CPUE	*n*	Fleet	CPUE	*n*	Fleet	CPUE	*n*	Fleet
1995	0.35 ± 0.10	94	5370							2.13 ± 0.15	17	2799
1996	1.08 ± 0.28	51	5370	0.80 ± 0.19	15	314	2.50 ± 0.13	16	355	1.90 ± 0.10	19	3037
1997				0.33 ± 0.12	18	400	1.43 ± 0.33	15	450	2.11 ± 0.37	19	2962
1998							0.25 ± 0.15	15	500			3018
1999							1.34 ± 0.11	12	200	1.76 ± 0.46	17	

($\bar{C}$) for the monitored port was assumed to be representative of the entire province and was extrapolated to estimate total annual bycatch using reported provincial fleet sizes (F) (Vietnam Fishery Service data) and a measure of annual vessel effort (E), taken from Project Seahorse surveys, of 20 days per month × 10 months per year = 200 days per year. A constant effort was assumed for all provinces and years. Total seahorse bycatch (B) for each province (i) and year (t) was calculated as

$$B_{it} = \bar{C}_{it} \cdot F_{it} \cdot E \tag{1}$$

This calculation resulted in the number of seahorses, which was then converted to kilograms using a value of 350 dried seahorses per kg, an average value obtained in global trade surveys (unpubl. data). Small variations in CPUE may be magnified by the large extrapolation, resulting in highly variable estimates of total catch. So for each extrapolation, a range was calculated using the 95% confidence limits for the observed $\bar{C}_{it}$, in order to provide an indication of the potential effect of variation in $\bar{C}$ on the total bycatch estimates.

Estimates of catch volumes must be interpreted cautiously due to the large extrapolations involved and the unknown sources of variation. Provincial estimates were based on a fleet size taken from government records and a constant fishing effort from surveys, both of unknown accuracy and variation. Government records were more likely to underestimate fleet sizes as the number of registered vessels at any port was generally less than the actual number operating (Do Huu Hoang pers. obs). Variation in CPUE rates among ports within a province was not quantified and we cannot be certain our monitored ports were representative of the entire province. Confidence limits provided reflect only variation in observed daily catch rates at monitored ports. Catch estimates are meant to assess the potential magnitude of the trade rather than be estimates of the actual annual landings. Due to the high level of uncertainty, we have not attempted to infer temporal trends in catch estimates and individual years are used as replicates to calculate average annual catch for each province.

Results

Description of seahorse fishery from surveys and biological monitoring

Three main species were identified by the authors in the bycatch of Vietnamese trawlers at Cua Be; *Hippocampus spinosissimus* ($n = 552$, SL ± sd = 128.3 ± 26.7 mm, Wt ± sd = 6.8 ± 4.2 g), *H. trimaculatus* ($n = 606$, SL ± sd = 133.3 ± 19.8 mm, Wt ± sd = 6.5 ± 4.1 g) and *H. kuda* ($n = 65$, SL ± sd = 131.0 ± 25.6 mm, Wt ± sd = 6.5 ± 4.0 g). Pregnant males of all three species were caught during all months, indicating year round breeding for the species, although any given individual may have bred for only part of each year.

The vast majority of landed seahorses was reportedly obtained as bycatch by trawlers targeting shrimp and demersal fish in inshore waters (less than 30–50 m deep) at night, according to interviews with fishers. Peak catch was reportedly between January and September. Trawl fishers in most ports in southern and central Vietnam, operating in the South China Sea or Gulf of Thailand, identified *H. trimaculatus* as the most commonly caught seahorse, followed by *H. spinosissimus*. Biological monitoring at Cua Be estuary, however, encountered relatively equal numbers of the two species (*H. trimaculatus* = 606; *H. spinosissimus* = 552). Only fishers based in Ha Tien (Kien Giang province) reported catching large numbers of *H. kuda*, mainly near the border with Cambodia. Few seahorses were reported in bycatch of trawlers operating in the Gulf of Tonkin in northern Vietnam. A small number of seahorses, mostly *H. kuda*, were hand-caught by swimmers or divers, often adolescents out to collect anything of value in estuaries, such as near Cua Be.

Catch monitoring rates and volumes

Despite low individual CPUE rates, the total fishery may have landed tonnes of seahorses annually in southern and central Vietnam. Individual trawlers caught on average <1 to slightly more than 2 seahorses per day (Table 1). Catch rates were highest for trawlers in the most southern provinces of Bac Lieu and Kien Giang, though still only at 1–2 seahorses per day (Table 1). However, given the large fleets reportedly operating, particularly for Kien Giang and Binh Thuan, there was potential to land large volumes of seahorses annually (Table 2). Overall provincial averages (and 95% CI), calculated from annual estimates of bycatch, were summed to produce an estimate of average total catch. Monitoring in four provinces suggested a combined average annual bycatch of 5900 kg (3227–8559 kg) (Table 2). In addition, earlier catch monitoring recorded annual bycatch of 500–600 kg in Khanh Hoa province (Vincent 1996), resulting in the estimated total bycatch of 6.5 t, or 2,275,000 individuals per year for five provinces.

Table 2. Mean annual seahorse bycatch and 95% confidence intervals (kg dried weight) for four provinces in southern Vietnam, and the provincial average and 95% confidence intervals calculated for all years monitored.

Year	Binh Thuan		Ca Mau		Bac Lieu		Kien Giang	
	Mean	95% CI	Mean	95% CI	Mean	95% CI	Mean	95% CI
1995	1074	483–1665					3407	2930–3884
1996	3314	1647–4981	144	76–211	507	455–559	3297	2947–3648
1997			75	21–130	368	204–532	3575	2362–4787
1998					71	0–154		
1999					153	138–178	3035	1478–4593
Provincial	2194	0–4389	110	41–179	275	79–441	3329	3107–3550

Data were extrapolated from CPUE rates observed in catch monitoring to the total provincial fleet.

Unknown volumes of seahorses were caught incidentally in other southern and central provinces. Direct catch monitoring was conducted in only 5 of 23 coastal provinces. Fishers, however, reported bycatch and trade of seahorses in Quang Nam ($n = 8$), Phu Yen ($n = 12$), Thua Thien ($n = 11$), and Vung Tau provinces ($n = 2$), albeit in lower numbers (CPUE = 0.13–0.88 seahorses day^{-1} boat^{-1}). Buyers in Da Nang (Quang Nam province) also cited the province of Binh Dinh as a source of seahorses. Fishers ($n = 2$) in the southern province of Tra Vinh gave questionably high bycatch rates (50 seahorses day^{-1} boat^{1}), but reported no trade in seahorses.

Trade routes from surveys

Dried seahorses caught in southern and central Vietnam were sent to three major markets within Vietnam; Ho Chi Minh City (HCMC), Hai Phong City and Da Nang, primarily for export to China (Table 3). The trade was generally concentrated through a small number of upper level buyers, who purchased from lower level local buyers or directly from fishers, and in turn supplied exporters. The main buyers in Khanh Hoa and Binh Thuan sent seahorses to all three markets, as well as possibly exporting directly to China. Most seahorses caught in Kien Giang and neighbouring Bac Lieu and Ca Mau, apparently went through one of three upper level buyers in Kien Giang, before being sent to Ho Chi Minh City. Buyers in Kien Giang, however, cited increased instances of agents from Ho Chi Minh coming to buy directly from fishers. Some seahorses from Bac Lieu and Ca Mau were also sent to buyers in Vung Tau province or directly to exporters in Ho Chi Minh or Hai Phong. Buyers in Vung Tau and reportedly those in Binh Dinh sent seahorses to Da Nang.

Few exporters ($n = 6$) were located during surveys, but those interviewed listed mainland China as the main destination for their dried seahorses. Buyers in Bac Lieu also stated they sold to Taiwanese operating out of Da

Table 3. Dried seahorse trade routes, trade volumes and number of respondents (n) from surveys of (a) upper level buyers in main source provinces surveyed and (b) exporters located.

Source	Destinations						Annual Volume (kg)	n
	China	HCMC	Haiphong	Da Nang	Vung Tau	Kien Giang		
(a) *Buyers*								
Binh Thuan		x		x			240–1000	5
Khanh Hoa	x	x	x	x			458	4
Kien Giang							1500–3000	3
Vung Tau				x			150–200	4
Bac Lieu[a]		x	x		x	x	200–400	3
Ca Mau[a]		x	x			x	50–100	1
Binh Dinh				x			?	?
Total							2348–4658	
(b) *Exporters*								
Ho Chi Minh City	x						400–550	2
Haiphong	x						240–300	3
Da Nang	x		x				900	1
Total							1540 – 1750	

Volumes were taken from most recent survey available between 1995 and 1999.

[a] Excluded from calculation of total volume traded, as they sent unknown volumes of dried seahorses to Kien Giang and Vung Tau.

Nang, and Taiwan Customs listed limited imports from Vietnam; 121 ± 111 kg per year between 1990 and 2002 (Republic of China (Taiwan) Statistics). Reciprocally, survey participants in China ($n = 12$) cited Vietnam as the major source for dried seahorses in interviews conducted in 1999 and 2000 (Project Seahorse, unpubl. data). Importers in Hong Kong and Taiwan also cited Vietnam as a source of dried seahorses in trade surveys conducted in those areas (Vincent 1996), though Vietnam was not listed in official Customs data for Hong Kong . Most seahorses sent to China were reportedly traded across the border at Mong Cai into Guangxi province or transferred to Chinese fishing vessels at sea. The trade reportedly began in 1988 but only became legal following the normalization of relations between China and Vietnam in 1991. Most trade remained 'unofficial' in that it was conducted among individual enterprises rather than through Government companies.

Domestic consumption from surveys

Small numbers of seahorses were consumed in Vietnam as traditional medicines, to cure general health problems and impotence and as an aphrodisiac. Seahorses and their derived products were sold through Traditional Chinese Medicine (TCM) outlets in Hanoi, Ho Chi Minh City and Quang Ninh City, and in the dry marine product market in Ninh Trang. Seahorses were also sold domestically as tonics, reportedly in order to assist the kidneys and invigorate general health (which often means the same thing in TCM), increase sexual potency and cure rheumatism and lumbago. Seahorses for tonic purposes were either sold fermented in alcohol in commercially prepared, ready-made tonics, or live for incorporation into alcohol-based tonics at home. The shops surveyed reported small annual sales, combined for a total annual domestic consumption of only 103–121 kg (Table 4). While more markets and shops may sell seahorses in Vietnam, surveys indicated that most seahorses landed were exported rather than consumed domestically.

Table 4. Domestic sales of dried seahorses based on surveys of retailers located in four major markets, showing estimated number of shops selling dried seahorses reported average sales per shop and calculated total annual sales for the city.

City	Shops (*n*)	Sales per shop (kg per annum)	Total Annual Sales (kg)
Ho Chi Minh City	25–30	0.5–1	12.5–30
Hanoi	11	0.4–0.5	4.4–5.5
Quang Ninh City	8	2	16
Nha Trang	28	2.5	70
Total			103–121

Export volumes from surveys

The vast majority of seahorses traded were reportedly exported. Total trade volume within Vietnam can therefore serve as an estimate of annual exports. While trade initially went through a large number of lower buyers, it was generally concentrated through a few upper level buyers in each province. Therefore, the total annual volume of the dried seahorse trade was estimated from the reported volumes of the upper level buyers identified in the source provinces who sent seahorses to exporters, Upper level buyers located in Kien Giang, Vung Tau, Khanh Hoa and Binh Thuan reported no trade amongst themselves so their volumes can be considered independent and may be summed (Table 3). Trade from Bac Lieu and Ca Mau was excluded from the total to avoid duplication, as an unknown portion may have gone to the buyers in Kien Giang and Vung Tau, though some went directly to exporters. For each province, we used the buyers' volumes from the most recent year. Annual values were not compared as the number of buyers surveyed varied among years, either because of changes in trade participation or in sampling effectiveness.

Upper level buyers ($n = 20$) sent an estimated 2348–4658 kg of dried seahorses each year to the main exporting centres (Table 3). Buyers in Kien Giang and Binh Thuan reported the largest volumes (Table 3), consistent with the provinces' respective estimated bycatch volumes (Table 2). The total volume traded by interviewed buyers was of a similar magnitude as the estimated total annual bycatch in the five provinces monitored (3700–9100 kg).

Annual export volumes (1540–1750 kg) calculated from exporters' information ($n = 6$) were considerably lower than volumes calculated from buyers' information (Table 3), probably because we didn't locate all exporters.

Economic values from surveys

Seahorses from Vietnam were considered high quality by TCM practitioners in other Asian countries because of their smoothness (Vincent 1996). Prices paid to fishers depended on size and type but were generally low and apparently declined during the study period (Table 5), for unknown reasons. Overall, trawl fishers were not particularly interested in seahorses, as the small catches contributed less than 5% of the trawlers' annual income, according to surveys, though divers targeting seahorses reported earning up to 35% of their annual income from seahorses.

On average, primary buyer maximum sell prices were 27% higher (range 0–100%) than the maximum prices (per kg) paid to fishers for the same area and year (Table 5). The reported prices paid to buyers at Ganh Hao Port in 1998 and 1999 were suspect as they were below the reported price paid to fishers. The decline in fisher sell price was mirrored in buyer sell price. The decline was most apparent in Rach Gia Port (Kien Giang) and Ganh Hao (Bac Lieu), the sites with the longest monitoring periods (Table 5). Upper level buyers who

Table 5. Sell and purchase prices (VND1000) for dried seahorses reported by fishers, primary buyers and upper level buyers in surveys conducted around Vietnam (1995–1999).

Province	Location	Year	Fishers	Primary buyers		Major buyers		
			Sell price (per SH)	Sell price (per kg)	Purchase Price (per SH)	Sell price (per kg)	Sell price by size Class (per kg)	Size Class (cm)
Kien Giang	Ha Tien	1996					1400; 1600	8–15; > 15
		1997			0.5–1.5	500–1200	500–800; 1100–1500	small; large
		1998			0.5–1.5	500–1300	500–800; 1100–1500	small; large
		1999	0.5–2	175–700	0.5–1.5	500–1400	1100–1200; 1400	6–10; 10–12
	Rach Gia	1995	4–7	1200–1300		1400–1450	1470	
		1996	3–7	1200–1400		1450–1600	1550	
		1997	2–3	700–1100		1000–1200	1200–1400	
		1999		625–1000	1–2	1000–1300	1300–1500	
	Rach Soi	1996		1000–1200	2–3	1500–1700		
	Tac Cau	1997				1500–1600		
Bac Lieu	Ganh Hao	1995			0.5		300–700	
		1996	1.5–3	700–800	0.5	1100–1200	1300	
		1997	0.5–1.5	175–525	0.5–1	350–700	300–500; 670–750; 900–1200	5–6; 6–11; 12–15
		1998	0.5–1.5	175–525		175–700	900–1300	
		1999	0.5–2	175–700	1–2	175–700	900–1300, 1400	unknown; 9–11
Ca Mau	Song Doc	1996	2–5	1000–1200		1200–1300	900–1250	
		1997	0.5–1.0	175–350	0.5–1.5			
Khanh Hoa	Nha Trang	1996					1650–1800	
HCMC	Ho Chi Minh City	1996	5–7	1750		800–1200		
Vung Tau	Vung Tau	1996	2–3	700–950			1400	
Binh Thuan	Phan Thiet	1995	3–10	1200–1500		1450–1550	1400	
		1996	2–8	100–1300		1350–1500		
		1997	2–3	400–950				

Table 5. Continued.

Province	Location	Year	Fishers	Primary buyers		Major buyers		
			Sell price (per SH)	Sell price (per kg)	Purchase Price (per SH)	Sell price (per kg)	Sell price by size Class (per kg)	Size Class (cm)
Quang Nam	Da Nang	1995					1600; 2500; 3200	< 15; 15–20; > 20
Hanoi		1995					2200–2300	
Range		All Years	0.5–1	100–500	0.5–3	175–1500		
		1995–96	1.5–10	100–1500	0.5–3	800–1700		
		1997–99	0.5–3	175–1100	0.5–2	175–1600		

For upper level buyers, sale prices were sometimes given by size class.

Table 6. Seahorse products for sale in Vietnam located during trade surveys, with description and retail prices with year located.

Product	Description (no. seahorses)	VND1000	US$	Year
Bô Than Tinh	*H*. sp. (2); small	80	7.30	1995
Ruou hai ma	*H. trimaculatus*(1)& ginseng	28	2.50	1996
Seahorse tonics	*H*. sp. (4); 90–115 mm	22.5	1.73	1998
	H. sp. (2); 135–170 mm	35	2.69	1998
	H. sp. (2); >170 mm	85	6.75	1998
Live seahorses	*H. kuda* (2); 150 mm	40	3.57	1996
	H. kuda (2)	40–50	3.08–3.85	1998
Dead seahorses	*H. kuda* (2)	20–25	1.79–2.23	1996
	H. kuda (2)	25–35	1.92–2.69	1998

Exchange rates for one US$ were VND11,000 in 1996 and VND13,000 in 1998.

sold to exporters in main centres reported receiving similar prices to the primary buyers, though with a wide range in price based on size (Table 5).

Although seahorses were of low value to fishers, they collectively provided sufficient income to make purchase by higher-level buyers worthwhile. Using the average annual catch of seahorses (6500 kg) and the range of reported value per kg paid to upper level buyers (VND300–1500 kg^{-1}), the total value of the seahorse trade may have been as much as VND2–10 billion (US$170,000–962,000) per year. The range of reported values excludes the largest, rarely encountered, size class > 15 cm, for which upper level buyers were reportedly paid VND300,000–1,600,000 kg^{-1} (US$26–148 kg^{-1}).

At the domestic retail level, individual seahorses sold in elixirs or live for tonics fetched considerably higher values than paid to fishers. Retail prices for seahorse products ranged between VND 20,000 and 85,000 (Table 6). Species identified were *H. trimaculatus* and *H. kuda*, suggesting local sources, though identification was not possible for some products.

Temporal trends in catch from surveys

Fishers were asked to describe and quantify temporal changes in the number of seahorses landed. The majority of fishers who responded ($n = 122$ of 143) reported that seahorse catches had declined over the last 2–5 years. A small number reported stable catches ($n = 14$), while only fishers in Ganh Hao (Bac Lieu) reported an increase in catch ($n = 7$). Most of those reporting a decline ($n = 89$ of 122) estimated a 30–60% decrease in seahorse catch in 2–5 years. Buyers also reported decreases in seahorse availability ($n = 21$ of 27) in most regions, with the exception being Ganh Hao (Bac Lieu) where buyers reported increased ($n = 2$) or stable supplies ($n = 1$). During surveys in 1996, we encountered buyers in Da Nang who had ceased trading seahorses when supplies were unable to meet demand from Taiwan. The majority of fishers ($n = 89$ of 102) and buyers ($n = 16$ of 19) reported no change in the size of seahorses caught.

Discussion

Low seahorse bycatch rates in southern and central Vietnam, magnified by large fishing effort, supported a commercial export of dried seahorses. This trade went unrecorded and unregulated through unofficial channels into China. Although no fisheries-independent data existed, fishers and buyers reported a decline in seahorse catch rates during the 1990s. The apparently large seahorse trade stresses the need for monitoring and evaluation of sample seahorse populations, fisheries and trades in order to meet CITES responsibilities for sustainable exports.

Individual bycatch rates for seahorses were low, with catch restricted primarily to the southern and central portions of Vietnam. On a daily basis only a few seahorses, predominately *H. spinosissimus* and *H. trimaculatus*, were taken in near shore trawl fisheries, with low numbers potentially reflecting the low density and patchy distribution observed for many seahorse species (Foster and Vincent 2004). Seahorse landings showed geographic variation, on a broad scale, with most landed in the southern and central provinces and reportedly few from the northern provinces. Whether this reflects a variation in seahorse abundance/distribution or a variation in fishing method is unknown.

Despite small individual catches, our estimates suggest that total landings and exports of dried seahorses may have measured tonnes annually (even without comprehensive surveys), albeit based on a large extrapolation to a total fishing effort value of unknown accuracy. The relative agreement in magnitude between estimates from catch monitoring and trade surveys provided some level of cross-validation. Moreover, our estimate was consistent with records of trade from neighbouring countries. Customs data from Taiwan and Hong Kong, for instance, document tonnes of dried seahorses originating from Thailand, the vast majority of which were taken as bycatch in trawlers (Vincent 1996). Vietnam's estimated seahorse bycatch would place it in the top five for global production of dried seahorses, with Thailand, Philippines, India, and Indonesia, according to trade surveys conducted (Project Seahorse, unpubl. data).

Exporting seahorses was a relatively new activity for Vietnam, probably arising from a coincidence between increased supply and opening of markets in the 1980s and 1990s. Total fishery production from Vietnam increased 250% from 1980 to 2001 (FAO statistics) as a result of fleet expansion and gear improvements mostly inshore (Ministry of Fisheries 1996). This increased trawling effort will have lead to increased seahorse bycatch. Around the same time, normalization of relations between China and Vietnam in the late 1980s and early 1990s, opened an export market for dried seahorses and other marine products (Li Yiming and Li Dinamo 1998). Most exports from Vietnam reportedly went to China, although the absence of Vietnam as a source country in official Chinese Customs data supports the conviction that most trade was unofficial and unreported. Guangxi province, cited as the main entry point to

China, is known to engage in substantial unregulated trade in wildlife from Vietnam (Li Wenjun et al. 1996; Li Yiming and Li Dinamo 1998).

This study provides no direct measure of the population status of seahorses in Vietnam, and no independent population assessments have ever been conducted. There was, however, strong agreement among fishers and buyers surveyed in Vietnam, and indeed around the world (Vincent 1996), that seahorse catches have declined. Declining catch rates, however, are indicators, not proof, of population declines. Moreover, assigning the portion of the decline due to fishing is complicated by other threats, including habitat destruction and pollution, Over-exploitation, along with habitat loss, was frequently cited for similar declines reported by fishers in other parts of Asia (Vincent 1996).

This paper provides information needed for implementation of the CITES Appendix II listing for seahorses in Vietnam. A recent review of Vietnam's fishery policies found no measures for the implementation of multilateral environmental agreements such as CITES (Tuan 2003). Unregulated trades have been cited as a concern for other species of wildlife (Le Dien Duc and Broad 1995; Li Wenjun et al. 1996; Li Yiming and Li Dinamo 1998) with as many as 190 vertebrate species traded across the Vietnam–China border, including species listed on CITES (Appendix I and II and under China's Wildlife Protection Law (Li Yiming and Li Dinamo 1998). With the listing of seahorses on CITES Appendix II, both China and Vietnam (as signatories), have responsibilities to monitor the trade. Identifying marine product exporters and importers in the trade routes reported here will be an important step in regulating that trade. Additionally it may benefit other species of concern to CITES often traded along with seahorses; such as shark (fin) and sea cucumbers, for which CITES has been evaluating options.

From a conservation perspective, non-selective trawling, rather than trade *per se*, posed the greatest threat to seahorse populations in Vietnam. Regulation, or even cessation, of the trade would do little to reduce seahorse landings. The CITES listing covers only the international trade in seahorses and provides no mechanism to address domestic trade or bycatch issues. Overall, seahorses were recorded in bycatch in more than 20 countries world wide (Project Seahorse, unpubl. data), and most seahorses in trade probably came from bycatch (Vincent 1996). Concerns have been raised about other rare bycatch species (Milton 2001; Stobutzki et al. 2001a, b), and the Code of Conduct for Responsible Fisheries (FAO 1995) requires consideration of the sustainability of all bycatch species. Devices designed for the prevention of bycatch, where employed, have shown mixed results, generally being more successful for large bodied or highly mobile species (Broadhurst 2000). It may, in any case, be difficult to engender much change in Vietnamese trawling for the sake of seahorses alone, given how few are caught and how little they are worth.

Significant numbers of seahorses were caught and traded in Vietnam, primarily from bycatch, without any monitoring or consideration of the effects on wild populations. While this exploitation creates a direct pressure on seahorse populations, it is also emblematic of problems facing many other species taken in unregulated fisheries (e.g. for traditional medicines, aquarium) or as bycatch. In this, seahorses may serve as a case-study for the effects of bycatch on small, less-studied species; their distinctive shape makes it possible to track incidental landings, their relatively sedentary behaviour facilitates population census, and their CITES status mandates formal attention to their status.

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References

Broadhurst M.K. 2000. Modifications to reduce bycatch in prawn trawls: a review and framework for development. Reviews in Fish Biology and Fisheries 10: 27–60.

Dao Xuan Loc and Hoang Phi 1991. Results of the surveys of *Hippocampus* seahorses in the coastal areas of the central provinces and the breeding of *Hippocampus kuda* seahorses in cement tanks [Tuyen Tap Nghien Cuu Bien III]. Collection of Marine Research works 3: 235–245 [in Vietnamese].

Do Huu Hoang, Truong Si Ky and Ho Thi Hoa 1998. Feeding behaviour and food of seahorses in Vietnam. In: The Marine Biology of the South China Sea III. Proceeding of the third International Conference on the Marine biology of the South China Sea, Hong Kong. Hong Kong University Press, pp. 307–320.

FAO 1995. Code of Conduct for Responsible Fisheries. Fisheries and Agriculture Organisation, Rome, Italy.

Foster S.J. and Vincent A.C.J. 2004. Life history and ecology of seahorses: implications for conservation and management. Journal of Fish Biology 65(1): 1–61.

Hodgson G. 1999. A global assessment of human effects on coral reefs. Marine Pollution Bulletin 38: 345–355.

Lau P.P.F. and Parry-Jones R. 1999. The Hong Kong Trade in Live Reef Fish for Food. TRAFFIC East Asia and World Wide Fund for Nature Hong Kong, Hong Kong.

Le Dien Duc and Broad S. 1995. Investigations into Tortoise and Freshwater Turtles Trade in Vietnam. IUCN, Gland, Switzerland.

Li Wenjun, Fuller T.K. and Wang Song 1996. A survey of the wildlife trade in Guangxi and Guangdong, China. TRAFFIC Bulletin 16: 9–16.

Li Yiming and Li Dinamo 1998. The dynamics of trade in live wildlife across the Guangxi border between China and Vietnam during 1993–1996 and its control strategies. Biodiversity and Conservation 7: 895–914.

Lourie S.A., Pritchard J.C., Casey S.P., Truong S.K., Hall H.J. and Vincent A.C.J. 1999a. The taxonomy of Vietnam's exploited seahorses (family Syngnathidae). Biological Journal of Linnean Society 66: 231–256.

Lourie S., Vincent A.C.J. and Hall H.J. 1999b. Seahorses: An Identification Guide to the World's Species and Their Conservation. Project Seahorse, London, UK.

Milton D.A. 2001. Assessing the susceptibility to fishing of populations of rare trawl bycatch: sea snakes caught by Australia's Northern Prawn Fishery. Biological Conservation 101: 281–290.

Ministry of Fisheries 1996. Technical, Financial and Economic Assessment of Capture Fisheries and Aquaculture in Vietnam. Final Report.

Ministry of Science, Technology, and Environment 1992. Red Data Book of Vietnam, Vol. 1. Animals, Science and Technology Publishing House, Hanoi.

Pajaro M.G., Meeuwig J.J., Giles B.G. and Vincent A.C.J. 2004. Biology, fishery and trade of sea moths (Pisces: Pegasidae) in the central Philippines. Oryx 38(4): 432–438.

Pajaro M.G., Vincent A.C.J., Buyhat D.Y. and Perante N.C. 1997. The role of seahorse fishers in conservation and management. In: Proceedings of the 1st International Symposium of Marine Conservation, Hong Kong. Hong Kong Marine Conservation Society, Hong Kong, pp. 118–126.

Sadovy Y.J. and Vincent A.C.J. 2002. Ecological issues and the trade in live reef fishes. In: Coral Reef Fishes. Elsevier Science, USA.

Stobutzki I.C., Miller M.J. and Brewer D. 2001a. Sustainability of fishery bycatch: a process for assessing highly diverse and numerous bycatch. Environmental Conversation 28: 167–181.

Stobutzki I.C., Miller M.J., Jones P. and Salini J.P. 2001b. Bycatch diversity and variation in a tropical Australian penaeid fishery; the implications for monitoring. Fisheries Research 53: 283–301.

Truong Si Ky and Ton Nu My Nga 1995. Reproduction of two species of seahorses, *Hippocampus histrix* and *H. trimaculatus* in Binh Thuan waters. In: Proceedings of the First Symposium on Marine Biology, October 1995. Nha Trang, Vietnam [In Vietnamese].

Tuan L.Q. 2003. Country Case Study: Trade in Fisheries and Human Development Vietnam. Asia Pacific Regional Initiative on Trade, Economic Governance and Human Development, United Nations Development Program, Hanoi, Vietnam.

Vincent A.C.J. 1996. The International Trade in Seahorses. TRAFFIC International, Cambridge, UK.

Wood E. 1985. Exploitation of Coral Reef Fishers for the Aquarium Trade. Marine Conservation Society, Ross-on-Wye, UK.

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Urban domestic gardens (VIII) : environmental correlates of invertebrate abundance

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Abstract. Domestic gardens associated with residential zones form a major component of vegetated land in towns and cities. Such gardens may play a vital role in maintaining biodiversity in urban areas, but variation in the abundance of organisms in gardens has been little explored. We report the results from a case study of 61 domestic gardens in the city of Sheffield, UK. Across 22 invertebrate groups, the median number of individuals recorded per garden was 49, 178, and 1012 in litter collections, pitfall and Malaise trap samples, respectively. Abundance was analysed by stepwise multiple regression and hierarchical *tree* analysis in relation to garden and landscape variables. The amount of variation explained in regression models ranged from 4 to 56%, for data based on pitfall and litter samples, and from 16 to 92% for data from Malaise traps. In total, 31 out of 36 explanatory variables entered into stepwise regression models, and 29 of them did so more than once. Although there was strong evidence only for approximately half of such relationships, in these cases the two methods of analysis corroborated one another. General correlates of invertebrate abundance were lacking, and likely reasons for inconsistencies in the relationships are discussed in the context of sampling and species biology. Correlates of the greatest significance occurred at both landscape (e.g. altitude) and garden scales (e.g. area of canopy vegetation). These factors were associated with species richness as well as abundance.

Introduction

Urbanisation causes wholescale transformation of the local environment, through its impact upon natural vegetation, climate, hydrology, and primary production (Sukopp and Starfinger 1999; Kinzig and Grove 2001). The scale of urbanisation is great: urban areas cover about 4% of the Earth's land surface, more than 4.71 million km^2 (UNDP, UNEP, World Bank & WRI 2000) – roughly equivalent to 19 times the area of the UK, or half that of the USA. Urbanisation is also accelerating worldwide (particularly in global biodiversity hotspots, Liu et al. 2003), therefore comprehending its effects, and consequently reducing its impact, are important goals for ecologists and conservationists.

The consequences of urbanisation include changes in the richness, composition, and individual species' abundance of animal and plant assemblages.

Urbanisation generally reduces native species richness across taxa (e.g. Blair and Launer 1997; Denys and Schmidt 1998; Thompson and Jones 1999; Germaine and Wakeling 2001), although certain groups may be favoured by the creation of novel habitats (e.g. Gilbert 1990; Eversham et al. 1996). Urbanisation tends to increase the proportion of alien species in an assemblage (Roy et al. 1999) with the effect that overall biodiversity may even be enhanced (Pyšek 1993; Blair 1996).

Land in towns and cities that supports vegetation and has freely draining surfaces, generically termed ‘green space’, can reduce the impact of urbanisation. Green space has the potential to lessen detrimental effects on species assemblages by preserving or creating habitat, and by retaining corridors through the urban matrix. A major component of urban green space is formed by domestic gardens associated with residential zones. The few estimates available for UK cities indicate that domestic gardens comprise 19–27% of the entire urban area (Gaston et al. in press), therefore they may play a critical role in maintaining biodiversity in such regions.

Domestic gardens can contain rich plant and animal assemblages (e.g. Owen 1991; Miotk 1996; Saville 1997), but with the exception of birds (BTO Garden BirdWatch scheme, Cannon 2000), the factors related to variation in biodiversity remain poorly understood; studies have focussed on either single gardens (e.g. Allen 1964; Smith 1989; Owen 1991) or a small number of taxa (e.g. Davis 1978; Vickery 1995; Bailey et al. 1998). It is difficult to predict what the relative roles of ‘internal’ and ‘external’ factors may be for biodiversity, since gardens are managed at an individual level, and vary widely in land cover composition and management intensity (e.g. ‘cleanliness’). At the same time, gardens form interconnected tracts of green space, so that they are also influenced by the configuration of vegetated land at a wider scale. Thus gardens differ essentially from isolated patches of green space – the subject of many previous studies of urban biodiversity (e.g. McGeoch and Chown 1997; Miyashita 1998; Denys and Schmidt 1998) – because they constitute much of the urban matrix. Here we report results from a systematic assessment of patterns in invertebrate abundance across a substantial sample of domestic gardens in a major city in the UK, encompassing variation in urban location, density of the built environment and garden age, size and management.

This work is part of a larger study, the Biodiversity of Urban Gardens in Sheffield (BUGS) project, an investigation of the resource that domestic gardens provide for biodiversity and ecosystem functioning (Gaston et al. in press; Smith et al. in press a), the factors that influence the levels of plant biodiversity associated with different gardens (Thompson et al. 2003, 2004) and ways in which features of gardens can be manipulated to enhance biodiversity (Gaston et al. 2005). We have examined patterns in invertebrate biodiversity in terms of both richness, mainly at the species level (the subject of a companion paper: Smith et al. in press b) and abundance of major taxonomic groups, the subject of this report.

Knowledge of abundance is relevant to understanding biodiversity for several reasons. First, abundance and richness are rarely independent, and the persistence of species, or their extent of distribution is often related to their local abundance (Soulé et al. 1988; Denys and Schmidt 1998; Gaston et al. 2000). Second, variation in the total abundance of a taxonomic group is likely to partly reflect the suitability of a habitat, or the availability of resources, for the group's constituent species. Thus abundance may provide useful information about the role of gardens for particular taxa. Third, in terms of ecological function, it is likely that the abundance of groups (in addition to species richness) will significantly influence their contribution to particular 'ecological services' (e.g. pest control, pollination, litter breakdown), and hence the importance of those processes in gardens (Loreau et al. 2002). Fourth, one, possibly unique aspect of garden biodiversity is that most owners will come into their closest contact with wildlife via the garden; therefore what occurs in gardens has great potential to influence people's appreciation of their local environment (Cannon 1999). For many people their perception of garden wildlife will be strongly influenced by the occurrence of the most abundant (and obvious) groups (e.g. bumblebees), while the often subtle differences between species may go unnoticed. A final, pragmatic reason is that for many groups of invertebrates, the resolution of large quantities of sampled material to species level may involve a disproportionate effort, or even be impossible (for example with immature specimens). Therefore examination of abundance data provides a way of exploring the role of gardens as a habitat even for groups which lack full information on species richness.

Methods

Study site

The city of Sheffield, South Yorkshire, UK (53°23′ N, 1°28′ W; Ordnance Survey (O.S.) grid reference SK 38) lies in the centre of England; it is largely surrounded by agricultural land, except where the urban area merges with that of Rotherham to the north-east. The administrative boundaries of the city enclose an area of more than 360 km^2, including farmland and a portion of the Peak District National Park. The study was carried out in the rear gardens (hereafter called 'gardens') of private, owner-occupied houses in the predominantly urbanised region of the city (about 143 km^2, defined as those 1 km × 1 km cells having more than 25% coverage by residential or industrial zones, as judged from O.S. 1:25,000 scale maps, Figure 1). The study focussed on rear gardens because they formed the major garden component of most properties.

Sixty-one gardens were selected as a stratified sample from a convenience sample of 161 householders derived from contacts among ancillary, clerical and academic staff at the University of Sheffield, and from members of the public at lectures or displays (see Discussion about potential sources of bias). This

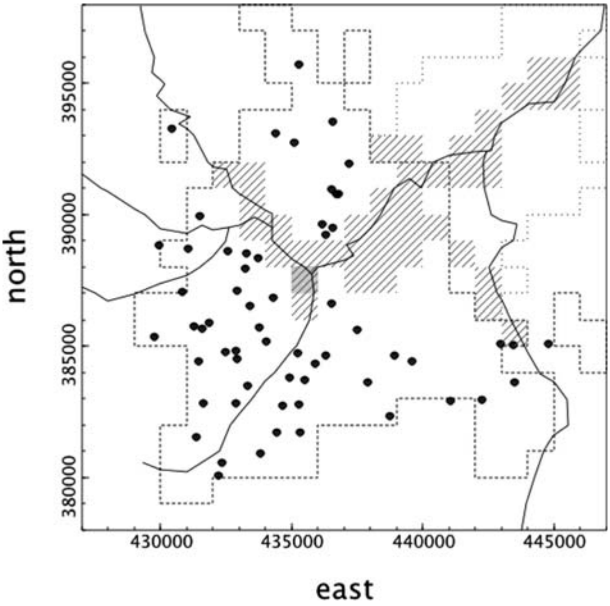

Figure 1. Map of the locations of the 61 study gardens in the predominantly urban area (heavy dashed line) of Sheffield, in relation to zones with > 50% industrial/commercial use (cross-hatching), principal rivers, and the adjoining town of Rotheram to the north-east (light dashed outline). The shaded square indicates 1 km^2 of the central business district, centred on the city hall. Map axes represent distances (m) on the Ordinance Survey national grid; the map covers 20 km by 20 km.

approach was chosen due to the great difficulty in the alternative of recruiting householders at random who were both sympathetic to research being conducted in their gardens, and able to offer daytime access. The sample size was the maximum permitted by the constraints of other aspects of the project (e.g. faunal sampling). By stratifying the sample along key axes of interest – house age and garden size – and selecting values along the entire length of each axis, our method enabled us to explore the influence on landcover composition of such axes, over their full ranges of variation. By this means the results from the study could be generalised to culturally similar areas in the UK even if the distribution of garden sizes differed. House age, approximate garden size, and location were the sole information used in generating the garden sample. Rear gardens ranged from 32 to 940 m^2 in area and their associated properties ranged from 5 to 165 years in age. Blocks of apartments were excluded from the study because they generally lacked private gardens.

Recording garden characteristics

Rear gardens were surveyed between July and September 2000. Principal dimensions were measured to the nearest 0.5 m, and a scale plan was drawn of each garden; this included the side portion on properties occupying corner plots. The plan incorporated boundaries (and their construction), buildings within the garden, and all forms of land use. The areas of each type of land use, and the lengths of linear features, were then estimated from the plan. Distance to the centre of the nearest 1 km×1 km cell having less than 25% coverage by residential or industrial zones was measured. Information on garden management and the intentional provision of resources for wildlife ('wildlife gardening') was gathered from garden owners using a questionnaire (see Appendix A for details). Altitude was recorded to the nearest 10 m, from O.S. 1:50,000 scale maps, and houses ranged between 40 and 250 m above sea level.

Recording vegetation

A complete list was made of all vascular plant taxa during the garden survey, and each taxon was allocated to alien or native categories (nomenclature and status followed Stace (1997) where possible, otherwise Wright 1984). Some plants were allocated to the native taxon (e.g. *Primula vulgaris*, *Aquilegia vulgaris*), even though many garden plants are of hybrid origin. Cultivars were not considered as separate taxa. Although the timing of the survey meant that some strict vernals (e.g. *Anemone blanda*) were missed, the remains of *Hyacinthoides*, *Narcissus* and *Tulipa* spp. were still visible. Measures of vegetation structure were produced by estimating the area covered by a canopy in the following height classes: <0.5, 0.5–1, 1–2, 2–3, and >3 m. The classes were mutually exclusive, and incorporated tree canopies (including those overhanging from outside the garden) but omitted mown lawn. The number of trees taller than 2 m was also recorded.

Garden measurements using digital data

The following variables were measured for each property using Ordnance Survey digital 'Land-line Plus' (1:1250) maps, imported to an ArcView GIS (Environmental Systems Research Institute, Inc.): total plot area, house area, and total garden area (calculated as the area of the plot excluding the house). A series of variables for land use surrounding each garden was also created. Measured for a circular area of 10,000 m^2 (1 ha) centred on each garden, the variables were: number of houses (where more than half of the area of the house was covered), area of roads, area of buildings, area of gardens (plots minus houses), and area of land not in the former categories. Within a 10,000 m^2 (1 ha) square plot centred on each garden, two other measures of local green space were taken from 1:1250 scale aerial photographs ('Cities Revealed', The GeoInformation Group, Cambridge, UK): the area of the contiguous block of green space in which the survey garden lay, and the total ground area of green space in the quadrat (non-built up, unmetalled ground, including gardens, parks, waste ground, woodland and landscaping).

Human population density was measured using POPSURF data at a 200 m grid cell resolution, based on 1991 UK population census data (Martin and Tate 1997). The value of the cell in which a garden lay was used as a measure of local population density. For three gardens where data were missing, a value was calculated from a bilinear interpolation of the four nearest cells.

Invertebrate sampling

Indices of the relative abundance of organisms in gardens (hereafter referred to as abundance) were measured by three methods, selected on the basis of their efficiency in gathering broadly comparable data for a wide range of taxa, across a large number of gardens simultaneously. These measures of abundance were valid for drawing comparisons between gardens, within taxa, where the sampled substrates were similar.

Pitfall trapping

White, disposable plastic coffee cups, 110 mm high and 70 mm wide at the rim, were used for pitfall traps. They were placed in triplicate in the cultivated borders of each of 60 out of the 61 gardens, as widely spaced as practicable. In one garden without borders, traps were placed along the boundary, which comprised fencing and a hedge. Each trap was half-filled with 50% alcohol, rather than ethylene glycol, due to the risk of being found by pets or children. When in use, each trap was covered with a ply-board rain shield, positioned 20 mm above the rim of the trap. Traps were run for 2 weeks at the beginning of each month, from June to October inclusive in 2000, resulting in a total of 15 samples for each garden.

Litter sampling

Samples of leaf litter and organic debris were collected in triplicate from each of the 61 gardens, on a single occasion between the end of July and mid-September 2000. Each sample was taken from a cultivated border, in a circular area of ca. 20 cm diameter, to a depth of ca. 5 cm, and samples within gardens were collected as far apart as possible. The surface substrate was collected if no litter was present. In one garden without borders, the samples were taken from the base of a boundary hedge. Organisms were extracted from the samples using Tullgren funnels, and collected into 70% ethyl alcohol. Organisms that remained in the dried litter samples, in particular snails, were recovered by hand searching.

Malaise trapping

Single Malaise traps (white roof, black walls) were erected in 16 out of the 61 gardens in order to sample flying insects (although samples also contained substantial numbers of arachnids); traps were placed in gardens that spanned the range of property sizes. Malaise traps were located in as standardised a manner as possible in each garden: at the edge of the lawn, with their long axis perpendicular to a border. The traps were operated for the first 2 weeks of June, July and September 2000 and invertebrates were collected in 70% ethyl alcohol.

The taxa sorted from samples were limited to those that could be easily allocated to a group without optical aids, or which would not have taken excessive time to extract; thus true fly (Diptera), springtail and mite families were largely excluded. Sorted specimens were generally grouped by family or order.

Analyses

As is often the case with analyses of this exploratory nature, there was a substantial number of independent variables of possible interest or importance. We examined our data for redundancy, and were able to remove a modest number of intercorrelated variables; in each case the retained variable had a clearer potential biological role, or had been measured with greater confidence. This enabled us to reduce the number of variables to 36, but further reductions would have become increasingly arbitrary as the pattern of intercorrelation was rather diffuse. This was reflected in the failure of a principal components analysis of the remaining independent variables to achieve useful reduction of the data.

In addition, the independent variables (excluding positional variables) were examined for evidence of spatial autocorrelation, but there was little evidence of anything other than weak, and idiosyncratic patterns. Essentially, there was no consistent pattern of gardens in close proximity being more similar in their characteristics than those which were far apart.

Whilst acknowledging that this left rather more variables than is ideal for model fitting, the approach to the analysis was exploratory: the primary aim was to identify what, if any, associations occurred between garden environments and relative abundance, and what evidence there was for general patterns across different groups of organisms. We chose not to try to control for the number of comparisons since, firstly, we were more interested in examining the full range of associations and their relative strengths; and secondly, the conceptual and methodological uncertainties with techniques for doing this would have resulted in arbitrary judgements as to how to apply such corrections (e.g. see Moran 2003). One consequence of this approach is that the weaker results must be viewed cautiously, and they are only presented in tables to give an overview. We used both multiple regression and tree modelling (binary recursive partitioning) to provide descriptive models of the relationships between the abundance of each group of organisms and the independent variables describing environmental characteristics. We are not suggesting that the models produced were either the only, or the best, for explaining the abundance of each group. However, for the first time they do provide a test of which types of garden features may be related to the abundance of various animal groups. The generality of these relationships and the existence of causal mechanisms remain to be explored.

Stepwise multiple regression was used to explore which environmental factors accounted for variation in abundance within each taxonomic group (see Appendix A for the list of factors). Data from triplicate samples (pitfall traps and litter samples) were pooled within each method, for each garden. Also, data were pooled across sampling times for pitfall and Malaise trap samples. Thus each taxon had one observation per sampling method in each garden, and each sampling method was analysed separately. For some sampling methods certain taxa were not analysed due to the small number of individuals. For example, although ants can form an important component of the invertebrate fauna in urban environments (Gibb and Hochuli 2002), they were omitted from the present study because they were absent from 65% of gardens, with only four gardens returning more than 20 individuals. Due to their numerical dominance in pitfall traps, and to their well-known ecology, ground beetles (Carabidae) were treated separately from other beetles.

Five of the independent variables had missing values for a few observations; if these factors failed to enter initial models they were removed in order to maximise degrees of freedom. The values of dependent variables were, when necessary, logarithmically transformed for analyses in order to homogenise variances and normalise residuals. Similarly, the areas of gardens and their internal land uses, of GIS-derived variables, lengths of internal walls and hedges, and proportions were logarithmically or arcsine square root transformed in order to linearise the relationship with the dependent variable.

Tree models (Crawley 2002; denoted *tree* for clarity) were used to check the robustness of our inferences from multiple regression. *Tree* models are well suited to situations where explanatory effects may be contingent, and effects are not simple linear responses. The process involved a sequential binary partitioning of the data with respect to the independent variables. The independent variable explaining the maximum deviance was selected first, and the data were split into two subgroups at a threshold value of this variable, such that the split gave the best reduction of total deviance in the group. This process was then repeated for each of the two subgroups, again selecting from all the independent variables, and continued with each successive subgroup until a group contained too few data to be further partitioned. Here we consider only the most important independent variables in each *tree* model, generally the results of the first two partitions (producing up to four groups, although partitioning sometimes stopped before). Fitting *tree* models was carried out using the *tree* package in R (Ihaka & Gentleman 1996).

Results

Twenty-two different invertebrate taxa were sorted across three sampling methods. The same nine taxa were identified from litter samples and pitfall traps, based on 5448 and 17,466 specimens respectively; 16 taxa were identified in Malaise traps, based on 15,570 individuals (Table 1). The median number of individuals recorded per garden (across taxa, for sorted groups) was 49, 178,

Table 1. Relative abundances of individuals from 22 different invertebrate taxa, and percentage occupancy of gardens, recorded in (panel a) litter samples – 61 gardens, (panel b) pitfall traps – 60 gardens, and (panel c) Malaise traps – 16 gardens.

	% gardens	Sum	Mean	Median	Minimum	Maximum
Panel a: litter samples						
Woodlice	100	3941	65.7	42.5	1	334
Snails	90.2	581	9.52	8	0	47
Millipedes	70.5	249	4.08	2	0	33
Beetles (others)	90.0	237	3.88	2	0	28
Spiders	90.2	224	3.67	3	0	20
Centipedes	60.6	89	1.46	1	0	9
Slugs	42.6	60	0.98	0	0	12
Harvestmen	36.0	50	0.82	0	0	6
Beetles (Carabidae)	16.6	17	0.28	0	0	4
Panel b: pitfall traps						
Woodlice	100	7903	132	70	4	1293
Slugs	100	3416	56.9	49	1	355
Beetles (Carabidae)	93.3	3144	52.4	27.5	0	272
Beetles (others)	100	1185	19.8	12.0	1	316
Spiders	100	842	14.0	10.0	1	67
Snails	83.3	436	7.27	4.5	0	59
Harvestmen	83.3	413	6.88	4	0	49
Millipedes	55.0	87	1.45	1	0	11
Centipedes	43.3	40	0.67	0	0	7
Panel c: Malaise traps						
Parasitoid wasps	100	3655	228.4	204.5	97	440
Hoverflies	100	2345	146.6	142.5	47	421
Moths	100	2080	130.0	101.5	45	317
True bugs	100	1223	76.4	62.0	25	288
Soldier-flies	93.8	1159	72.4	57.5	0	248
Bumble bees	100	1131	70.7	52.0	10	246
Social wasps	100	856	53.5	30.0	6	236
Beetles	100	672	42.0	36.5	14	100
Craneflies	100	645	40.3	32.5	5	82
Long-legged-flies	100	621	38.8	30.5	3	187
Sawflies	100	372	23.2	17.5	4	60
Spiders	100	338	21.1	17.5	6	47
Dance-flies	93.8	274	17.1	8.5	0	118
Solitary bees	75.0	80	5.00	2	0	27
Solitary wasps	81.2	61	3.81	2	0	21
Harvestmen	62.5	58	3.63	1.5	0	15

and 1012 in litter, pitfall and Malaise trap samples, respectively. Woodlice dominated the samples of ground-dwelling organisms. Comprising 72.3% of the total sorted litter samples, they were more than six times as abundant as the next taxon, snails; woodlice formed 45.2% of the total sorted pitfall samples, and were approximately four times more numerous than beetles or slugs. As might be expected from the mobility of organisms, pitfall traps recorded more individuals than litter samples in all sorted taxa except snails, centipedes, and millipedes. Flies were the dominant group in Malaise trap samples even before sorting (32.4% of the sorted catch, with hoverflies alone forming 15.1%), although parasitoid wasps were also strongly represented, accounting for 23.5% of the total sorted catch. In the following sections each invertebrate taxon is treated in turn, with results from regression analyses followed by those from the *tree* models.

Beetles (Arthropoda, Insecta: Coleoptera)

Ground beetles (Carabidae). Abundance of ground beetles in pitfall traps was positively related to the area of green space surrounding a garden, followed by the number of trees; habitat diversity was negatively related (Table 2, panel a). This result was partially reflected in the *tree* analysis (Table): the primary split was on the contiguous area of green space in which the garden lay, with secondary splits on garden 'permeability' (i.e. percentage of boundary not comprising walls) and number of alien plant taxa (panel a of Tables 3 and 4).

Beetles other than Carabidae. No variables entered the model for other beetles based solely on litter sampling. For pitfall traps, the only significant factor common to the regression on ground beetles was the area of green space, although the area of vegetation canopy above 2 m was also positively associated (and this variable is closely correlated to number of trees). The richness of native plant taxa, number of surrounding houses, and intensity of garden management were further positively associated with non-Carabidae abundance; distance on a northerly axis and area of hard surfaces in a garden were negatively related (Table 2, panel a). The area of canopy above 2 m high was also the primary split in the *tree* analysis, and the higher group only further subdivided on the area of hard surfaces (panel a of Tables 3 and 4). For beetles in Malaise traps, a negative relationship with altitude was the sole factor in the model, accounting for over half the variation in abundance (Table 2, panel b). This relationship was corroborated by the *tree* analysis, where altitude was also the only split (panel b of Tables 3 and 4).

Spiders (Arthropoda, Arachnida: Aranea)

Less than 10% of the variation in spider abundance was explained by the multiple regression, either for litter or pitfall data. Single factors entered each model: the proportion of vegetative material in litter samples for the former, and area of surrounding gardens for the latter (Table 2, panel a). For the *tree* analyses, the primary split for spiders in litter was the area of canopy above 2 m high; thereafter, the lower group divided on the size of the green space fragment. Concerning spiders in pitfall traps, data split on garden permeability, with the upper group further dividing on house age (panel a of Tables 3 and 4).

A strong, negative association with altitude, and a weaker positive relationship with length of garden walls, accounted for more than half the variation in spider abundance in Malaise trap samples (Table 2, panel b); altitude contributed 97% of that explained. The sole split in the *tree* analysis was on the garden perimeter–area ratio (panel b of Tables 3 and 4).

Harvestmen (Arthropoda, Arachnida: Opiliones)

The abundance of harvestmen in litter samples was related positively to garden size, proportion of permeable boundary and house age, but negatively to altitude. Only marginally significant factors entered the model based on pitfall samples (Table 2, panel a). In the *tree* analyses, harvestmen in litter were associated positively with area of vegetation above a level of 2 m; secondary splits were on the area of green space in the garden and the length of boundary abutting other gardens (panel a of Tables 3 and 4). For pitfall samples, harvestmen were more abundant in gardens with smaller proportions of boundary abutting green space. Native plant taxon richness and altitude formed the secondary splits (panel a of Tables 3 and 4). A greater proportion of the variation in abundance was explained for harvestmen in Malaise trap samples. Variation was positively related to the areas of lawn and vegetation canopy below 2 m and negatively to the area of surrounding gardens (Table 2, panel b). The latter result was corroborated by the *tree* analysis, with harvestmen being more abundant at sites with a smaller area of surrounding gardens (panel b of Tables 3 and 4).

Slugs (Mollusca: Gastropoda)

The abundance of slugs in pitfall traps was strongly positively related to the area of vegetation canopy above 2 m in height, and to the richness of alien plant taxa; the area of hard surfaces was strongly negatively related (Table 2, panel a). According to the *tree* analysis, slug abundance declined in gardens to the east, with data then splitting on the area of canopy above 2 m high and the structural diversity of the vegetation (panel a of Tables 3 and 4).

Snails (Mollusca: Gastropoda)

Models for snails in pitfall traps and litter explained very similar degrees of variation, and included relatively large numbers of factors (Table 2, panel a).

Table 2. Stepwise multiple regression: matrices showing the relationships between independent variables (environmental and housing characteristics; no. in italics refers to description of variable in Appendix A) and the relative abundance of individuals in invertebrate taxa (see Methods for details) for (panel a) data from pitfall traps (P) and litter samples (L), and (panel b) data from Malaise traps.

Panel a: Pitfall trap and litter samples:		Ground beetles	Beetles (others)	Spiders	Spiders	Harvestmen	Harvestmen	Slugs	Snails	Snails	Centipedes	Centipedes	Millipedes	Woodlice	Woodlice
Source of data:		P	P	L	P	L	P	P	L	P	L	P	L	L	P
Model d.f.:		4, 54	6, 52	1, 59	1, 58	4, 54	3, 57	3, 56	7, 50	8, 46	2, 56	3, 54	1, 59	4, 56	2, 57
Model r^2_{adj}:		0.38	0.46	0.06	0.07	0.40	0.17	0.41	0.56	0.53	0.08	0.16	0.04	0.25	0.18
Alien taxon richness	*2*							**2**							
Native taxon richness	*3*		1												
Distance east	*5*								**−2**	**−2**					
Distance north	*6*		**−2**												**2**
House age	*7*					1									
Altitude	*8*					**−2**	(1)								
Habitat diversity	*10*	−1													
Structural diversity	*11*								1	1					
Garden area	*12*					**2**									
Perimeter–area ratio	*13*								**−2**						
Area of lawn	*14*									−1		1			
Area of hard surface	*16*		**−3**					**−3**				**−3**		1	
Presence of pond	*17*	(−1)					(1)			−1					
Presence of composting	*18*									1					1
Canopy < 2 m	*19*								−1						
Canopy > 2 m	*20*		**3**					**3**						**3**	
No. of trees	*21*	2													
Length of hedges	*23*								1	**3**					
Length of walls	*24*								1	**2**			(1)		
% permeable boundary	*26*					**2**									

% green on boundary	*27*						(−1)				(1)						
No. of houses	*29*		1														
Area of gardens	*30*				1						(−1)			−1			
Total green space	*31*	**3**	**2**											−1			
Green space fragment	*32*											(1)					
Management index	*33*		1						**−3**								
Use of slug pellets	*34*									**−3**							

Panel b: Malaise trap samples:

		Beetles	Spiders	Harvestmen	Bumble bees	Solitary bees	Solitary wasps	Social wasps	Sawflies	Parasitoids	Moths	True bugs	Craneflies	Dance-flies	Long-legged flies	Soldier-flies	Hoverflies
Model d.f.:		1, 14	2, 12	3, 12	1, 14	3, 10	4, 9	4, 10	4, 11	3, 11	2, 13	3, 14	4, 11	3, 12	1, 14	2, 13	5, 10
Model r^2_{adj}:		0.54	0.63	0.56	0.16	0.86	0.81	0.91	0.64	0.86	0.48	0.60	0.90	0.52	0.41	0.58	0.92
Native taxon richness	*3*					**3**											**3**
Distance east	*5*										1	(1)					
Distance north	*6*								1	**3**							
House age	*7*												**−2**				
Altitude	*8*	**−3**	**−3**					**−3**					**3**				
Rural proximity	*9*											−1		**2**			
Habitat diversity	*10*										1					**3**	
Structural diversity	*11*															**−1**	
Garden area	*12*												**−3**				
Perimeter–area ratio	13							**2**									**−3**
Area of lawn	*14*			1			**2**										
Presence of pond	*17*				(1)												**2**
Presence of composting	*18*						**2**										
Canopy < 2 m	*19*			**2**													

Table 2. Continued.

Panel b: Malaise trap samples:		Beetles	Spiders	Harvestmen	Bumble bees	Solitary bees	Solitary wasps	Social wasps	Sawflies	Parasitoids	Moths	True bugs	Craneflies	Dance-flies	Long-legged flies	Soldier-flies	Hoverflies
Model d.f.:		1, 14	2, 12	3, 12	1, 14	3, 10	4, 9	4, 10	4, 11	3, 11	2, 13	3, 14	4, 11	3, 12	1, 14	2, 13	5, 10
Model r^2_{adj}:		0.54	0.63	0.56	0.16	0.86	0.81	0.91	0.64	0.86	0.48	0.60	0.90	0.52	0.41	0.58	0.92
Canopy > 2 m	*20*							**3**									
No. of trees	*21*								**2**	**3**			**3**		**2**		
Length of hedges	*23*								**−2**					(−1)			
Length of walls	*24*		(1)														
Local population density	*28*						**2**							1			**3**
No. of houses	*29*																**3**
Area of gardens	*30*			−1		**−2**	−1		−1								
Total green space	*31*							**3**									
Green space fragment	*32*									**−3**		1					
Wildlife index	*35*					**−2**											

In each cell, '+' or '–' indicate the direction of the relationship; for level of significance: **3** = $p < 0.001$, **2** = $p < 0.01$, 1 = $p < 0.05$, (1) = $0.10 > p > 0.05$.

Table 3. Tree analysis: matrices showing the relationships between independent variables (environmental and housing characteristics; no. in italics refers to Appendix A) and the relative abundance of individuals in invertebrate taxa (see Methods for details) for (panel a) data from pitfall traps (P) and litter samples (L), and (panel b) data from Malaise traps.

Panel a: pitfall trap and litter samples

Source of data:		Ground beetles P	Beetles (others) P	Spiders L	Spiders P	Harvestmen L	Harvestmen P	Slugs P	Snails L	Snails P	Centipedes L	Centipedes P	Millipedes L	Woodlice L	Woodlice P
Alien taxon richness	*2*	B+													B–
Native taxon richness	*3*						B+								
Distance east	*5*							A–	B–	B–			B–		
Distance north	*6*														A+
House age	*7*				B+										
Altitude	*8*						B+								
Structural diversity	*11*							B–							
Area of lawn	*14*								B–						
Area vegetated	*15*					B–				A+					
Area of hard surface	*16*		B–												
Canopy > 2 m	*20*		A+	A+		A+		B+						B+	
No. of trees	*21*														
Boundary with gardens	*25*					B–									
% permeable boundary	*26*	B–			A+										
% green on boundary	*27*						A–								
Local population density	*28*											B–			
Area of gardens	*30*										A–				
Total green space	*31*												A– B+		
Green space fragment	*32*	A+		B–					A+					A+ B–	B+
Management index	*35*										B+	A–			

Table 3. Continued.

Panel b: Malaise trap samples		Beetles	Spiders	Harvestmen	Bumble bees	Solitary bees	Solitary wasps	Social wasps	Sawflies	Parasitoids	Moths	True bugs	Craneflies	Dance-flies	Long-legged flies	Soldier-flies	Hoverflies
Native taxon richness	*3*					A+	A+										
Distance east	*5*											A+					
Altitude	*8*	A−															
Perimeter–area ratio	*13*		A−		A−									A−			
Area vegetated	*15*															A−	
Presence of pond	*17*							A+							A+		A+
Canopy > 2 m	*20*												A+				
Length of walls	*24*									A+							
% boundary with gardens	*25*										A+						
No. of houses	*29*								A+								
Area of gardens	*30*			A−													

In each cell, 'A' and 'B' indicate the 1st and 2nd variables, respectively, on which the data split, and '+' and '–' show the direction of the relationship. Data for all groups from Malaise traps split only once.

Table 4. *Tree* analyses showing details for up to the first two partitions of data for the relative abundance of individuals in invertebrate taxa: (panel a) data from pitfall traps (P) and litter samples (L), and (panel b) data from Malaise traps (see Analyses for details).

Taxon		1st partition	Threshold		Above, below	2nd partition	Threshold		Above, below
Ground beetles	P	Green space fragment	936 m^2	+	28.4	% permeable boundary	90%	–	11.3
									46.7
					3.90	Alien taxon richness	49.3 species	+	8.34
									1.82
Beetles (others)	P	Canopy > 2 m	6.93 m^2	+	15.1	Area of hard surface	35.4 m^2	–	10.3
									23.8
					4.98	—			
Spiders	L	Canopy > 2 m	11.5 m^2	+	5.13	—			
					2.75	Green space fragment	2917 m^2	–	1.43
									3.96
Spiders	P	% permeable boundary	37%	+	19.1	House age	30 yrs	+	22.5
									11.8
					7.76	—			
Harvestmen	L	Canopy > 2 m	23.5 m^2	+	1.2	Area vegetated	18.4 m^2	–	0.0
									0.7
					0.2	Boundary with gardens	33.5 m	–	0.7
									2.7
Harvestmen	P	% green on boundary	0.89	–	4.3	Native taxon richness	50.0 species	+	7.2
									2.4
					12.0	Altitude	175 m	+	21.0
									7.2
Slugs	P	Distance east		–	37.3	Canopy > 2 m	8.9 m^2	+	42.8
									18.4
					82.4	Structural diversity	0.6	–	52.7
									129.1
Snails	L	Green space fragment	1441 m^2	+	9.7	Distance east		–	2.4
									12.0
					3.0	Area of lawn	38.0 m^2	–	1.52

Table 4. Continued.

Taxon		1st partition	Threshold		Above, below	2nd partition	Threshold		Above, below
									4.12
Snails	P	Area vegetated	172.4 m^2	+	17.9	—			
					4.2	Distance east		–	1.32
									4.84
Centipedes	L	Area of gardens	2854 m^2	–	1.2	Management index	9.5	+	1.7
									0.6
					3.6	—			
Centipedes	P	Management index	4.5	–	0.4	Local population density	2.35 ha^{-1}	–	0.4
									1.2
					2.2	—			
Millipedes	L	Total green space	4471 m^2	–	2.8	Total green space	7217 m^2	+	10.4
									1.8
					9.3	Distance east		–	4.3
									16.4
Woodlice	L	Green space fragment	1090 m^2	+	51.4	Canopy > 2 m	10.5 m^2	+	63.2
									21.2
					16.2	Green space fragment	374 m^2	–	9.0
									37.2
Woodlice	P	Distance north		+	160.7	Alien taxon richness	60.4 species	–	69.5
									313.3
					44.9	Green space fragment	936 m^2	+	58.2
									21.1

Columns show the independent variables at either the primary or secondary partitions, and their associated threshold values, directions of relationship ('+' and '-'), and values of sub-group means above and below the split.
Threshold values of the Distance east were relative and are not shown. Data for all groups from Malaise traps split only once. Pitfall trap and litter samples.

Table 5. Malaise trap samples.

Taxon	1st partition	Threshold		Above, below
Beetles	Altitude	140 m	–	23.6 46.6
Spiders	Perimeter–area ratio	0.295	–	13.0 28.1
Harvestmen	Area of gardens	5881 m^2	–	0.3 6.4
Bumble bees	Perimeter–area ratio	0.290	+	116.4 38.4
Solitary bees	Native taxon richness	50.4 species	+	6.3 1.9
Solitary wasps	Native taxon richness	43.9 species	+	3.4 1.4
Social wasps	Presence of pond		+	61.8 26.6
Sawflies	No. of houses	28.5 houses	+	31.1 14.9
Parasitoids	Length of walls	18.9 m	+	304.8 148.2
Moths	% boundary with gardens	91%	+	146.6 71.0
True bugs	Distance east		+	79.4 43.2
Craneflies	Canopy > 2 m	41.1 m^2	+	62.1 17.0
Dance-flies	Perimeter–area ratio	0.29	+	17.1 5.34
Long-legged-flies	Presence of pond		+	35.0 10.3
Soldier-flies	Area vegetated	105 m^2	–	13.8 93.5
Hoverflies	Presence of pond		+	182.4 88.7

Distance on an easterly axis, structural diversity of the vegetation, and lengths of hedges and walls in gardens were common to both models, though the latter two effects were greater for pitfall data. Respectively, the use of slug pellets (molluscicides) and the index of management intensity had strong negative relationships with snail abundance in pitfall traps and litter, accounting for 21 and 36% of explained variation in models.

The area of green space fragment was the primary split in the *tree* analysis for litter data, with the sub-groups splitting on distance east and area of lawn. For snails in pitfall traps, the data split on area of vegetated land uses in a garden. The lower group only then split on distance east, and as for litter data, snails were more abundant in the west (panel a of Tables 3 and 4).

Centipedes (Arthropoda: Chilopoda)

Centipede abundance in litter was not strongly related to any factors. The area of hard surfaces had the strongest, and negative, effect on centipede abundance in pitfall traps, while the area of lawn was weakly positively related (Table 2, panel a). The area of surrounding gardens was negatively related to abundance in litter in the *tree* analyses; only the data above the split bisected further, on index of garden management intensity. Abundance in pitfall traps was negatively associated with the index of garden management intensity; the data split further, for the upper group only, on local human population density (panel a of Tables 3 and 4).

Millipedes (Arthropoda: Diplopoda)

No variables were strongly related to millipede abundance in either litter or pitfall samples (Table 2, panel a). In the *tree* analysis, the primary split was on the surrounding area of green space, with secondary splits on area of green space and distance east (panel a of Tables 3 and 4).

Woodlice (Arthropoda: Crustacea, Isopoda)

The model for litter data for woodlice explained slightly more variation, with four factors, than that for pitfall traps, in which only two entered (Table 2, panel a). No factors were common to both models, the most important for litter was the positive relationship with extent of vegetation canopy above 2 m, while for pitfalls it was distance north. There was weak evidence for negative associations between abundance in litter and both the area of gardens and total green space. In the *tree* analyses (panel a of Tables 3 and 4), the litter data split first on green space fragment area, and secondarily on area of canopy above 2 m and, again, green space fragment area. The pitfall data split on distance north, and then on green space fragment area alien plant taxon richness.

Bumble bees (Arthropoda, Insecta, Hymenoptera: Apidae)

No significant relationships existed for bumble bee abundance (Table 2, panel b). The *tree* analysis indicated that abundance was greater in gardens with a large perimeter–area ratio (i.e. in smaller gardens, panel b of Tables 3 and 4).

Solitary bees (Arthropoda, Insecta, Hymenoptera: Apoidea)

Native plant richness was positively related to abundance of solitary bees, and explained 56% of variation in the regression model (Table 2, panel b); the area of gardens in the surroundings, and an index of wildlife gardening, were negatively related. Data divided also on native plant richness in the *tree* analysis (panel b of Tables 3 and 4).

Solitary wasps (Arthropoda, Insecta, Hymenoptera: Specoidea, Vespoidea)

The regression model also explained a large proportion of the variation in solitary wasp abundance. Positive relationships existed with area of lawn, the presence of composting, and local human population density. In common with solitary bees, abundance was negatively related to the area of surrounding gardens (Table 2, panel b). Similarly, the primary split in the *tree* analysis was native plant richness (panel b of Tables 3 and 4).

Social wasps (Arthropoda, Insecta, Hymenoptera: Vespidae)

Virtually all the variation in abundance of social wasps was explained by four factors (Table 2, panel b), of which two positively related ones, canopy vegetation above 2 m and area of surrounding green space, explained 34 and 26% respectively. Other variables strongly associated with social wasp abundance were altitude (negatively), and the garden perimeter–area ratio (positively). The sole split in the *tree* analysis was on the presence of ponds (panel b of Tables 3 and 4).

Sawflies (Arthropoda, Insecta, Hymenoptera: Symphyta)

Sawfly abundance was related positively to number of trees in a garden and distance north, and negatively to the length of hedges and area of surrounding gardens (Table 2, panel b); number of trees accounted for 32% of the variation in abundance. The number of houses in the surrounding 1 ha was the sole split in the *tree* analysis (panel b of Tables 3 and 4).

Parasitoid wasps (Arthropoda, Insecta, Hymenoptera: Ichneumonidae)

As for sawflies, number of trees and distance north were important effects in the regression model for parasitoid wasps, with trees explaining 61% of variation in abundance. Parasitoid abundance was negatively related to the area of green space in which the garden lay (Table 2, panel b). The *tree* analysis indicated that parasitoids were more abundant in gardens with a greater length of walls (panel b of Tables 3 and 4).

Moths (Arthropoda, Insecta: Lepidoptera, excluding butterflies, Papilionoidea)

There was some evidence for strong relationships for moths with the distance east and garden habitat diversity, which explained nearly half the variation in moth abundance (Table 2, panel b). The percentage of garden boundary abutting green space formed the primary split in the *tree* model (panel b of Tables 3 and 4).

True bugs (Arthropoda, Insecta: Hemiptera, excluding Sternorrhyncha)

True bug abundance was related positively to the area of green space in which a garden lay, and it increased towards the rural edge (Table 2, panel b). The *tree* analysis indicated a sole split on distance east (panel b of Tables 3 and 4).

Craneflies (Arthropoda, Insecta, Diptera: Tipulidae, Pediciidae, Limoniidae and Ptychopteridae)

The regression analysis for craneflies accounted for 90% of variation in abundance, and a positive association with the number of trees was twice as important as the next factor, altitude (also positive, unlike most cases with other taxa). Garden area and house age were strongly negatively related (Table 2, panel b). According to the *tree* analysis (panel b of Tables 3 and 4), craneflies were more abundant in gardens with more vegetation canopy above 2 m.

Dance-flies (Arthropoda, Insecta, Diptera: Empididae)

Distance from the rural edge and local human population density were positively associated with the abundance of dance-flies (Table 2, panel b). In the *tree* analysis perimeter–area ratio was the sole split (panel b of Tables 3 and 4).

Long-legged-flies (Arthropoda, Insecta, Diptera: Dolichopodidae)

The number of trees was the only factor related (positively) to abundance of long-legged-flies, accounting for 41% of variation (Table 2, panel b); in the *tree* model (panel b of Tables 3 and 4) long-legged-flies were more abundant in gardens with ponds compared to those without.

Soldier-flies (Arthropoda, Insecta, Diptera: Stratiomyidae)

Abundance was strongly positively related to habitat diversity in a garden, and weakly negatively related to structural diversity (Table 2, panel b). The *tree* model indicated that soldier-flies were more abundant in gardens with relatively less vegetated landcover (panel b of Tables 3 and 4).

Hoverflies (Arthropoda, Insecta, Diptera: Syrphidae)

Native plant richness, local human population density, number of houses and presence of ponds all had strong positive relations with hoverfly abundance, while the perimeter–area ratio of the garden was negatively associated (Table 2, panel b). In the *tree* model (panel b of Tables 3 and 4), hoverflies were very much more abundant in gardens containing ponds.

Discussion

Our need to work intensively in gardens for all the components of the BUGS project meant that survey gardens were drawn from owner-occupiers who were either relatively interested in their gardens or sympathetic to the presence of university researchers (but not necessarily motivated by their gardens). Our sample possessed relatively more large (detached) houses, and fewer small (terraced) ones: terraced, semi-detached and detached houses comprised 16, 56, and 28% of the sample respectively, compared to 50, 44, and 6% occurring in a random sample ($n = 218$) of Sheffield gardens (Gaston et al. in press). Thus the results of the study need to be interpreted in this context. Nevertheless, it is also clear that a substantial majority of UK residents invests time and interest in the garden: a random survey of Sheffield garden owners indicated that more than 75% enjoyed their garden environment, while less than 10% valued nothing about their garden (Dunnett and Qasim 2000). Our experience also revealed that owners' interest in the project or in wildlife issues did not necessarily match effort spent on the garden, due to constraints on time such as young children or a busy job. We therefore believe that our approach allowed us to survey the full range of variation in interest and creativity one might expect to encounter in a random sample (and possibly more): from gardens used daily to those largely untouched for 10 years; from gardens including wildlife meadows and ponds to those with nothing but a lawn. Further, our sample contained the full span of garden sizes as found in a random sample (Dunnett and Qasim 2000), which permitted us fully to investigate landcover in relation to garden area.

For the twenty-two invertebrate taxa examined, a broad range of factors were significantly related to their abundance in gardens. These factors operated across geographical scales, from characteristics of gardens and their management, to effects at the level of the landscape. Thirty-one out of 36 explanatory variables entered stepwise regression models at least once, and 29 did so more than once. As was found for similar analyses of species richness in the same study (Smith et al. in press b), the amount of variation explained by models varied, though in many cases it was reasonably large (Table 2). For data based on pitfall and litter samples, the total ranged from 4 to 56%, yet for Malaise traps it ranged from 16 to 92%, with the majority of models accounting for more than 50% of variation in abundance. Strong, consistent patterns did not emerge for the effects of factors across taxa. Results of the *tree* analyses partially supported the relationships identified in regression models (Table 3): in 16 out of 30 analyses (53%), the primary or secondary splits in the data occurred on variables, or closely correlated ones, that also featured in regressions.

Geographical scales of explanatory factors

The abundances of invertebrate taxa were related to variables external and internal to gardens. Of the former, the distances on easterly (snails and moths) and northerly (beetles other than Carabidae, sawflies and parasitoid wasps) axes represented the largest scales at which correlations occurred, over distances of more than 10 km. Altitude, varying by more than 200 m across the sample gardens, was strongly negatively related to the abundances in Malaise traps of beetles, spiders and social wasps, but positively to craneflies. Independent evidence for an effect of local climate on garden biodiversity is provided by the species composition of garden lawns in Sheffield. Most of the variation in the vascular plant composition of lawns was explained by Principal Components Analysis axes correlated with the west-east decline in altitude, such that plants of woodland or damp habitats were more common in the west, while weeds of waste ground were more common in the east (Thompson et al. 2004).

Measures of the extent of green space surrounding each study garden (within the 1 ha cell) featured strongly in models only occasionally: these were either the summed area of surrounding gardens (solitary bees), the summed area of all green space (beetles and social wasps), or the size of the contiguous green space fragment in which the garden lay (parasitoid wasps). Further, the directions of relationships were sometimes contrary to expectation if one predicted that green space area should have been positively correlated with the numbers of invertebrates in gardens. The general absence of strong effects for the suite of green space variables has two implications. Either the range of variation in green space extent was insufficient to detect effects, or other correlates of abundance were more important. As the total amount of green space ranged between 28 and 79% of the 1 ha cell centred on each garden, the second explanation seems more probable. Total green space was at least strongly related to the abundance of beetles in pitfall and litter samples, and to ground beetles in particular; but this finding is not supported by evidence for ground beetles in London gardens, where green space was measured at a larger scale (correlation of $\log_{10}$ abundance with % green space in a 20 ha cell, $r = -0.13$, $n = 15$, $p > 0.05$; from data in Davis 1978).

The majority of variables that correlated with abundance occurred at the scale of the garden itself (17 out of 23, 74%, for data from pitfall and litter samples, and 15 out of 24, 62%, for data from Malaise trap samples), and this pattern was reflected in the *tree* analyses too (11 out of 15 variables, 73%, on which data split for pitfall and litter data, and 8 out of 11, 73%, for Malaise trap data). The predominant factors were those associated with vegetation structure in gardens: canopy above 2 m was strongly positively related to beetles (other than Carabidae) and slugs in pitfall traps, while the area of hard surfaces was strongly negatively related to centipedes, beetles (other than Carabidae) and slugs in pitfall traps; woodlice in litter were also strongly positively related to canopy > 2 m. Sawflies, parasitoid wasps, craneflies and long-legged flies in Malaise trap samples were all strongly positively associated with the number of trees in gardens (itself closely correlated with canopy > 2 m, Smith et al. in press a). The significance of vegetation structure has been demonstrated previously for mammals: various height classes of vegetation were more important than measures of urbanisation in determining the abundances of small mammals in urban habitat patches (Dickman and Doncaster 1987). In contrast, the diversity of vegetation structures did not appear as important. Structural diversity probably is significant when considered across all taxa in a garden, whereas individual taxa are perhaps only associated with specific components of the vegetation.

On the basis of previous research in urban environments (e.g. McGeoch and Chown 1997; Miyashita et al. 1998), some garden variables that might have been expected to be important correlates of biodiversity in gardens played relatively minor roles. For example, measures of patch size and richness – garden area and land use diversity – entered models rarely. Garden area and house age were strongly negatively related to cranefly abundance alone, and habitat diversity was only strongly positively associated with soldier-flies. Such a result might have arisen because gardens comprise much of the surrounding habitat matrix; therefore the fauna recorded in a particular garden is not isolated from external populations, and thus less influenced by patch characteristics. It is possible that had we studied smaller organisms, such as the soil mesofauna, then effects due to the ‘patch’ sampled (e.g. a flower bed or area of uncut lawn) may have become apparent. Having said this, disturbance in gardens due to movements in soil and plant material, and during general re-design of gardens, are likely to homogenise invertebrate assemblages. The members of relatively sessile taxa, such as molluscs, centipedes and millipedes, were virtually ubiquitous in Sheffield gardens (Smith et al. in press b).

The species richness of plants in gardens also featured infrequently in models, although native plant richness formed strong positive relationships with the abundance of solitary bees and hoverflies, and these taxa are known to be closely associated with flora. This result was corroborated by the *tree* analysis, and by the strong relationship between the species richness of solitary bees and total plant richness (Smith et al. in press b; a further analysis, replacing native richness by % native taxa, to control for the positive correlation between the sizes of alien and native components, did not alter the result). Similarly, measures of garden management or disturbance – the use of slug pellets and the index of management intensity – were only strongly (negatively) related to snails in pitfall and litter traps respectively. The composition of litter was only weakly related to one out of the seven groups (spiders) in litter samples.

Although some plausible relationships are noted above, there were numerous cases where associations between an invertebrate group and an independent variable were obscure. For some of these cases the variables are probably correlated with other factors of real significance. Examples include slugs and woodlice related to canopy above 2 m, and snails related to the lengths of hedges and walls in gardens; all these instances could be linked to the provision of shelter or litter. Other explanatory variables, however, are less obvious, e.g. the association of garden perimeter–area ratio (greater in smaller gardens) with snails in litter, social wasps, and hoverflies. The presence of ponds and, again, perimeter–area ratio were the primary splits for 6 out of 16 groups in the *tree* analyses of Malaise trap data (Table 3, panel b), yet the reason for their inclusion is unclear.

Inconsistencies in explanatory factors

The correlates of invertebrate abundance were relatively inconsistent between taxa, and they mirror the results for species richness in the same study of Sheffield gardens (Smith et al. in press b). There are several possible reasons for this. First, as stressed previously, it is likely that some of the apparent associations were chance results: a large number of variables was examined, and evidence for many of the relationships was weak; respectively, only 44 and 66% of the significance values for factors in models of pitfall/litter and Malaise data had a probability <0.01. However, even for factors with strong evidence, the direction was often dependent on the taxon. Second, a wide range of taxa was studied: one would expect different factors to be associated with the abundance of taxa of dissimilar life histories and biology, e.g. predatory spiders compared to omnivorous molluscs. Third, the three sampling methods operated at different scales. Pitfall trapping and litter sampling were effective over relatively small areas, at the sampling point itself, or in the immediate vicinity. Therefore the taxa that such methods sampled, typically woodlice, millipedes, centipedes, and ground-dwelling beetles, arachnids and molluscs, should have better reflected local factors. In contrast, Malaise traps sampled a predominantly aerial, mobile fauna (likely to have originated from outside as well as within the garden), so that the recorded taxa should have reflected broader-scale factors. Although this latter prediction was confirmed for species richness (Smith et al. in press b), it was not borne out for abundance, where the number of factors related to the scale of the garden was similar between sampling methods.

Inferences from abundance and species richness

Urbanisation frequently leads to declines in species richness and in abundance within species. However, overall abundance of a taxon (as measured across species) may fall at a slower rate because certain species, often termed ‘urban exploiters', thrive in urban environments as other species disappear (Blair 1996; Denys and Schmidt 1998; Germaine and Wakeling 2001). Thus the abundance of organisms in a taxon may not necessarily be closely linked to the group's species richness. In the present study, some of the important explanatory factors related to abundance were also associated with species richness (Smith et al. in press b). The strongest cases were: canopy above 2 m and the number of trees for beetle abundance and species richness, respectively; distance east and altitude (which are negatively correlated) for beetle abundance and richness in Malaise traps; distance north for sawflies; altitude for spiders in Malaise traps; length of walls for snails; and plant richness for solitary bees. Such congruence suggests that where the abundance of particular invertebrate groups was high, numbers were enhanced due to a relatively large number of species, rather than to a small number of species that contributed a disproportionate number of individuals.

Indeed, when gardens were ranked according to abundance and species richness, 9 out of 16 invertebrate group-sampling method combinations (a subset of taxa, as species richness had not been evaluated for all) showed strong correlations between the two measures of biodiversity (Spearman Rank correlations on untransformed variables: beetles in pitfall traps: $r_s = 0.61$, $p < 0.001$; beetles in Malaise traps: $r_s = 0.78$, $p < 0.001$; spiders in litter: $r_s = 0.46$, $p < 0.001$; spiders in pitfall traps: $r_s = 0.63$, $p < 0.001$; spiders in Malaise traps: $r_s = 0.54$, $p < 0.05$; snails: $r_s = 0.69$, $p < 0.001$; millipedes: $r_s = 0.81$, $p < 0.001$; solitary bees: $r_s = 0.96$, $p < 0.001$; and solitary wasps: $r_s = 0.87$, $p < 0.001$). Correlations were not significant for slugs, centipedes, woodlice, bumble bees, sawflies, craneflies and true bugs; the first four of which were species-poor, but often very widespread and abundant groups. Thus for a range of relatively species-rich invertebrate groups, the significant correlations indicate that certain gardens are associated with both high species richness and abundance.

Conclusions

Many factors were related to invertebrate abundance in urban gardens, although very few assumed importance for more than a few taxa. This lack of evidence for general determinants of abundance is to be expected, as a consequence of the range of sampling methods used and the wide variety of invertebrate taxa examined, with their associated differences in mobility and resource requirements. The present study contrasts with work on habitat fragments, which has found strong effects related to patch characteristics; instead, urban gardens are interconnected over large areas and individual garden size is therefore less directly significant. In trying to extract those environmental correlates of greatest importance, the suite of variables associated with garden vegetation and its structure would be foremost. Providing mature vegetation and trees in urban gardens could be the best way of enhancing abundance in the widest possible range of taxa. Such action is largely under the control of garden owners, although the current trend in the UK for new houses to possess small gardens may discourage owners from planting trees. Further, as abundance was closely linked to species richness for a significant proportion of the taxa in this study, then appropriate garden management could have benefits for overall biodiversity.

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Appendix A. Independent variables used in analyses of relative abundance (see methods)

(1) Richness of higher plant taxa in garden; (2) richness of alien higher plant taxa in garden; (3) richness of native higher plant taxa in garden; (4) proportion of alien higher plant taxa; (5) easting, Ordnance Survey National Grid map coordinate; (6) northing, Ordnance Survey National Grid map coordinate; (7) age of house calculated in 2000; (8) altitude, m above sea level; (9) rural proximity: distance in km from centre of nearest 1 km cell with $<25\%$ urban land use; (10) habitat diversity: Simpson's diversity index for land uses in each garden; (11) structural diversity: Simpson's diversity index for vegetation canopy cover classes: <0.5, 0.5–1, 1–2, 2–3, and >3 m in each garden; (12) area of rear garden in m^2; (13) perimeter–area ratio: ratio of 'exposed' (i.e. excluding perimeter along rear of house) garden perimeter to garden area; (14) area of grass in rear garden (cut + uncut portions); (15) area of non-grass green space in rear garden (grass paths + cultivated border + vegetable patch + neglected/uncultivated); (16) area of non-green space in rear garden (hard paths + patios + green house + sheds + garage + decking); (17) presence of ponds in a rear garden (scored 1 or 0); (18) presence of compost bins or heaps in a rear garden (scored 1 or 0); (19) area of vegetation canopy 0–2 m (excluding mown grass); (20) area of vegetation canopy >2 m; (21) no. of trees >2 m tall in rear garden; (22) exposed perimeter length of rear garden (i.e. excluding perimeter along rear of house); (23) length of hedges in rear garden, m; (24) length of walls in rear garden, m; (25) length of garden boundary abutting other gardens, m; (26) proportion of garden boundary permeable to movement by animals (i.e. not composed of mortared walls); (27)

proportion of boundary abutting green space; (28) human population density (no. $40 \times 10^3 m^{-2}$, or 4 ha^{-1}), POPSURF 1991 census data; 26–29 recorded from GIS, for 1 ha circular plot centred on survey garden: (29) no. of houses (where > half of property is included), (30) area of domestic gardens, (31) area of all green space, (32) area of contiguous green space fragment; (33) management intensity index- summation of following values of management variables, data from questionnaire: (a) index of intensity of weeding (weak 1–5 strong), (b) index of intensity of pruning vegetation (weak 1–5 strong); (c) index of intensity of watering borders (weak 1–5 strong), (d) dead-heading flowers (scored 1 or 0), (e) collecting fallen leaves in autumn (scored 1 or 0), (f) use of fertiliser in garden (scored 1 or 0), (g) use of herbicides in garden (scored 1 or 0), (h) use of pesticides in garden (scored 1 or 0); (34) use of slug pellets (scored 1 or 0); (35) wildlife management index – summation of following wildlife gardening variables, data from questionnaire: (a) bird feeding (scored 1 or 0), (b) provision of nest box for birds (scored 1 or 0), (c) other management specifically to attract wildlife (scored 1 or 0); (36) estimate of proportion of vegetative matter in litter sample, averaged across replicates in a garden.

References

Allen A.A. 1964. The Coleoptera of a suburban garden. Entomologist's Record and Journal of Variation 76: 261–264.

Bailey S.E.R., North M.C. and Cook L.M. 1998. Slugs and snails and thrushes' anvils: children's surveys of slugs and snails. Journal of Conchology Special Publication 2: 171–178.

Blair R.B. 1996. Land use and avian species diversity along an urban gradient. Ecological Applications 6: 506–519.

Blair R.B. and Launer A.E. 1997. Butterfly assemblages and human land use: species assemblages along an urban gradient. Biological Conservation 80: 113–125.

Cannon A. 1999. The significance of private gardens for bird conservation. Bird Conservation International 9: 287–297.

Cannon A. 2000. Garden BirdWatch Handbook, 2nd edn. British Trust for Ornithology, Thetford.

Crawley M.J. 2002. Statistical Computing: An Introduction to Data Analysis using S-Plus. John Wiley and sons, Chichester, UK.

Davis B.N.K. 1978. Urbanisation and the diversity of insects. In: Mound L.A. and Waloff N. (eds), Diversity of Insect Faunas. Oxford, Blackwell Scientific, pp. 126–138.

Denys C. and Schmidt H. 1998. Insect communities on experimental mugwort (*Artemisia vulgaris* L.) plots along an urban gradient. Oecologia 113: 269–277.

Dickman C.R. and Doncaster C.P. 1987. The ecology of small mammals in urban habitats. I. Populations in a patchy environment. Journal of Animal Ecology 56: 629–640.

Dunnett N. and Qasim 2000. HortTechnology 10: 40–45.

Eversham B.C., Roy D.B. and Telfer M.G. 1996. Urban, industrial and other manmade sites as analogues of natural habitats for Carabidae. Annals Zoologica Fennici 33: 149–156.

Gaston K.J., Blackburn T.M., Greenwood J.J.D., Gregory R.D., Quinn R.M. and Lawton J.H. 2000. Abundance–occupancy relationships. Journal of Applied Ecology 37: 39–59.

Gaston K.J., Smith R.M., Thompson K. and Warren P.H. 2005. Urban domestic gardens (II): experimental tests of methods for increasing biodiversity. Biodiversity and Conservation.

Gaston K.J., Warren P.H., Thompson K. and Smith R.M. in press. Urban domestic gardens (IV): the extent of the resource and its associated features. Biodiversity and Conservation.

Germaine S.S. and Wakeling B.F. 2001. Lizard species distributions and habitat occupation along an urban gradient in Tucson, Arizona, USA. Biological Conservation 97: 229–237.

Gibb H. and Hochuli D.F. 2002. Habitat fragmentation in an urban environment: large and small fragments support different arthropod assemblages. Biological Conservation 106: 91–100.

Gilbert O.L. 1990. The lichen flora of urban wasteland. Lichenologist 22: 87–101.

Ihaka R. and Gentleman R. 1996. R: a language for data analysis and graphics. Journal of Computational and Graphical Statistics 5: 299–314.

Kinzig A.P. and Grove J.M. 2001. Urban–suburban ecology. In: Levin S.A. (ed.), Encyclopedia of Biodiversity, Vol. 5. Academic Press, San Diego, pp. 733–745.

Liu J., Daily G.C., Ehrlich P.R. and Luck G.W. 2003. Effects of household dynamics on resource consumption and biodiversity. Nature 421: 530–533.

Loreau M., Naeem S. and Inchausti P. (eds) 2002. Biodiversity and Ecosystem Functioning: Synthesis and Perspectives. Oxford University Press, Oxford.

Martin D. and Tate N. 1997. Surpop V2.0: Introduction. http://census.ac.uk/cdu/surpop.htm.

McGeoch M.A. and Chown S.L. 1997. Impact of urbanization on a gall-inhabiting Lepidoptera assemblage: the importance of reserves in urban areas. Biodiversity and Conservation 6: 979–993.

Miotk P. 1996. The naturalized garden – a refuge for animals? – first results Zoologischer Anzeiger 235: 101–116.

Miyashita T., Shinkai A. and Chida T. 1998. The effects of forest fragmentation on web spider communities in urban areas. Biological Conservation 86: 357–364.

Moran M.D. 2003. Arguments for rejecting the sequential Bonferroni in ecological studies. Oikos 100: 403–405.

Owen J. 1991. The Ecology of a Garden: the First Fifteen Years. Cambridge University Press, Cambridge.

Pyšek P. 1993. Factors affecting the diversity of flora and vegetation in central European settlements. Vegetatio 106: 89–100.

Roy D.B., Hill M.O. and Rothery P. 1999. Effects of urban land cover on the local species pool in Britain. Ecography 22: 507–515.

Saville B. 1997. The Secret Garden: Report of the Lothian Secret Garden Survey. Lothian Wildlife Information Centre, Edinburgh.

Smith C. 1989. Butterflies and moths in suburbia. Nature in Cambridgeshire 31: 19–27.

Smith R.M., Gaston K.J., Warren P.H. and Thompson K. in press. Urban domestic gardens (V): relationships between landcover composition, housing and landscape. Landscape Ecology 20(2): 235–253.

Smith R.M., Warren P.H., Thompson K. and Gaston K.J. in press. Urban domestic gardens (VI): environmental correlates of invertebrate species richness. Biodiversity and Conservation.

Soulé M.E., Bolger D.T., Alberts A.C., Wright J., Sorice M. and Hill S. 1988. Reconstructed dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands. Conservation Biology 2: 75–92.

Stace C. 1997. New Flora of the British Isles, 2nd edn. Cambridge University Press, Cambridge.

Sukopp H. and Starfinger U. 1999. Disturbance in Urban Ecosystems. Ecosystems of the World 16. In: Walker L.R. (ed.), Ecosystems of Disturbed Ground. Elsevier Science, Amsterdam, pp. 397–412.

Thompson K., Austin K.C., Smith R.M., Warren P.H., Angold P. and Gaston K.J. 2003. Urban domestic gardens (I): putting small-scale plant diversity in context. Journal of Vegetation Science 14: 71–78.

Thompson K., Hodgson J.G., Smith R.M., Warren P.H. and Gaston K.J. 2004. Urban domestic gardens (III): composition and diversity of lawn floras. Journal of Vegetation Science 15: 371–376.

Thompson K. and Jones A. 1999. Human population density and prediction of local plant extinction in Britain. Conservation Biology 13: 185–189.

United Nations Development Programme, United Nations Environment Programme, World Bank and World Resources Institute 2000. World Resources 2000–2001: People and Ecosystems – the fraying web of life. Elsevier Science, Amsterdam.

Vickery M.L. 1995. Gardens: the neglected habitat. In: Pullin A.S. (ed.), Ecology and Conservation of Butterflies. Chapman & Hall, London, pp. 123–134.

Wright M. 1984. The Complete Handbook of Garden Plants. Michael Joseph, London.

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Effects of livestock grazing on aboveground insect communities in semi-arid grasslands of southeastern Arizona

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Abstract. Despite the importance of invertebrates in grassland ecosystems, few studies have examined how grassland invertebrates have been impacted by disturbances in the southwestern United States. These grasslands may be particularly sensitive to one common disturbance, livestock grazing, because they have not recently evolved in the presence of large herds of bison, an important mammalian herbivore. This study examined how livestock grazing influenced vegetation-associated insect communities in southeastern Arizona. Insect abundance, richness, diversity, community composition, and key environmental variables were compared between sites on active cattle ranches and sites on a 3160 ha sanctuary that has not been grazed by cattle for over 25 years. Vegetation-associated insect communities were found to be sensitive to livestock grazing. Overall abundance of these insects was lower on grazed grasslands, and certain insect orders appeared to be negatively affected by livestock grazing; beetles were less rich, flies were less diverse, and Hymenoptera were less rich and diverse on grazed sites. Conversely, Hemiptera were more diverse on grazed sites. Species composition of vegetation-associated insect communities also differed and was significantly correlated with percent vegetation cover and number of shrubs. Insect species responsible for these differences were taxonomically diverse, and included herbivores and predators/parasites. When compared to other studies conducted in areas of the United States that fall within the historic range of bison, this study suggests that invertebrates in areas outside this range may be more sensitive to grazing pressure.

Abbreviations: ANOVA – analysis of variance; CCA – canonical correspondence analysis; MDA – multigroup discriminant analysis; NMDS – nonmetric multidimensional scaling; PCoA – principal coordinate analysis; PCA – principal component analysis

Introduction

Livestock grazing is only one of several human activities that threaten the world's grasslands, yet in certain areas, such as in the western United States, its widespread prevalence has generated great interest among conservation biologists and managers in understanding its ecological effects (e.g., Brussard et al. 1994; Fleischner 1994; Noss 1994). In response to this interest, numerous studies have examined the effects of livestock grazing on grassland plants, birds, reptiles, and mammals (see Fleischner 1994; Jones 2000 for reviews). In contrast, far fewer studies have examined the effects of livestock grazing on invertebrates, despite the fact that grassland invertebrates comprise an overwhelming proportion of animal biomass and biodiversity, form a major component of terrestrial food webs, and play pivotal roles in ecosystem functions, including decomposition, pollination, seed dispersal, pest control, soil conditioning, and nutrient cycling (Wilson 1987; Kellert 1993; Whitford et al. 1995; Coleman and Hendrix 2000). Livestock grazing alters various environmental factors that should impact invertebrates, including vegetation characteristics, soil compactness, and microhabitat temperature and humidity (Whitford et al. 1995; Loftin et al. 2000). Studies examining the responses of invertebrates to disturbance suggest that they can be as sensitive to changes in these environmental factors as vertebrates and plants, but that patterns in invertebrate diversity are not necessarily correlated with patterns in vertebrate or flowering plant diversity (Majer 1983; Yen 1987; Burbidge et al. 1992; Milchunas et al. 1998), Thus, as Wilson (1987) pointed out over a decade ago, studies on how human disturbance affects invertebrate communities are vital for pursuing the goals of conservation biology.

The most extensive research on the effects of livestock grazing on grassland invertebrate communities has taken place in Europe. Early studies in England were motivated by a concern for preserving the biodiversity of grassland invertebrates *per se*, and a wide variety of invertebrate taxa were examined (Morris 1967, 1968, 1969a, b). European researchers have continued to expand on this work over the last decade (Gibson et al. 1992a, b; Dennis et al. 1997; Bonte et al. 2000; Bell et al. 2001; Kruess and Tscharntke 2002a, b). These studies indicate that (1) livestock grazing can affect grassland invertebrate communities, primarily through their effect on the composition, quality, and architecture of vegetation, and (2) certain invertebrate groups are more sensitive to livestock grazing than others.

In contrast to European work, most studies of livestock grazing of grassland invertebrates in the United States have had a more narrow focus. Numerous studies have examined the effect of livestock grazing on grasshopper communities (e.g., Capinera and Sechrist 1982; Jepson-Innes and Bock 1989; Quinn and Walgenbach 1990; Miller and Onsager 1991; Welch et al. 1991). This research has been motivated both by the fact that some grasshopper species are considered to be serious rangeland and crop pests and by the fact that grasshoppers are dominant herbivores in many grassland systems in the United States (Otte 1981). Of the relatively few studies that have expanded our knowledge of livestock grazing on grassland invertebrates in the United States, most have examined belowground non-insect invertebrates (e.g., Leetham and Milchunas 1985; Wall-Freckman and Huang 1998; Kay et al. 1999).

Although these studies have provided valuable insights on livestock grazing effects on grassland invertebrates and added much to our knowledge of specific geographic regions, several important gaps in our knowledge remain. First, in contrast to European work, the relatively narrow focus of studies in the United States limits our knowledge about the effects of livestock grazing on grassland invertebrate communities in general, and how particular groups may be differentially affected. Second, we know very little about how livestock grazing affects invertebrate communities in grasslands whose recent evolutionary history does not include herds of large herbivores. Grasslands and their associated fauna that have evolved in the presence of large herbivores are expected to be relatively insensitive to, or even dependent upon, grazing by domestic livestock compared to grasslands with no recent evolutionary history of large herbivores (Mack and Thompson 1982; Fielding and Brusven 1996; Pykala 2000). Most European grasslands have been subjected to grazing for millennia, both by native grazers and domestic livestock (Pykala 2000), and almost all studies in the United States have been conducted in areas that fall within the historic range of the American bison (*Bison bison*). Yet a large portion of the far western and southwestern United States has not been exposed to large herds of native herbivores since the Pleistocene (McDonald 1981). Thus, there is a pressing need for studies that examine how invertebrate communities associated with these potentially more sensitive grasslands are affected by livestock grazing (Loftin et al. 2000).

This study seeks to address these gaps in our knowledge by examining how livestock grazing affects a variety of invertebrates in grasslands of southeastern Arizona. The Audubon Appleton-Whittell Research Ranch, a 3160 ha sanctuary in southeastern Arizona that has not been grazed by cattle since 1967, provides an excellent opportunity to examine long term effects of grazing cessation. Surrounded by active cattle ranches, the Ranch is one of the largest sanctuaries of ungrazed grassland in the southwestern United States. Most other sites used in comparative studies of grazing involve enclosures of ungrazed grasslands less than 50 acres (Fleischner 1994). In addition, the Ranch has been the site of numerous studies of other taxa, including vegetation, mammals, and birds (e.g., Bock et al. 1984; Brady et al. 1989; Bock and Bock 1993). Studies at the Ranch have shown strong vegetative responses to the cessation of livestock grazing (Brady et al. 1989; Bock and Bock 1993) and support the hypothesis that plants in these grasslands are more sensitive to livestock grazing than plants of the Central Plains of the United States.

The study described here focuses on a diverse group of invertebrates, insects, and addresses four objectives by comparing insect communities at multiple ungrazed sites on the Ranch with paired grazed sites on adjacent cattle ranches. These objectives are to: (1) determine if insect community structure differs between grazed and ungrazed lands, (2) identify insect groups that may be sensitive to livestock grazing, (3) compare the effect of two types of grazing regimes (traditional and holistic approaches) on insect communities, and (4) determine whether any observed differences in insect community structure between grazed and ungrazed sites are related to key environmental variables (percent plant cover, number of shrubs, vegetation structure, and microhabitat temperature and relative humidity).

Study area

The study was conducted at Audubon's Appleton-Whittell Research Ranch located on the Sonoita Plain in Santa Cruz County, Arizona. Operated by the National Audubon Society, the Ranch is a 3160 ha sanctuary of private and public land, which is surrounded by active cattle ranches. Although the Ranch was grazed by livestock until 1967, I use "ungrazed" to describe the grasslands within the Research Ranch boundary. By "ungrazed" I mean that it is no longer disturbed by active livestock grazing; I do not suggest that the area has returned to its "pregrazed" condition, whatever that may have been.

Four 30 × 30 m ungrazed sites on the Research Ranch were paired with four 30 × 30 m grazed sites on adjacent active cattle ranches. Sites were paired based on similarities in elevation, topography, soil type, and general vegetation and sites within a pair were separated by between 1.0 and 1.8 km. Distance between pairs of sites varied between 1.8 and 6 km, with an average distance of 4.3 km. Two of the grazed sites (Sites 2-D and 4-D) were managed using holistic resource management practices (Savory 1999) that involve using high density stocking rates (one animal unit per 6 ha) with short duration rotation. The other two grazed sites (Sites 1-D and 3-D) were managed with traditional grazing practices that involve using lower stocking rates (approximately one animal unit per 39 ha) with season-long grazing.

Because of its size and the length of time it has been ungrazed, the Research Ranch provides one of the greatest contrasts between grazed and ungrazed grasslands in the southwestern United States, and as such represents the logical point to start investigations into the effects of livestock grazing in the area. Although the four ungrazed sites are all located on the Research Ranch, there is no reason to believe that their location on the Research Ranch reflects any commonality other than the cessation of livestock grazing in 1967 for the following reasons: (1) the sites are widely separated, and (2) the only management practice conducted on the Research Ranch sites between 1967 and the time the study was conducted was the removal of livestock. In other words, no specific management practices, other than the removal of livestock, have taken place on the Research Ranch that would make it different from any other area in the region where livestock had been removed. However, the results of this study are generalized only to the grasslands of the Research Ranch and the surrounding cattle ranches to avoid pseudoreplication (Hurlbert 1984).

Sampling methods

Environmental sampling

Several environmental characteristics were measured at each site. Relative humidity and temperature were measured 2.5 cm above the soil surface with a Fisherbrand® Printing Hygrometer/Thermometer at 9 regularly spaced locations within each site. All pairs of sites were sampled, in varying order, on 11 days in the late summer and early fall of 1993 between 1000 and 1600. In August 1994, percent vegetative cover was measured at each site by visually estimating the percent vegetative cover to the nearest 5% in each of 54, 1 m^2, wire rings used to delineate subsample boundaries (Onsager and Henry 1978). In addition, the total number of the most common shrub found in the study area, *Baccharis pteroniodes*, was counted, and the maximum height of each was measured to give an estimate of habitat structure.

Insect sampling

I employed a repetitive sampling regime of the eight sites because repetitive sampling over more limited areas has been found to be a more efficient strategy for collecting cryptic, covert, or rare species than non-repetitive sampling efforts spread over larger areas (Dobyns 1997). Vegetation-associated insects were sampled in the same location with sweep net (Martin 1977) three times in 1993 (September–November) and four times in 1994 (June–August). At each site, sweep net sampling was conducted once a day for four days per sampling bout, so that each pair of sites could be sampled once during four time periods throughout the day: mid-morning, late-morning, early afternoon, and late afternoon. Thus, during each bout, each site was sampled once during each of the four sampling periods. Each sampling effort consisted of 100 arc-shaped sweeps.

Insects were identified to the lowest taxonomic level possible. Specimens that could not be identified to species were separated into recognizable taxonomic units (i.e., taxa based on morphological similarity) (Rees 1983). Estimates of richness and diversity obtained by using recognizable taxonomic units have been found to be comparable to those obtained by specialists who identify to known species (Oliver and Beattie 1993). Data from both years were combined because of the non-overlapping temporal distribution of sampling (i.e., different parts of the season were sampled each year).

Data analysis

Environmental data

Data used in parametric analyses were tested for normal distribution using Lillefors test (SYSTAT 1997) and transformed before analyses, if necessary. If data could not be transformed to meet the assumption of normality, nonparameteric statistics were used. Differences in average relative humidity and temperature for each pair of sites (ungrazed site – grazed site) were calculated and average differences were compared to zero using a one sample *t*-test. Shrub abundance at ungrazed and grazed sites was compared using a

Mann–Whitney *U* test. Data on percent vegetation cover and structure (as estimated by the height of *B. pteroniodes*) were analyzed for differences associated with grazing history using an ANOVA blocked by paired sites. Means are reported ± one standard error.

Insect data

Total abundance, species richness, and species diversity of insects in grazed and ungrazed sites were conducted at two taxonomic resolutions: for all insects combined and for each of the six most common insect orders. Abundance was simply the absolute number of individuals found at each site and richness was the total number of species present at each site. Diversity was calculated using the Shannon-Wiener Index, which not only reflects richness but also takes the evenness of species abundances into account (Smith 1986). Abundance, richness, and diversity were analyzed with ANOVA, blocked by paired sites.

To determine whether species composition of insect communities differed between grazed and ungrazed sites, patterns in insect community composition were examined using multivariate statistical techniques. Specifically, ordination methods were used to examine whether sites showed any patterns in species space relative to grazing history. Data sets were first reduced by eliminating rare species. Rare species were considered to be any species whose average abundance was less than 0.15% of the total insects captured. Rare species are typically removed from data analyzed with multivariate techniques because their presence may be due more to chance than to any underlying ecological condition, and their inclusion in analyses may increase the statistical "noise" and mask underlying patterns (Gaston 1994).

After reduction, a similarity index was calculated for each combination of sites. Percentage similarity (also known as Renkonen's index) was used because it performs well over a diverse set of ecological data sets, and sample size and diversity have only small effects on the performance of the index in measuring actual similarity between sampling units (Gauch 1982; Ludwig and Reynolds 1988; Krebs 1989). Similarity indices were used in a principal coordinate analysis (PCoA), which in combination with principal component analysis (PCA), was employed to detect general ordination patterns of the sites in species space. PCoA was used because it is an ordination method which is robust against non-linear relationships between sampling units (Gauch 1982; Pimentel 1993) and PCA was used to assign species loadings to ordination axes. The resulting configurations were rescaled using nonmetric multidimensional scaling (NMDS).

The significance of patterns found in species space with relationship to grazing types was determined using multigroup discriminant analysis (MDA), a technique that evaluates the within and between variation of *a priori* groups (Digby and Kempton 1987) and calculates generalized distances and 95% confidence radii about group centroids. I conducted two MDAs: one comparing ungrazed sites vs. grazed sites, and one comparing ungrazed sites vs. holistically managed grazed sites vs. traditionally grazed sites.

Finally, to determine whether any of the environmental variables measured explained patterns observed in the ordination, Spearman rank correlations were calculated for each environmental variable and the site scores of the first two NMDS ordination axes (Jongman et al. 1995; Quinn and Keough 2002). Performing an ordination and secondarily relating the ordination to environmental variables are preferred when the primary purpose of a study is to detect patterns in community structure *per se* and of secondary interest is whether any of the environmental variables measured explain those patterns (Jongman et al. 1995; McCune and Grace 2002). In this study, the major goal was to detect patterns in insect communities that might be associated with livestock grazing, with a secondary goal of determining whether any of the abiotic and vegetative variables measured might be associated with observed differences. Alternative methods, such as canonical correspondence analysis (CCA), are not appropriate under these circumstances. CCA ignores community structure that is unrelated to measured environmental variables and, as such, is best suited for studies designed to determine whether specific environmental variables play any role in structuring communities, not to determine whether the strongest community patterns are related to environmental variables (Jongman et al. 1995; McCune and Grace 2002).

Results

Environmental variables

The average difference in temperature between ungrazed and grazed sites (0.04 ± 0.65 °C) was not significantly different from zero ($T = 0.05$, $p = 0.96$). Similarly, the average difference in relative humidity between ungrazed and grazed sites (2.1 ± 1.51%) did not differ significantly from zero ($T = 1.4$, $p = 0.26$). In contrast, several characteristics of vegetation differed between ungrazed and grazed sites. Total percent vegetation cover was significantly greater on ungrazed sites (57.7 ± 1.80%) than grazed sites (30.8 ± 3.31%) ($F = 9.5$, $p = 0.03$). The abundance of the common shrub, *B. pteroniodes*, was also significantly greater on ungrazed sites (120 ± 44.9) than grazed sites (11 ± 3.3) ($U = 0$, $p = 0.02$). However, vegetation structure, as measured by the average height of *B. pteroniodes* (40.9 ± 1.56 cm for ungrazed sites, 31.1 ± 6.9 cm for grazed sites), did not differ significantly between grazed and ungrazed sites ($F = 1.8$, $p = 0.24$).

Insects associated with vegetation

A total of 6058 adult individuals collected in 1993 and 1994 were sorted into 229 species in 10 orders: Coleoptera, Diptera, Hemiptera, Homoptera, Hymenoptera, Lepidoptera, Mantodea, Neuroptera, Orthoptera, and Phasmida. Insects were more abundant on ungrazed sites, although species richness and diversity did not differ significantly between ungrazed and grazed sites (Table 1). Six of the most common insect orders were examined for differences in abundance, richness, and diversity (Table 1). On ungrazed sites, Coleoptera were more rich, Diptera were more diverse, and Hymenoptera were both more rich and diverse. In contrast, Hemiptera were less diverse on ungrazed sites.

The data set was reduced prior to multivariate analysis by eliminating rare species, resulting in 5661 individuals of 41 species being used in all multivariate analyses. Eigenvalues and percent variance explained for the first six principal coordinate axes are reported in Table 2. Because axes 3–6 explained relatively little variation compared to axes 1–2, they are not considered further. Rescaled ordination of the data revealed an obvious pattern in insect species space between grazed and ungrazed sites along axis 1 (Figure 1), which explained 52.6% of the variation. MDA was used to analyze the magnitude of these differences. A test of overall discrimination based on equality of centroids showed that groups differed significantly ($\lambda = 0.03$, $F = 23.1$, $p = 0.01$) and

Table 1. Differences in abundance, richness, and diversity for all insects combined and for the six most common insect orders collected by sweep net.

Group	Ungrazed	Grazed	*F*-value
All Insects			
Abundance	957.8 ± 159.54	561.5 ± 110.32	**$F = 12.1$, $p = 0.04$**
Richness	77.0 ± 5.79	68.0 ± 2.38	$F = 1.3$, $p = 0.39$
Diversity	3.7 ± 0.22	3.8 ± 0.27	$F = 0.1$, $p = 0.79$
Coleoptera			
Abundance	109.0 ± 39.89	101.8 ± 44.00	$F = 0.01$, $p = 0.92$
Richness	18.5 ± 1.32	14.5 ± 0.87	**$F = 19.2$, $p = 0.02$**
Diversity	2.9 ± 0.39	2.1 ± 0.42	$F = 2.6$, $p = 0.21$
Diptera			
Abundance	21.0 ± 5.61	25.3 ± 2.32	$F = 0.7$, $p = 0.47$
Richness	14.0 ± 2.61	11.5 ± 0.87	$F = 2.0$, $p = 0.25$
Diversity	3.6 ± 0.24	2.9 ± 0.08	**$F = 9.6$, $p = 0.05$**
Hemiptera			
Abundance	254.8 ± 97.28	21.5 ± 3.62	$F = 5.9$, $p = 0.09$
Richness	7.3 ± 0.95	6.5 ± 0.87	$F = 0.3$, $p = 0.64$
Diversity	0.4 ± 0.09	1.8 ± 0.45	**$F = 9.4$, $p = 0.05$**
Homoptera			
Abundance	431.8 ± 95.27	322.0 ± 83.86	$F = 1.0$, $p = 0.40$
Richness	12.0 ± 0.71	11.8 ± 0.85	$F = 0.1$, $p = 0.71$
Diversity	2.01 ± 0.11	1.66 ± 0.23	$F = 1.9$, $p = 0.27$
Hymenoptera			
Abundance	8.3 ± 1.60	3.0 ± 0.71	$F = 7.4$, $p = 0.07$
Richness	7.0 ± 1.23	2.7 ± 0.48	**$F = 10.5$, $p = 0.05$**
Diversity	2.7 ± 0.27	1.4 ± 0.23	**$F = 16.2$, $p = 0.03$**
Orthoptera			
Abundance	128.8 ± 29.57	83.3 ± 21.83	$F = 2.6$, $p = 0.20$
Richness	14.5 ± 2.02	17.8 ± 1.18	$F = 1.0$, $p = 0.38$
Diversity	3.3 ± 0.15	3.6 ± 0.13	$F = 1.4$, $p = 0.32$

Means are reported ± one standard error. *F* values with a $p \leq 0.05$ are in bold face font.

Table 2. Eigenvalues, percent variance, and cumulative variance for principal coordinate axes associated with insect data.

Axes	1	2	3	4	5	6
Eigenvalue	7050.33	2761.40	1551.78	1066.88	724.53	545.87
Percent variance	52.60	20.60	11.58	7.96	5.41	1.86
Cumulative percent	52.60	73.20	84.78	92.73	98.14	100.00

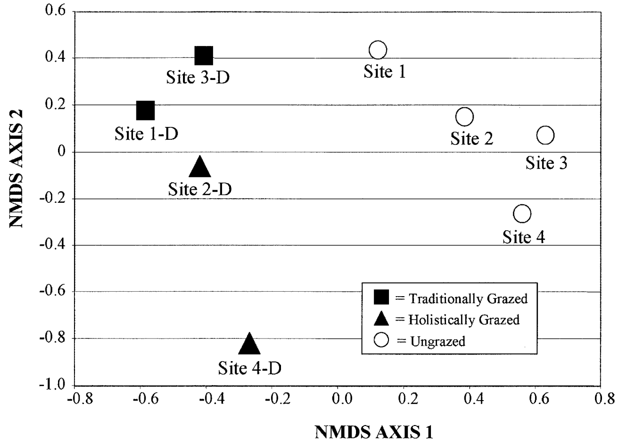

Figure 1. Nonmetric multidimensional scaling (NMDS) ordination of species collected at grazed and ungrazed sites.

univariate testing along the first two principal coordinate axes showed that ungrazed and grazed sites separated significantly along axis 1 (Table 3). The generalized distance, or the distance between grazed and ungrazed centroids in discriminant space expressed in units of standard deviations, was 9.6 and the 95% confidence radii for both groups were 1.59.

Table 3. Insect Species MDA Manova Table: Univariate testing for group differences along the first two principal coordinate axes between (A) ungrazed and grazed sites and (B) ungrazed, holistically grazed, and traditionally grazed sites.

Coordinate axis	Among mean square	Within mean square	*F*-Ratio	Probability	Adjusted probability
A. Between ungrazed and grazed sites along the first two principal coordinate axes					
1	0.880	0.020	43.69	<0.001	0.003
2	0.052	0.158	0.33	0.879	0.972
B. Among ungrazed, holistically grazed, and traditionally grazed sites along the first two principal coordinate axes					
1	0.447	0.021	20.85	0.005	0.018
2	0.262	0.095	2.75	0.156	0.493

The particular insect species correlated with principal component axis 1, and the strength and direction of the relationship, are shown in Table 4. Thirteen species showed a positive correlation with axis 1, meaning that they are associated with ungrazed sites, while three species showed a negative correlation with axis 1, indicating that they are associated with grazed sites.

Rescaled ordination of the data also suggests a pattern in insect species space between traditionally and holistically grazed sites along axes 1 and 2 (Figure 1). A test of overall discrimination based on equality of centroids of ungrazed, holistically grazed, and traditionally grazed sites was suggestive of differences ($\lambda = 0.01$, $F = 4.1$, $p = 0.10$) and univariate testing along principal coordinate axes 1 and 2 showed group differences along axis 1 (Table 3). However, generalized distances between groups show that the centroids of both types of grazed groups were much closer to each other than either was to the ungrazed group; the generalized distance between ungrazed sites and traditionally and holistically grazed sites was 8.95 and 10.43, respectively, and the distance between holistically and traditionally grazed sites was 2.89. The confidence radius for the ungrazed centroid was 1.59 and confidence radii for both grazed centroids were 8.98.

Relationship of insect community composition and environmental variables

Rank correlations for sweep net data showed that both percent vegetative cover and shrub number were significantly positively correlated with NMDS ordination scores for axis 1 (Table 5).

Table 4. Principal component correlations for 16 species or morphospecies with common names of lowest taxonomic unit to which identified.

Order	Species, Genus, or Family – Common Name	Correlation
Orthoptera	*Opeia obscura* (Thomas) – Obscure Grasshopper	0.265
Coleoptera	Melyridae – Soft-Winged Flower Beetle	0.255
Homoptera	Cercopidae – Froghopper/Spittlebug	0.251
Homoptera	*Acanalonia conica* (Say) – Acanalonid Planthopper	0.250
Orthoptera	*Eritettix simplex* (Scudder) – Velvetstriped Grasshopper	0.246
Orthoptera	*Dactylotum variegatum* (Scudder) – Rainbow Grasshopper	0.241
Diptera	Bombyliidae – Bee Fly	−0.228
Orthoptera	*Poecilotettix pantherinus* (F. Walker) – Panther Spotted Grasshopper	0.221
Coleoptera	Curculionidae – Snout Beetle	0.220
Orthoptera	*Amphitornus coloradus* (Thomas) – Striped Grasshopper	0.220
Homoptera	Cicadellidae – Leafhopper	0.217
Orthoptera	*Oecanthus* sp. – Tree Cricket	0.211
Orthoptera	*Cordillacris crenulata* (Bruner) – Crenulatewinged Grasshopper	−0.209
Hemiptera	*Extarademus macer* (Van Duzee) – Lygaeid Bug	0.195
Homoptera	*Cuerna arida* (Oman and Beamer) – Cicadellid Leafhopper	0.190
Orthoptera	*Trachyrhachis mexicana* Saussure – Bandwinged Grasshopper	−0.155

Correlations of species with principal component axis 1 (only those greater than 0.15 are reported).

Table 5. Spearman rank correlations of values of environmental variables at each site with the NMDS ordination scores at the same site.

Environmental Variable	Axis 1	Axis 2
Relative humidity	0.45	−0.17
Temperature	0.41	−0.24
Percent vegetative cover	0.74*	0.21
Shrub number	0.83*	−0.17
Shrub height	0.31	0.48

*$p < 0.05$.

Discussion

Responses of vegetation-associated insects

This study found that vegetation-associated insect communities of grazed and ungrazed grassland sites in southeastern Arizona differed strongly. Overall, insects were significantly more abundant in ungrazed areas than in grazed areas, a result also found in European studies involving several insect orders associated with vegetation (Morris 1967, 1968, 1969a; Kruess and Tscharntke 2002a). In addition, several insect groups in this study showed differences between grazed and ungrazed sites at the order level. On ungrazed sites, beetle communities were more rich, flies were more diverse, and Hymenoptera were more rich and diverse compared to grazed sites. Some of these results are similar to those found by Kruess and Tscharntke (2002a, b), who found that species richness of Hymenoptera and Coleoptera was higher on ungrazed grasslands than on grazed pastures in Germany.

Differences in total abundance of all vegetation-associated insects, and specific differences in richness and diversity of particular orders may be related to differences in vegetative characteristics between ungrazed and grazed sites. Average percent vegetative cover on ungrazed grasslands was almost double of that on grazed grasslands, and average shrub abundance was over 10-times greater on ungrazed grasslands. Thus, the abundance of resources available for phytophagous insects is much higher on ungrazed sites, and may translate to bottom up effects on higher trophic levels, leading to a greater overall abundance of all insects. In addition, although species composition of vegetation was not measured in this study, previous studies on the Research Ranch have found that ungrazed sites have a greater diversity of plants than grazed sites (Bock et al. 1984; Brady et al. 1989), and this increased complexity of vegetation may account for greater richness and/or diversity of certain insect groups. This may be particularly true of beetles, flies, and Hymenoptera, many of which have close associations with particular plants.

In contrast to these groups, Hemiptera in this study were more diverse on grazed sites than on ungrazed sites. This pattern is undoubtedly due to one sap-feeding species of lygaeid bug, *Blissus omani*, which was much more abundant in ungrazed sites and accounted for 94% of all Hemiptera captured. Thus, the overwhelming abundance of this one species in ungrazed sites is responsible for the decreased diversity observed in Hemiptera in ungrazed sites.

This study also showed that species composition of vegetation-associated insect communities between grazed and ungrazed areas was quite different, and that these differences were significantly correlated with two vegetation characteristics, percent vegetation cover and shrub abundance (Table 5). While most of the work in the United States on the effects of livestock grazing on invertebrates has focused on grasshoppers, this study found that species affected by grazing were taxonomically diverse, falling into five different orders (Orthoptera, Coleoptera, Homoptera, Diptera, and Hemiptera) (Table 4). Less than half of the most heavily affected species were grasshoppers. The majority of affected species in the five orders were positively correlated with ungrazed sites, with only two grasshopper species strongly associated with grazed sites. The results concerning grasshoppers in this study are similar to those obtained by Jepson-Innes and Bock (1989) in their study of an ungrazed site on the Ranch and a grazed site on an adjacent cattle ranch. Although analyzed at a coarser scale (grasshopper subfamily), their results are comparable to this study. They found that grasshopper community composition differed between the two sites, with patterns in grasshopper subfamilies in the summer consistent with the pattern displayed by six out of the seven grasshopper species found to be responsive to grazing in this study. In this study, other plant feeders besides grasshoppers were also found to load significantly on the first principal component axis, including a snout beetle, a tree cricket, a true bug, and four Homopteran hopper species (Table 4).

Not all species sensitive to livestock grazing were herbivores, however. A species of soft winged flower beetles (Melyridae), whose adults and larvae are predaceous and common on flowers (Borror et al. 1992) was found to be positively associated with ungrazed grasslands. A strong association with flowers has been found to be important in determining invertebrate community composition in European studies; Morris (1967) found that species associated with flowers had higher abundances in ungrazed plots in English chalklands. In contrast, a bee fly (Bombyliidae), whose larvae are either parasitic on immature stages of other insects or predaceous on grasshopper eggs (Borror et al. 1992), was positively associated with grazed grasslands. This is in contrast to a study by Kruess and Tscharntke (2002b), who found that parasitism rates of digger wasps were higher on ungrazed grasslands.

Unlike the clear differences between community composition of vegetation-associated insects in grazed and ungrazed areas, differences between traditional and holistic grazing practices in this community were not obvious. Although multivariate techniques tended to separate out insect communities according to these two grazing practices, the generalized distances between traditional and holistic groups was small compared to the distances separating each from ungrazed communities. Because of the small sample size in this study, more study of the effects of holistic management techniques on grassland insects is necessary to determine its influence on insect community composition. However, this study, like others conducted on vegetation on the Ranch (Brady et al. 1989; Bock and Bock 1993), does not support Savory's theory that the removal of grazing animals will have long term deleterious effects on the grassland, or the specific prediction that, after an initial improvement, grasslands on the Research Ranch would deteriorate, leading to a loss of diversity (Savory 1986). No overall differences in diversity or richness in insects between grazed and ungrazed sites were found in this study.

Evolutionary history of grasslands and sensitivity of invertebrates to grazing

When contrasted with other studies of insect community responses in grasslands of the United States, this study provides evidence that insects in grasslands without a recent evolutionary history with large herds of mammalian herbivores may be more sensitive to grazing pressure than grasslands that have evolved in their presence. Although a few studies of grasshopper communities in regions within the historic range of bison have found decreased abundance or changes in community composition associated with grazing (Capinera and Sechrist 1982; Quinn and Walgenbach 1990; Fielding and Brusven 1995), numerous other studies have shown that grasshoppers and other insects are either positively influenced or not affected by livestock grazing in these areas. For example, several early studies (Coyner 1939; Weese 1939; Smith 1940) from the tall-grass prairie region of central Oklahoma documented greater total abundances of a variety of insect taxa, including grasshoppers, in response to increased grazing intensity. This pattern has also been found in Kansas and Nebraska, where greater grazing intensity was associated with higher abundances of grasshoppers (Campbell et al. 1974; Joern 1982). Milchunas et al. (1998) report data from Lavigne et al. (1972) that show that aboveground macroarthropod abundance was higher in lightly grazed grasslands than in ungrazed grasslands in the Central Plains Experimental Range of Colorado. In addition, arthropod diversity in that area also showed a bell shaped pattern, with the highest diversity associated with moderately and lightly grazed lands, and the lowest diversity with ungrazed grasslands, indicating that diversity was actually increased by low to moderate levels of livestock grazing. Other studies conducted within the historic range of bison (e.g., Holmes et al. 1979; Miller and Onsager 1991; Welch et al. 1991) have found little response of insect communities to livestock grazing. In contrast to these studies, the results reported here show that livestock grazing in an area outside that range is associated with decreased total abundance and differing community composition, and not with increased insect diversity. However, this conclusion must be interpreted with caution given the difficulty of comparing grazing intensity across studies. Although the level of grazing intensity at these sites were judged to be moderate, based on the stocking levels and the condition of the grassland, the possibility exists that the grazing intensity in this study corresponds to high intensity grazing reported in other studies. If so, then additional studies examining a range of grazing intensities needs to be conducted in the area to establish if low to moderate levels of grazing result in similar patterns.

Implications for conservation

The results of this study highlight the need for examining a variety of taxa in order to obtain a more complete picture of how human impacts affect invertebrate communities. While studies of dominant groups, such as grasshoppers, provide information useful to conservationists, patterns seen in these taxa may not be reflective of trends in other important invertebrates. As in European studies, this study showed that livestock grazing was found to affect multiple functional groups and a wide variety of taxa. In addition, some taxa as a whole appear to be sensitive to grazing, and may warrant particular management attention. In this study, Hymenoptera, many of which are important pollinators, appeared to be particularly sensitive to livestock grazing, and further studies are needed to examine the extent of this effect and its ramifications for ecosystem function.

This study suggests that several characteristics associated with vegetation may be important in driving many of the differences observed in vegetation-associated insect communities. However, multiple abiotic and biotic factors are undoubtedly responsible for community differences, and the relative importance of these variables surely varies species by species. While determining specific mechanistic reasons of how particular environmental variables associated with livestock grazing affect insects is interesting ecologically, it is less important for directing conservation efforts. In other words, even if one or two specific effects of livestock grazing (e.g., soil compaction, vegetative cover) could be identified as the most important environmental variables driving patterns in most insect species, it is unlikely this knowledge would change options available for land managers. There is no obvious way to change grazing practices so that only one variable (e.g., soil compaction) is affected without also affecting other variables associated with grazing. Because of this, priority should be placed on understanding how grazing as a whole, through its multiple effects on numerous environmental factors, affects insect species and communities and the important ecological functions associated with them.

The importance of considering invertebrates in grassland management cannot be overstated. Because invertebrates comprise the major component of animal diversity and fulfill important ecosystem functions, an understanding of how this diversity can be protected must be a high priority for conservation biologists. This study shows that the composition of vegetation-associated insect communities differs between grazed and ungrazed areas in a southwestern United States grassland, indicating that overall diversity should theoretically be higher in a landscape which includes a mosaic of both types of environments. This is a management strategy suggested by several scientists working with invertebrates in Europe (Dennis et al. 1997; Bell et al. 2001; Kruess and Tscharntke 2002b), where livestock grazing has the added benefit of suppressing exotic plant invasions (Dennis et al. 1997). However, given the prevalence of livestock grazing in grasslands in the southwestern and western United States, overall diversity of invertebrate communities can potentially be maximized by emphasizing the protection of grasslands from livestock grazing.

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References

Bell J.R., Wheater C.P. and Cullen W.R. 2001. The implications of grassland and heathland management for the conservation of spider communities: a review. Journal of Zoology (London) 255: 377–387.

Bock C.E. and Bock J.H. 1993. Cover of perennial grasses in southeastern Arizona in relation to livestock grazing. Conservation Biology 7: 371–377.

Bock C.E., Bock J.H., Kenney W.R. and Hawthorne V.M. 1984. Responses of birds, rodents, and vegetation to livestock exclosures in a semidesert grassland site. Journal of Range Management 37: 239–242.

Bonte D., Maelfait J.-P. and Hoffmann M. 2000. The impact of grazing on spider communities in a mesophytic calcareous dune grassland. Journal of Coastal Conservation 6: 135–144.

Borror D.J., Triplehorn C.A. and Johnson N.F. 1992. An Introduction to the Study of Insects. Saunders College Publishing, Fort Worth, Texas.

Brady W.W., Stromberg M.R., Aldon E.F., Bonham C.D. and Henry S.H. 1989. Response of a semidesert grassland to 16 years of rest from grazing. Journal of Range Management 42: 284–288.

Brossard P.F., Murphy D.D. and Tracy C.R. 1994. Cattle and conservation biology-another view. Conservation Biology 8: 919–921.

Burbidge A.H., Leichester K., McDavitt S. and Majer J.D. 1992. Ants as indicators of disturbance at Yanchep National Park, Western Australia. Journal of the Royal Society of Western Australia 75: 89–95.

Campbell J.B., Arnett W.H., Lambley J.D., Jantz O.K and Knutson H. 1974. Grasshoppers (Acrididae) of the Flint Hills Native Tall Grass Prairie in Kansas. Kansas State University Agricultural Experiment Station, Research Paper 19.

Capinera J.L. and Sechrist T.S. 1982. Grasshopper (Acrididae)-Host plant associations: response of grasshopper populations to cattle grazing intensity. Canadian Entomologist 114: 1055–1062.

Coleman D.C. and Hendrix P.F. (eds) 2000. Invertebrates as Webmasters in Ecosystems. CAB International, New York.

Coyner W.R. 1939. A report of the effect of overgrazing on the Acrididae. Proceedings of the Oklahoma Academy of Science 19: 83–85.

Dennis P., Young M.R., Howard C.L. and Gordon I.J. 1997. The response of epigeal beetles (Col.: Carabidae, Staphylinidae) to varied grazing regimes on upland *Nardus stricta* grasslands. Journal of Applied Ecology 34: 433–443.

Digby P.G.N. and Kempton R.A. 1987. Multivariate Analysis in Community Ecology. Chapman and Hall, London.

Dobyns J.R. 1997. Effects of sampling intensity on the collection of spider (Araneae) species and the estimation of species richness. Environmental Entomology 26: 150–162.

Fielding D.J. and Brusven M.A. 1995. Grasshopper densities on grazed and ungrazed rangeland under drought conditions in southern Idaho. Great Basin Naturalist 55: 352–358.

Fielding D.J. and Brusven M.A. 1996. Livestock Grazing and Grasshoppers: An Interregional Perspective. University of Idaho, College of Agriculture, Bulletin Number 786.

Fleischner T.L. 1994. Ecological costs of livestock grazing in western North America. Conservation Biology 8: 629–644.

Gaston K.J. 1994. Rarity. Chapman and Hall, London.

Gauch H.G. 1982. Multivariate Analysis in Community Ecology. Cambridge University Press, Cambridge, UK.

Gibson C.W.D., Brown V.K., Losito L. and McGavin G.C. 1992a. The response of invertebrate assemblies to grazing. Ecography 15: 166–176.

Gibson C.W.D., Hambler C. and Brown V.K. 1992b. Changes in spider (Araneae) assemblages in relation to succession and grazing management. Journal of Applied Ecology 29: 132–142.

Holmes N.D., Smith D.S. and Johnston A. 1979. Effect of grazing by cattle on the abundance of grasshoppers on fescue grassland. Journal of Range Management 32: 310–311.

Hurlbert S.H. 1984. Pseudoreplication and the design of ecological experiments. Ecological Monographs 54: 187–211.

Jepson-Innes K. and Bock C.E. 1989. Response of grasshoppers (Orthoptera: Acrididae) to livestock grazing in southeastern Arizona: differences between seasons and subfamilies. Oecologia 78: 430–431.

Joern A. 1982. Distributions, densities and relative abundances of grasshoppers (Orthoptera: Acrididae) in a Nebraska sandhills prairie. Prairie Naturalist 14: 37– 45.

Jones A. 2000. Effects of cattle grazing on North American arid ecosystems: a quantitative review. Western North American Naturalist 60: 155–164.

Jongman R.H.G., Ter Braak C.J.F. and Van Tongeren O.F.R. (eds) 1995. Data Analysis in Community and Landscape Ecology. Cambridge University Press, Cambridge, UK.

Kay F.R., Sobhy H.M. and Whitford W.G. 1999. Soil microarthropods as indicators of exposure to environmental stress in Chihuahuan Desert rangelands. Biology and Fertility of Soils 28: 121–128.

Kellert S.R. 1993. Values and perceptions of invertebrates. Conservation Biology 7: 845–855.

Krebs C.J. 1989. Ecological Methodology. Harper and Row, New York.

Kruess A., and Tscharntke T. 2002a. Contrasting responses of plant and insect diversity to variation in grazing intensity. Biological Conservation 106: 293–302.

Kruess A. and Tscharntke T. 2002b. Grazing intensity and the diversity of grasshoppers, butterflies, and trap-nesting bees and wasps. Conservation Biology 16: 1570–1580.

Lavigne R.J., Kumar R., Leetham J.W. and Kieth V. 1972. Population densities and biomass of aboveground arthropods under various grazing and environmental stress treatments on the Pawnee Site 1971. USIBP-Grassland Biome Technical Report Number 204. Natural Resource Ecology Laboratory, Ft. Collins, Colorado.

Leetham J.W. and Milchunas D.G. 1985. The composition and distribution of soil microarthropods in the shortgrass steppe in relation to the soil water, root biomass, and grazing by cattle. Pedobiologia 28: 311–325.

Loftin S.R., Bock C.E., Bock J.H. and Brantley S.L. 2000. Desert grasslands. In: Jemison R. and Raish C. (eds), Livestock Management in the American Southwest: Ecology, Society, and Economics. Elsevier, New York, pp. 53–96.

Ludwig J.A. and Reynolds J.F. 1988. Statistical Ecology: A Primer on Methods and Computing. John Wiley and Sons, New York.

Mack R.N. and Thompson J.N. 1982. Evolution in steppe with few large, hooved mammals. The American Naturalist 119: 757–773.

Majer J.D. 1983. Ants: bio-indicators of minesite rehabilitation, land-use, and land conservation. Environmental Management 7: 375–383.

Martin J.E.H. 1977. The Insects and Arachnids of Canada, Part 1: Collecting, Preparing, and Preserving Insects, Mites, and Spiders. Research Branch, Canada Department of Agriculture, Biosystematics Research Institute, Ottawa.

McCune B. and Grace J.B. 2002. Analysis of Ecological Communities. MjM Software Design, Gleneden Beach, California.

McDonald J.N. 1981. North American Bison; Their Classification and Evolution. University of California Press, Berkeley.

Milchunas D.G., Lauenroth W.K. and Burke I.C. 1998. Livestock grazing: Animal and plant biodiversity of shortgrass steppe and the relationship to ecosystem function. Oikos 83: 65–74.

Miller R.H. and Onsager J.A. 1991. Grasshopper (Orthoptera: Acrididae) and plant relationships under different grazing intensities. Environmental Entomology 20: 807–814.

Morris M.G. 1967. Differences between the invertebrate faunas of grazed and ungrazed chalk grassland. I. Responses of some phytophagous insect to cessation of grazing. Journal of Applied Ecology 4: 459–474.

Morris M.G. 1968. Differences between the invertebrate faunas of grazed and ungrazed chalk grassland. II. The faunas of sample turves. Journal of Applied Ecology 5: 601–611.

Morris M.G. 1969a. Differences between the invertebrate faunas of grazed and ungrazed chalk grassland. III. The heteropterous fauna. Journal of Applied Ecology 6: 475–487.

Morris M.G. 1969b. Populations of invertebrate animals and the management of chalk grasslands in Britain. Biological Conservation 1: 225–231.

Noss R.F. 1994. Cows and conservation biology. Conservation Biology 8: 613–616.

Oliver I. and Beattie A.J. 1993. A possible method for the rapid assessment of biodiversity. Conservation Biology 7: 562–568.

Onsager J. A. and Henry J.E. 1978. A method for estimating the density of rangeland grasshoppers (Orthoptera: Acrididae) in experimental plots. Acrida 6: 231–237.

Otte D. 1981. The North American Grasshoppers. Vol I. Acrididae: Gomphocerinae and Acridinae. Harvard University Press, Cambridge, Massachusetts.

Pimentel R.A. 1993. BioStatII: A Multivariate Statistical Toolbox: Tutorial Manual. Sigma Soft, San Luis Obispo, California.

Pykala J. 2000. Mitigating human effects on European biodiversity through traditional animal husbandry. Conservation Biology 14: 705–712.

Quinn G.P. and Keough M.J. 2002. Experimental Design and Data Analysis for Biologists. Cambridge University Press, Cambridge, UK.

Quinn M.A. and Walgenbach D.D. 1990. Influence of grazing history on the community structure of grasshoppers of a mixed-grass prairie. Environmental Entomology 19: 1756–1766.

Rees C.J.C. 1983. Microclimate and the flying Hemiptera fauna of a primary lowland rainforest in Sulawesi. In: Sutton S.L., Whitmore T.C., Chadwick and A.C. (eds), Tropical Rainforest: Ecology and Management. Blackwell Scientific Publications, Oxford, pp. 121–136.

Savory A. 1986. Pointing fingers. The Savory Letter 4(October): 1–4.

Savory A. 1999. Holistic Resource Management. Island Press, Washington, D.C.

Smith C.C. 1940. The effect of overgrazing and erosion upon the biota of the mixed-grass prairie of Oklahoma. Ecology 21: 381–389.

Smith R.L. 1986. Elements of Ecology. Harper and Row, New York.

SYSTAT 1997. SYSTAT 7.0 for Windows. SPSS Inc., Chicago, Illinois.

Wall-Freckman D. and Huang S-P. 1998. Response of the soil nematode community in a shortgrass steppe to long-term and short-term grazing. Applied Soil Ecology 9: 39–44.

Weese A.O. 1939. The effect of overgrazing on insect populations. Proceedings of the Oklahoma Academy of Science 19: 95–99.

Welch J.L., Redak R. and Kondratieff B.C. 1991. Effect of cattle grazing on the density and species of grasshoppers (Orthoptera: Acrididae) of the Central Plains Experimental Range, Colorado: a reassessment after two decades. Journal of the Kansas Entomological Society 64: 337–343.

Whitford W.G., Forbes G.S. and Kerley G.I. 1995. Diversity, spatial variability, and functional roles of invertebrates in desert grassland ecosystems. In: McClaran M.P. and Van Devender T.R. (eds.), The Desert Grassland. University of Arizona Press, Tucson, Arizona, pp. 152–195.

Wilson E.O. 1987. The little things that run the world (the importance and conservation of invertebrates). Conservation Biology 1: 344–346.

Yen A.L. 1987. A preliminary assessment of the correlation between plant, vertebrate and Coleoptera communities in the Victorian malleein. In: Majer J.D. (ed.), The Role of Invertebrates in Conservation and Biological Survey. Western Australian Department of Conservation and Land Management, pp. 73–88.

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Medicinal plants of the Argentine Yungas plants of the Las Yungas biosphere reserve, Northwest of Argentina, used in health care

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Abstract. We have compared the species richness of medicinal plants and the differential patterns of use amongst settlements in the Andean communities of Northwest Argentina which have differing levels of isolation. About 259 ethnoespecies, belonging to 74 plant families, were included, representing between 70 and 80% of the total estimate. The results indicate that *Coronopus didymus* is the most relevant and important species. The method of use of medicinal plants and the ailments treated by *rural doctors* compared to those of the layperson is different. Native and exotic plants are used differently according to the body system treated. There are some relationships between internal and external use and body systems and recipes. The greater medicinal species richness found in the less isolated locations is due to external enriching cultural influences.

Introduction

The main goal of early Ethnobotanical studies was the documentation of endangered knowledge whilst today many projects collect data for biodiversity conservation and community development, focusing on the ecological feasibility of the indigenous management strategies (Frei et al. 2000). An implicit assumption of these studies is that plants are economically, culturally and ecologically important (Frei et al. 2000; Hersh-Martínez 2002). The recognition of this human component of the traditional ecological knowledge and of forest landscape management held by the resident cultures has led to a model of 'community-based' conservation (Gadgil et al. 1993). But it is important to recognize that, in many cases, local people have developed behaviors which have had a conservational impact without these initial aims; practices that, in general, look for the best results in local economy. It is important to remember that management of natural resources is foremost a question about social relations, that is to say, about the social net who is regulating the access to these resources (Kalland 2000).

In the same sense, Ethnobotanical studies have become increasingly valuable in the development of health care and conservation programs in different parts of the world (Balick 1996). In each culture the importance of each medicinal plant varies; some are hardly ever used, while others are important medicinal resources. Even so, numerous papers have called attention to the lack of information on the relative importance of medicinal plants (or other useful plants) within a culture (Moerman 1996; Ankili et al. 1999).

Many rural populations throughout the tropics rely on medicinal plants because of their effectiveness, the lack of modern alternatives and their cultural preferences. However, the distribution and extent of local knowledge and the use of medicinal plants in these societies are being altered by exposure to modern culture, increased trade and access to modern conveniences (including modern medicines). In fact, local knowledge cannot be treated as an insulated domain, since the majorities are interacting with exogenous knowledge (Osseweijer 2000).

On the other hand, forest conversion and land degradation can reduce the availability of medicinal plants and can also affect local knowledge of interests in medicinal plant use (Caniago and Siebert 1998).

In the present work the use of medicinal plants in populations residing within the Argentine Yungas Biosphere Reserve is investigated. Within the zone studied are the Baritú National Park and the National Reserve 'El Nogalar.' Both reserves are of recent creation (in 2002 and 2003, respectively) but the National Park dates back to 1974. According to Brown (1995) and Brown et al. (2001), this region has the highest biodiversity levels and rural population numbers in the Montane Cloud Forest of Argentina, but also it represents one of the biomes within the national territory most threatened by productive activities such as logging, grazing forest conversion into cropland.

Today, Pre-Columbian and Spanish colonial influences are still to be seen in the area but modern influences are constantly altering the traditional medical systems and the use of medicinal plants, as noted by Frei et al. (1998) with respect to Mexican communities. Recently, several studies concerning the use of medicinal plants have been undertaken in Northwestern Argentina (Iharlegui and Hurrell 1992; Hurrell and de la Sota 1996; Lupo and Echenique 1997). The community health issue has also been investigated on a few occasions from an anthropological viewpoint (Torres 1982; Palma 1994; Madrid de Zito Fontan and Palma 1997). Some studies on ethnomedicine have been undertaken in neighboring areas of the Salta province (Hurrell 1990, 1991; Martinez and Pochettino 1992) but there is only one ethnopharmacological study dealing specifically with the medicinal plants used within the Yungas biogeographic province (Hilgert 2001).

Ellen and Harris (2000) have defined indigenous knowledge as local, orally transmitted and constantly reinforced by experience; they have also expressed the importance of not placing local knowledge outside culture. Taking into account the above mentioned concept, the goals of the present paper are the documentation of the usage of medicinal plants in rural communities of the Yungas Biosphere Reserve of Northwest Argentina. Besides, the methods of use, the parts of the plant used and the documentation of the cultural value of the use of medicinal plants are analyzed. Finally, how this knowledge is distributed among the population and the comparison among communities with different socio-economic features and environmental conservation status are also treated.

Methods

Study site

The area is located on the eastern slope of the Cordillera Oriental in the north of the Province of Salta, Argentina, close to the Bolivian border. The localities studies were; Abra de Minas, Lipeo and Baritú, located at the limit and within the Baritú National Park, and the neighboring areas of La Mamora (Bolivia), El Condado, La Misión, Los Toldos and El Arazay (Figure 1). The climate is tropical continental with hot and rainy summers and cold and dry winters. Mean annual temperatures range from 14 to 26.5 °C with orographic rains (rains that occur by condensation of humid air rising up high mountain slopes) concentrated between September and March and with an annual rainfall of 700–1400 mm (Bianchi and Yánez 1992; Hunzinger 1995).

From a biogeographic point of view the area corresponds to the Yungas Province (Montane Cloud Forest) within the Amazonian Domain within the Neotropical Region. This biome can be divided into three environmental units: the Submontane Subtropical Forest, the Montane Moist Forest and the Temperate Cloud Forest (which includes Fog Grasslands) (Cabrera 1976).

The communities under study are considered to be part of the Andean cultural world. The inhabitants of these settlements are Andean with strong Spanish influence. They speak only Spanish although many Quechuan expressions are found in their speech. For the most part the inhabitants live under marginal socio-economic conditions. A brief analysis of the regional economy shows the coexistence of shifting agriculture, transhumance, harvesting, nomadic cattle-breeding, hunting and fishing and finally, access to paid work in temporary or permanent jobs (Hilgert 2001).

In order to gain access to the area it is necessary to leave the country via the frontier crossing, drive approximately 70 km on Bolivian roads, and then re-enter Argentina. Up to 2001 and before the inauguration of an international bridge, it was necessary to cross two river beds, which were impassable during some or all of the rainy season. At the present time Abra de Minas, Lipeo and Baritú only have communication by foot or horse for most of the year and these settlements. Table 1 provides a comparing the key socio-economic and environmental features of each study area.

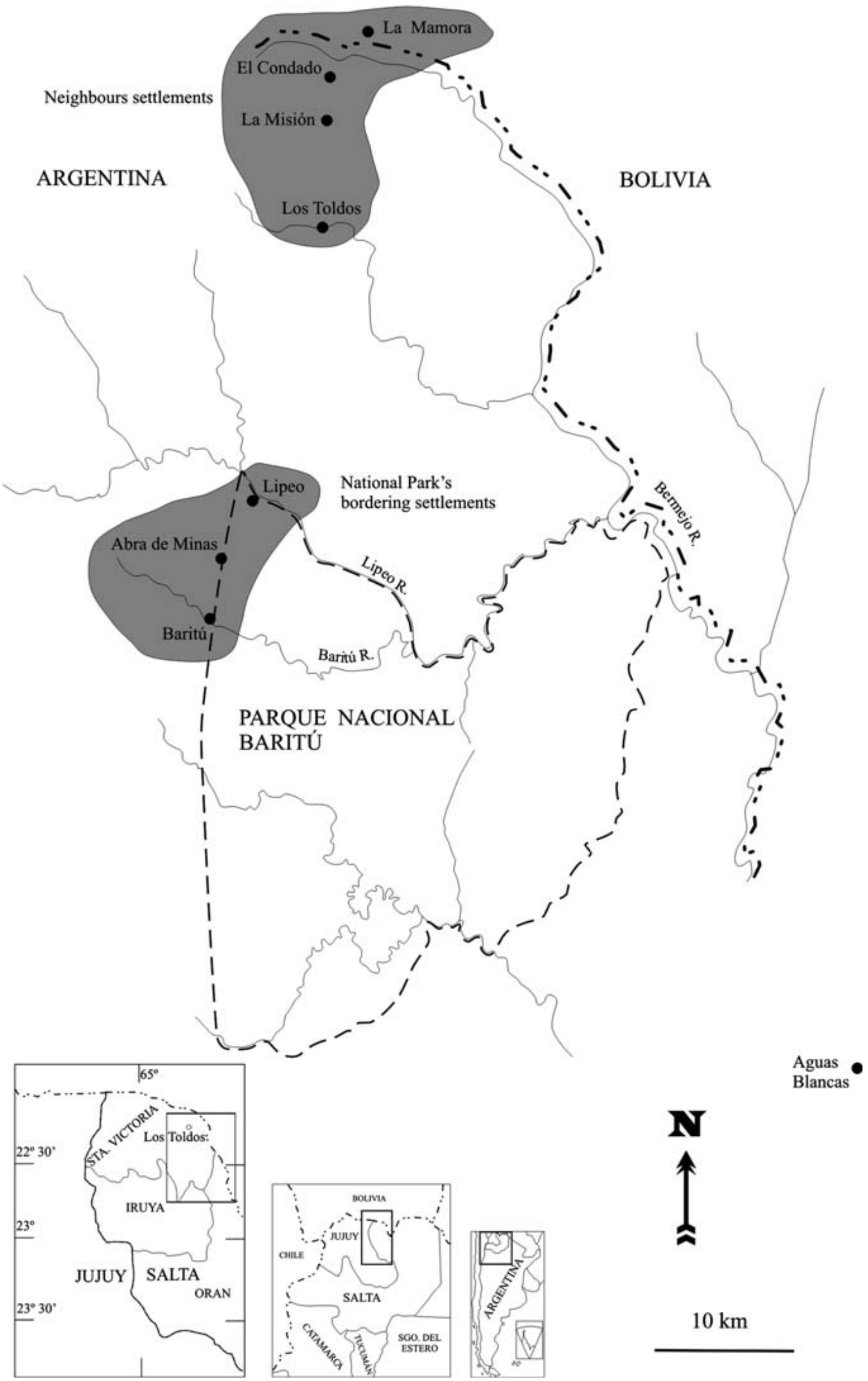

Figure 1. Baritu National Park.

Table 1. Socio-economic and environmental features of each study area.

	NP settlements			Neighbors settlements			
	Baritú	Abra de Minas	Lipeo	Los Toldos	La Misión	El Condado	La Mamora
MOSL	1500	1800	1100	1600	1100	900	1100
Vegetation type	Temperate cloud and Montane moist forest	Temperate cloud forest	Montane moist and Submontane subtropical forest	Temperate cloud and Montane moist forest	Montane moist and Submontane subtropical forest	Submontane subtropical forest	Montane moist and Submontane subtropical forest
Disturb level	Low	Low	Low	Medium	Medium	High	High
# Families	16	2	21	124	102	101	no data
First degree school	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Second degree school	No	No	No	Yes	No	No	No
Percentage analphabet mothers	74	no data	65	42	57	66	no data
Hospitals	No	No	No	Yes	No	No	Yes
Health centers	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Stores	No	No	Yes	Yes	Yes	Yes	Yes
Telephone	No	No	No	Yes	No	No	Yes
Electricity	No	No	No	Yes	Yes	Yes	Yes
Car roads	In dry season	In dry season	In dry season	All year	All year	All year	All year
Public means of transportation	No	No	No	Yes	Yes	Yes	Yes

Data collection

During seven visits from 1994 to 2000 a total of 104 surveys were undertaken of 39 rural families interviewed using a semi structured questionnaire. For the present article these families were considered as two groups. The first group consisted of 19 families from Abra de Minas, Lipeo and Baritú, where a total of 39 families live (i.e. the work was undertaken using 48% of the inhabitants of or near to the Baritú National Park). The second group consisted of 18 families divided among the populations of El Condado, La Misión, Los Toldos and El Arazay in Argentina and 2 families in La Mamora (Bolivia). So, in Argentina the second group represents 5.5% of the total 327 families, we have no data about this percentage for the Bolivian city. The individuals were asked about the medicinal plants they used, the parts of the plant used, the methods of preparation and administration, the dosage, the duration of the treatment and the illness being treated. Plants were collected with the local help and were pressed and dried at the Museo de Ciencias Naturales of the Universidad Nacional de Salta, Argentina. The nomenclature used follows Zuloaga et al. (1994) and Zuloaga and Morrone (1996, 1999).

Data analysis

An 'event' is defined as the process of asking an individual on one day about the uses they know for one species, according to methods proposed by Phillips and Gentry (1993) and Phillips (1996).

The theoretical total of locally used medicinal plants was estimated in addition to the percentage representation of the species mentioned in the present study. Due to the distinct level of isolation and historical characteristics, these calculations considered separately the locations at the limit of, or within, the Baritú National Park (Abra de Minas, Lipeo and Baritú) and other more distant neighboring places (La Mamora, El Condado, La Misión, Los Toldos, El Arazay). Non-parametric estimators were used (Chao2, Jacknife1, Jacknife2) taking each informant as a sampling unit and using the EstimateS 6.0b1 program (Colwell 2000). Based on the values of species for sample calculated by EstimateS (an average of 50 simulations randomizing the observed samples) the smoothing to the species accumulation functions (Clench equation, logarithmic and linear dependence models) was analyzed with the statistical software Statistica 98 Edition (StatSoft Inc. 1998). We consider that Chao1 calculations are not applicable to this type of data as this estimator is based on rare species which are represented by only one or two individuals (in our case, verbal references) in a sample (informant) and the species that have only one or two uses will be only referenced once. As such, this type of species will deflect the calculations, resulting in overestimations of the total expected species. For this case, the individuals (references) of a survey differ from those of a natural population of a live species in which it is possible to record numerous individuals of a species by sample (Moreno 2000). The relative importance (RI) for each species was estimated, according to Bennet and Prance (2000), based on the normalized number of pharmacological properties attributed by each species and the normalized number of body systems affected by each one. Spearman correlations were undertaken between the RI and the methods of administration and the recipes. In order to analyze the differential use of native and exotic species we classify its following Zuloaga et al. (1994) and Zuloaga and Morrone (1996, 1999) adding data about natives endemics of Argentina and naturalized adventitious (Table 2). The amounts of native/exotic species used for body systems were compared using a Chi squared test. The same operation was undertaken to compare the method of application and the types of recipes used by the individuals known as 'médicos rurales' (*rural doctors*) to those of the rest of the interviewed individuals, using the number of events for each case. For these last two comparisons a discriminant analysis was also undertaken using native/exotic and *rural doctor*/layperson respectively as classificatory variables, using the frequency of the reference of each species by body system for the first case and the method of use and the recipe for the second case. All the statistical tests were undertaken using the SPSS software application for Windows (SPSS Inc. 2000).

Results

Health system

The inhabitants of the region maintain traditional health practices and therefore the underlying notion of the origin of a disease is very important for determining diagnosis and treatment. They recognize three origins for ailments; natural, socio-cultural (i.e. when a food taboo is not respected), and supernatural (i.e. witch-craft, air diseases). The last two types can be diagnosed and treated only by a *rural doctor*. Diseases of natural origin, like cough, dyspepsia, headache, postpartum pain are usually solved within the family and it is not necessary to have formal training nor to carryout any ritual process.

The hot and cold theory holds an important place in the local medicine lore. This is the theory as described by the inhabitants of the Zenta River Basin, near to the present area, (Hilgert 2001) who consider a healthy body to have a certain corporal temperature that can be altered by the influence of external factors, i.e. sun, water, or an inadequate behavior. For example if some person ate 'cold' food (like lettuce) in excess, this cold would cause a templary imbalance and he or she would have digestive problems afterwards he or she is considered to be suffering from 'cold.' The imbalance also could become from an excessive exposure to cold and humidity, or heat and dryness these may cause cold or hot.

Against 'hot' and 'cold' diseases, usually plants with an opposite condition are used, however sometimes neutral condition's beverages are prepared to

Table 2. Relative importance value of medicinal plants.

Species, family (Herbarium number according to collector)	Vernacular name	#BS	Rel BS	#PH	Rel PH	RI	Status
Coronopus didymus (L.), Brassicaceae (H 1987 MCNS)	quimpe, quimpy	11	1	30	1	100.0	NA
Rosa sp., Rosaceae (H 2261 MCNS)	rosa, rosa remedio	11	1	13	0.43	71.5	EX
Citrus limon (L.) Burm., Rutaceae (H 1590 MCNS)	limón	9	0.81	17	0.56	68.5	EX
Sambucus nigra L. subsp. *peruviana* (Kunth) R. Bolli, Caprifoliaceae (H 2142 MCNS)	mololo	9	0.81	17	0.56	68.5	NA
Citrus sinensis (L.) Osbeck, Rutaceae (H 2053 MCNS)	naranja, naranja dulce	10	0.91	13	0.43	67.0	EX
Malva parviflora L., Malvaceae (H 2503 MCNS)	malva	9	0.81	16	0.53	67.0	AD
Erythroxylum coca Lam. var. *coca*, Erythroxylaceae (H 2108 M-MCNS)	coca	8	0.72	18	0.60	66.0	EX
Nicotiana tabacum L., Solanaceae (H 2368 MCNS)	tabaco	9	0.81	13	0.43	62.0	EX
Acacia macracantha H. B. K., Fabaceae (H 2581 MCNS)	churqui, tusca	7	0.63	14	0.46	54.5	NA
Myroxylon peruiferum L.f., Fabaceae (H 2377 MCNS)	quina colorada, quina del campo, quina	8	0.72	11	0.36	54.0	NA
Ruta chalepensis L., Rutaceae (H&A 1399 MCNS)	ruda	7	0.63	13	0.43	53.0	EX
Plantago australis Lam., Plantaginaceae (H 2534 MCNS)	llantén	8	0.72	9	0.30	51.0	NA
Cinchona ledgeriana Monees., Rubiaceae (H 1631 M-MCNS)	quina amarilla, quina blanca, quina castilla	8	0.72	8	0.26	49.0	EX
Cortaderia selloana (Schult. et Schult. f) Asch. Et Graebn., Poaceae (H 1772 MCNS)	cortadera	8	0.72	8	0.26	49.0	NA
Verbena litoralis Kunth, Verbenaceae (H 2499 MCNS)	verbena	8	0.72	8	0.26	49.0	NA
Cinnamomum porphyrium (Griseb.) Kosterm, Lauraceae (H 2022 M-MCNS)	laurel del campo	7	0.63	9	0.30	46.5	NA
Eucalyptus camaldulensis Dehnh., Myrtaceae (H 1845 MCNS)	eucaliptus	7	0.63	9	0.30	46.5	EX
Matricaria recutita L., Asteraceae (H 2438 MCNS)	manzanilla	7	0.63	9	0.30	46.5	AD
Solanum palitans C. V. Morton, Solanaceae (H 1618 MCNS)	ñusco	7	0.63	9	0.30	46.5	EN

Table 2. Continued.

Species, family (Herbarium number according to collector)	Vernacular name	#BS	Rel BS	#PH	Rel PH	RI	Status
Acacia aroma Gill. ex Hook et Arn., Fabaceae (H 2400 MCNS)	tusca	7	0.63	8	0.26	44.5	NA
Allium sativum L., Liliaceae (N 1578 M-MCNS)	ajo	7	0.63	8	0.26	44.5	EX
Linum usitatissimum L., Linaceae (N 1621 M-MCNS)	linaza	7	0.63	8	0.26	44.5	EX
Ocimun basilicum L., Lamiaceae (H 2058 MCNS)	albahaca	7	0.63	8	0.26	44.5	EX
Salvia gilliesii Benth., Lamiaceae (H 2321 M-MCNS)	salvia gateadora, salvia del cerro	7	0.63	8	0.26	44.5	NA
Schinus molle L., Anacardiaceae (H. 2540 MCNS)	molle	7	0.63	8	0.26	44.5	AD
Melissa officinalis L., Lamiaceae (H 1059 M-MCNS)	toronjil	6	0.54	10	0.33	43.5	EX
Xanthium catharticum HBK, Asteraceae (H 2167 MCNS)	espinillo	6	0.54	10	0.33	43.5	NA
Petiveria alliaceae L., Phytolaccaceae (H 2383 MCNS)	calaschi	7	0.63	7	0.23	43.0	NA
Zea mays L. var. *ocho rayas*, Poaceae (H 1563 MCNS)	maíz	7	0.63	7	0.23	43.0	EX
Ageratum conyzoides L., Asteraceae (H&Lo 969 MCNS)	borraja del campo, borrajilla	5	0.45	9	0.30	42.0	NA
Buddleja brasiliensis Jacq. ex Spreng., Buddlejaceae (H 2182 MCNS)	san juan c'ora	6	0.54	9	0.30	42.0	NA
Maytenus cuezzoi Leg., Celastraceae (H 2565 M-MCNS)	lloque	6	0.54	9	0.30	42.0	EN
Citrus aurantium L., Rutaceae (H 2051 MCNS)	naranja agria	6	0.54	8	0.26	40.0	EX
Fagara coco (Gill.) Engler, Rutaceae (H 2199 M-MCNS)	sauco	6	0.54	8	0.26	40.0	NA
Rosa rubiginosa L., Rosaceae (H&A 1445 MCNS)	rosa, rosa remedio	6	0.54	8	0.26	40.0	EX
Rosmarinus officinalis L., Lamiaceae (H 2103 MCNS)	romero	6	0.54	8	0.26	40.0	EX
Taraxacum officinale Weber ex F. H. Wigg., Asteraceae (H 1436 MCNS)	retama, achicoria, k'ana yuyo	6	0.54	8	0.26	40.0	AD
Satureja boliviana (Benth.) Briquet, Lamiaceae (H 2528 MCNS)	muña	5	0.45	10	0.33	39.0	NA

Table 2. Continued.

Species, family (Herbarium number according to collector)	Vernacular name	#BS	Rel BS	#PH	Rel PH	RI	Status
Pavonia sepium St. Hil., Malvaceae (H 1099 MCNS)	abrojo	6	0.54	7	0.23	38.5	NA
Prunus amygdalus Batsch., Rosaceae	almendras	6	0.54	7	0.23	38.5	EX
Senencio crepidifolius DC., Asteraceae (H 2500 MCNS)	arnica	6	0.54	6	0.20	37.0	NA
Anthemis cotula L., Asteraceae (H&A 1410 MCNS)	manzanilla	5	0.45	8	0.26	35.5	AD
Satureja parvifolia (Phil.) Epling, Lamiaceae (H 2269 M-MCNS)	muña	5	0.45	8	0.26	35.5	NA
Peperomia alata Ruiz et Pav., Piperaceae (H&G 2391 MCNS)	anís del monte	6	0.54	5	0.16	35.0	NA
Achyrocline alata (Kunth) DC, Asteraceae (H 2481 MCNS)	amaicha blanca, vila vila	5	0.45	7	0.23	34.0	NA
Jacaranda mimosifolia D. Don, Bignoniaceae (H&G 2397 MCNS)	tarco	5	0.45	7	0.23	34.0	NA
Piper anduncum L. var. *anduncum*, Piperaceae (H&G 2336 MCNS)	matico	5	0.45	7	0.23	34.0	NA
Plantago myosurus Lam., Plantaginaceae (H 2222 MCNS)	llantén	5	0.45	7	0.23	34.0	NA
Tanacetum parthenium (L.) Sch. Bip, Asteraceae (H&A 1479 M-MCNS)	ajenco, a. amarillo	5	0.45	7	0.23	34.0	EX
Peperomia fiebrigii C. DC., Pieraceae (H&G 2345 MCNS)	siemprevida	4	0.36	9	0.30	33.0	NA
Equisetum bogotense H. B. K., Equisetaceae (H&A 1394 MCNS)	cola de caballo chica	5	0.45	6	0.20	32.5	NA
Tagetes campanulata Griseb., Asteraceae (H&A 1478 MCNS)	rosa amarilla, rosa pascua	5	0.45	6	0.20	32.5	NA
Artemisia absinthium L., Asteraceae (H 2433 MCNS)	ajenco, a. blanco	4	0.36	8	0.26	31.0	EX
Lepechinia vesiculosa (Benth.) Epling., Lamiaceae (H 1899 MCNS)	salvia grande, salvia blanca	4	0.36	8	0.26	31.0	NA
Amaranthus hypochondriacus L. var. *powellii* (S. Watson) Ped., Amaranthaceae (H 1976 MCNS)	aroma	5	0.45	5	0.16	30.5	NA
Dahlia sp., Asteraceae (H 1975 MCNS)	dalia	5	0.45	5	0.16	30.5	EX
Dianthus caryophyllus L., Caryophyllaceae (H 2468 MCNS)	clavel de huerta	5	0.45	5	0.16	30.5	EX

Table 2. Continued.

Species, family (Herbarium number according to collector)	Vernacular name	#BS	Rel BS	#PH	Rel PH	RI	Status
Equisetum giganteum L., Equisetaceae (H&L 1617 MCNS)	cola de caballo grande	5	0.45	5	0.16	30.5	NA
Eugenia uniflora L., Myrtaceae (H 2057 MCNS)	arrayán, a. colorado	5	0.45	5	0.16	30.5	NA
Ilex paraguariensis A. St. Hill., Aquifoliaceae (H 1565 M-MCNS)	yerba	5	0.45	5	0.16	30.5	EX
Tagetes sp., Asteraceae	comadrita	5	0.45	5	0.16	30.5	NA
Arundo donax L., Poaceae (H 2577 MCNS)	caña hueca	4	0.36	7	0.23	29.5	AD
Citrus aurantifolia (Christm.) Sw., Rutaceae (H&G 2388 MCNS)	lima	4	0.36	7	0.23	29.5	EX
Macfadyena unguis-cati (L.) A. H. Gentry, Bignoniaceae (H 2192 MCNS)	garra de gato	5	0.45	4	0.13	29.0	NA
Helianthus annuus L., Asteraceae (H 1327 MCNS)	mirasol	5	0.45	4	0.13	29.0	EX
Opuntia ficus indica (L.) Mill., Cactaceae (H&L 1859 M-MCNS)	penca, tuna	5	0.45	4	0.13	29.0	AD
Baccharis trimera (Less.) DC., Asteraceae (H 2501 MCNS)	carqueja	4	0.36	5	0.16	26.0	NA
Cajophora lateritia (Hook.) Koltzch, Loasaceae (H 2225 MCNS)	itapalla	4	0.36	5	0.16	26.0	NA
Duranta serratifolia (Griseb.) Kuntze, Verbenaceae (H 2147 MCNS)	espinillo	4	0.36	5	0.16	26.0	NA
Not identified	livi livi	4	0.36	5	0.16	26.0	
Origanum x appli (Domin) Boros, Lamiaceae (H 2242 MCNS)	orégano	4	0.36	5	0.16	26.0	EX
Stachytarpheta cayennensis (Rich) M. Vahl. f., Verbenaceae (H&A 2387 MCNS)	verbena	4	0.36	5	0.16	26.0	NA
Tabebuia impetiginosa (Mart. ex DC.) Standl., Bignoniaceae (Krap. 26581 CTES)	lapacho morado	4	0.36	5	0.16	26.0	NA
Urera caracasana (Jacq.) Gris., Urticaceae (H&G 2394 MCNS)	itapalla, orteguilla	4	0.36	5	0.16	26.0	NA
Amaranthus quitensis Kunth., Amaranthaceae (H&G 2393 MCNS)	aroma	4	0.36	4	0.13	24.5	NA
Anredera cordifolia (Ten.) Steenis, Basellaceae (H 2256 MCNS)	papa santa, hierba santa	4	0.36	4	0.13	24.5	NA

Table 2. Continued.

Species, family (Herbarium number according to collector)	Vernacular name	#BS	Rel BS	#PH	Rel PH	RI	Status
Canna indica L., Cannaceae (H 1972 MCNS)	achera	4	0.36	4	0.13	24.5	NA
Cucurbita ficifolia Bouché, Cucurbitaceae (H 1571 M-MCNS)	cayote	4	0.36	4	0.13	24.5	EX
Cydonia oblonga Mill., Rosaceae (H&A 1456 M-MCNS)	membrillo	4	0.36	4	0.13	24.5	EX
Prunus persica (L.) Batsch., Rosaceae (H 2049 MCNS)	durazno	4	0.36	4	0.13	24.5	EX
Rhipsalis lorentziana Griseb., Cactaceae (H&A 1462 MCNS)	huasca huasca, peinquillita	4	0.36	4	0.13	24.5	NA
Roripa nasturtium-aquaticum (L.) Hayek, Brassicaceae (H&G 2404 MCNS)	berro	4	0.36	4	0.13	24.5	AD
Saccharum officinarum L., Poaceae (H 1583 M-MCNS)	azúcar, caña dulce	4	0.36	4	0.13	24.5	EX
Scoparia dulcis L., Scrophulariaceae (H 2162 MCNS)	yerba de víbora	4	0.36	4	0.13	24.5	NA
Solanum trichoneuron Lillo, Solanaceae (H 2161 MCNS)	hediondilla	4	0.36	4	0.13	24.5	EN
Tillandsia usneoides (L.) L., Bromeliaceae (H 2187 MCNS)	sacha blanca	4	0.36	4	0.13	24.5	NA
Tournefortia paniculata Cham., Boraginaceae (H 1088 MCNS)	alcanflor	4	0.36	4	0.13	24.5	NA
Trichocereus arboricola Kimnach, Cactaceae (H&G 2399 M-MCNS)	cardón, c. blanco	4	0.36	4	0.13	24.5	NA
Pluchea sagittalis (Lam.) Cabrera, Asteraceae (H 2392 MCNS)	cuatro cantos	3	0.27	6	0.20	23.5	NA
Punica granatum L., Punicaceae (H 1643 M-MCNS)	granada castilla	3	0.27	6	0.20	23.5	EX
Aloe vera (L.) Burm. F., Liliaceae	penca aloe vera, sabila	4	0.36	3	0.10	23.0	EX
Cynodon dactylon L., Poaceae (H 2164 MCNS)	brama blanca	4	0.36	3	0.10	23.0	AD
Adiantum lorentzii Hieron., Pteridaceae (H&A 1457 MCNS)	culandrillo	3	0.27	5	0.16	21.5	NA
Aloysia polystachya (Griseb.) Mold., Lamiaceae (H 2409 M-MCNS)	burrito	3	0.27	5	0.16	21.5	NA
Apium graveolens L., Apiaceae (H&A 1447 MCNS)	apio	3	0.27	5	0.16	21.5	AD

Table 2. Continued.

Species, family (Herbarium number according to collector)	Vernacular name	#BS	Rel BS	#PH	Rel PH	RI	Status
Mimosa polycarpa Kunth. var *subandina* Barneby, Fabaceae (H 2220 MCNS)	celosita chica	3	0.27	5	0.16	21.5	NA
Solanum sisymbriifolium Lam.var. *sisymbriifolium*, Solanaceae (H 2637 MCNS)	vila vila	3	0.27	5	0.16	21.5	NA
Oreopanax kuntzei Harms, Araliaceae (H 1375 MCNS)	higuerilla	4	0.36	2	0.06	21.0	NA
Borago officinalis L., Boraginaceae (H 2462 M-MCNS)	borraja castilla, b. de huerta	3	0.27	4	0.13	20.0	AD
Chrysanthemum sp., Asteraceae (H 2255 MCNS)	papa de margarita, margarita	3	0.27	4	0.13	20.0	EX
Mentha x piperita L. var. *citrata* (Ehrh.) Briq., Lamiaceae (H 1640 MCNS)	menta	3	0.27	4	0.13	20.0	EX
Microgramma squamulosa (Kaulf.) de la Sota, Polypodiaceae (H&G 2346 MCNS)	pori pori, poli poli, canchalagua	3	0.27	4	0.13	20.0	NA
Persea americana Mill., Lauraceae (H 2074 MCNS)	palta anisada	3	0.27	4	0.13	20.0	AD
Rhipsalis floccosa Pfeiff. subsp. *tucumanensis* (Web.) Barth., Cactaceae(H 2024 MCNS)	huasca huasca, calaguala	3	0.27	4	0.13	20.0	NA
Smilax campestris Griseb., Smilacaceae (H 2320 M-MCNS)	zarzaparilla	3	0.27	4	0.13	20.0	NA
Acaulimalva nubigena (Walp.) Krapov., Malvaceae (H 2465 M-MCNS)	altea	3	0.27	3	0.10	18.5	NA
Achyrocline flaccida (Weinm) DC, Asteraceae (H 2435 MCNS)	amaicha, vila vila	3	0.27	3	0.10	18.5	NA
Amburana cearensis (Allemao) A. C. Sm., Fabaceae (H 1620 M-MCNS)	roble	3	0.27	3	0.10	18.5	NA
Bocconia integrifolia Humb. y Bonpl., Papaveraceae (H 2541 MCNS)	mil hombres, palo amarillo	3	0.27	3	0.10	18.5	NA
Capsicum annuum L., Solanaceae (H 1894 MCNS)	ají	3	0.27	3	0.10	18.5	EX
Cedrella lilloi DC, Meliaceae (H 2634 MCNS)	cedro	3	0.27	3	0.10	18.5	NA
Cinnamomum zeylanicum Blume, Lauraceae (H 2330 M-MCNS)	canela	3	0.27	3	0.10	18.5	EX

Table 2. Continued.

Species, family (Herbarium number according to collector)	Vernacular name	#BS	Rel BS	#PH	Rel PH	RI	Status
Cucurbita maxima Duchesne var . *maxima*, Cucurbitaceae (H 1961 MCNS)	zapallo	3	0.27	3	0.10	18.5	EX
Dodonaea viscosa Jacq., Sapindaceae (H 1012 MCNS)	chacatea	3	0.27	3	0.10	18.5	NA
Eupatorium bupleurifolium DC., Asteraceae (H&Lo 950 MCNS)	prementina	3	0.27	3	0.10	18.5	NA
Fagara naranjillo (Griseb.) Engl., Rutaceae (Jörg. 2585 SI)	naranjillo	3	0.27	3	0.10	18.5	NA
Gochnatia palosanto Cab., Asteraceae (H 1619 M-MCNS)	palo santo	3	0.27	3	0.10	18.5	NA
Hordeum vulgare L., Poaceae (H 1581 M-MCNS)	cebada	3	0.27	3	0.10	18.5	EX
Lactuca sativa L., Asteraceae (H 1569 M-MCNS)	lechuga	3	0.27	3	0.10	18.5	EX
Laurus nobilis L., Lauraceae (N 1576 M-MCNS)	laurel	3	0.27	3	0.10	18.5	EX
Lavandula sp., Lamiaceae	alhucema	3	0.27	3	0.10	18.5	EX
Myristica fragans Houtt., Myristicaceae (H 2104 M-MCNS)	nuez moscada	3	0.27	3	0.10	18.5	EX
Phoradendron tucumanense Urb., Viscaceae (H 1347 MCNS)	suelda con suelda	3	0.27	3	0.10	18.5	NA
Plantago major L., Plantaginaceae (H 2439 MCNS)	llantén	3	0.27	3	0.10	18.5	EX
Schinus meyeri Barkley, Anacardiaceae (H. 2149 MCNS)	chirimolle	3	0.27	3	0.10	18.5	NA
Schkuhria pinnata (Lam.) Kuntze, Asteraceae (H 2507 MCNS)	hallapichana	3	0.27	3	0.10	18.5	NA
Solanum sp., Solanaceae	yerba del golpe	3	0.27	3	0.10	18.5	NA
Solanum tuberosum L., Solanaceae (H 1907 MCNS)	papa	3	0.27	3	0.10	18.5	NA
Syzygium aromaticum (L.) Merr. et Perry, Myrtaceae (H 1580 M-MCNS)	clavo de olor	3	0.27	3	0.10	18.5	EX
Tournefortia lilloi M. Johnston, Boraginaceae (H&A 1428 MCNS)	alcanflor	3	0.27	3	0.10	18.5	NA
Triticum aestivum L., Poaceae (H 1584 M-MCNS)	trigo	3	0.27	3	0.10	18.5	EX
Chaptalia nutans (L.) Polak., Asteraceae (H 2521 MCNS)	pelodilla, marancel, rejón	2	0.18	5	0.16	17.0	NA

Table 2. Continued.

Species, family (Herbarium number according to collector)	Vernacular name	#BS	Rel BS	#PH	Rel PH	RI	Status
Chenopodium ambrosioides L., Chenopodiaceae (H 1978 MCNS)	paico	2	0.18	5	0.16	17.0	NA
Tripodanthus acutifolius (Ruiz et Pav.) Tiegh, Loranthaceae (H 1096, 2248 MCNS)	corpo	2	0.18	5	0.16	17.0	NA
Blumembachia sp., Loasaceae (H 2599 M-MCNS)	itapalla del cerro	3	0.27	2	0.06	16.5	NA
Acantholippia salsoloides Griseb., Verbenaceae (H 1612 M-MCNS)	rica rica	2	0.18	4	0.13	15.5	NA
Citrus medica L., Rutaceae (H 2328 M-MCNS)	sidra, cidra	2	0.18	4	0.13	15.5	EX
Tagetes filifolia Lag., Asteraceae (H 2180 MCNS)	anís del campo	2	0.18	4	0.13	15.5	NA
Tecoma stans (L.) Juss., Bignoniaceae (H 2532 MCNS)	guaran guay	3	0.27	1	0.03	15.0	NA
Anadenanthera colubrina (Vell.) Bernan var. *cebil* (Griseb.) Alts, Fabaceae (H&G 2398 MCNS)	cebil	2	0.18	3	0.10	14.0	NA
Apium sp., Apiaceae	apio del campo	2	0.18	3	0.10	14.0	NA
Bidens pilosa L. var. *minor* (Bl.) Sherff., Asteraceae (H&Lo 990 MCNS)	saitilla blanca, saitilla	2	0.18	3	0.10	14.0	NA
Buddleja tucumanensis Griseb., Buddlejaceae (H 2570 MCNS)	san juan c'ora	2	0.18	3	0.10	14.0	NA
Coffea arabica L., Rubiaceae (H 1641 M-MCNS)	café	2	0.18	3	0.10	14.0	EX
Cuminum cyminum L., Apiaceae (H 1593 M-MCNS)	comino	2	0.18	3	0.10	14.0	EX
Fagara rhoifolia (Lam.) Engl., Rutaceae (H&Lo 982 MCNS)	sauco hediondo, sauquillo	2	0.18	3	0.10	14.0	NA
Mentha x rotundifolia (L.) Huds., Lamiaceae (H 1639 M-MCNS)	yerba buena	2	0.18	3	0.10	14.0	AD
Not identified	oreja de perro	2	0.18	3	0.10	14.0	
Not identified (H 2267 MCNS)	alcanflor	2	0.18	3	0.10	14.0	
Not identified (H 2484 MCNS)	oreja de palo	2	0.18	3	0.10	14.0	
Ocotea puberula (Rich.) Nees, Lauraceae (N 2197 M-MCNS)	laurel	2	0.18	3	0.10	14.0	NA
Peperomia arifolia Miq., Piperaceae (H 2036b MCNS)	anís del monte	2	0.18	3	0.10	14.0	NA
Peperomia tetraphylla (G. Forst) Hook et Arn., Piperaceae (H 1426 MCNS)	siemprevida chica	2	0.18	3	0.10	14.0	NA
Peperomia theodori Trelease, Piperaceae (H 1105 MCNS)	siempreviva	2	0.18	3	0.10	14.0	NA

Table 2. Continued.

Species, family (Herbarium number according to collector)	Vernacular name	#BS	Rel BS	#PH	Rel PH	RI	Status
Senecio cremeiflorus Mattf., Asteraceae (H&A 1442 MCNS)	lampazo	2	0.18	3	0.10	14.0	EN
Vassobia breviflora (Sendtn.) Hunziker, Solanaceae (H 2411 MCNS)	pucancho, uchucho	2	0.18	3	0.10	14.0	NA
Viola sp. L., Violaceae (H 2455 M-MCNS)	violeta	2	0.18	3	0.10	14.0	EX
Achyrocline hyperchlora Blake, Asteraceae (H&Lo 974 MCNS)	amaicha	2	0.18	2	0.06	12.0	NA
Argenome subfusiformis Ownbey, Papaveraceae (H&L 1834 MCNS)	cardo santo	2	0.18	2	0.06	12.0	NA
Baccharis coridifolia DC, Asteraceae (H 2157 MCNS)	romerillo	2	0.18	2	0.06	12.0	NA
Baccharis grisebachii Hieron, Asteraceae (H 2460 M-MCNS)	quinchamal	2	0.18	2	0.06	12.0	NA
Campyloneurum aglaolepis (Alston) de la Sota, Polypodiaceae (H&A 1427 MCNS)	pori pori, poli poli, canchalagua	2	0.18	2	0.06	12.0	NA
Canavalia sp., Fabaceae	habilla	2	0.18	2	0.06	12.0	NA
Diatenopteryx sorbifolia Radlk., Sapindaceae (H 2376 MCNS)	suiquillo	2	0.18	2	0.06	12.0	NA
Eupatorium hookerianum Griseb., Asteraceae (H&Lo 995 MCNS)	hediondilla negra	2	0.18	2	0.06	12.0	NA
Euphorbia sp., Euphorbiaceae (H 2455 MCNS)	piedrita	2	0.18	2	0.06	12.0	
Gunnera apiculata Schindl., Gunneraceae (H&L 1745 MCNS)	querusilla colorada, quirusilla	2	0.18	2	0.06	12.0	NA
Malus sylvestris Mill., Rosaceae (H&A 1409 MCNS)	manzana	2	0.18	2	0.06	12.0	EX
Manihot esculenta Crantz., Euphorbiaceae (H&L 1616 M-MCNS)	mandioca	2	0.18	2	0.06	12.0	EX
Mimosa debilis H. B. K. ex. Willd., Fabaceae (H&Lo 947 MCNS)	celosita grande	2	0.18	2	0.06	12.0	NA
Not identified	muela hedionda	2	0.18	2	0.06	12.0	
Not identified (H 2041 MCNS)	polvillo	2	0.18	2	0.06	12.0	
Not identified (H 2509 MCNS)	violeta del campo	2	0.18	2	0.06	12.0	
Oncidium bifolium Sims, Orchidiaceae (H 2276 MCNS)	banderilla, pajarilla	2	0.18	2	0.06	12.0	NA

Table 2. Continued.

Species, family (Herbarium number according to collector)	Vernacular name	#BS	Rel BS	#PH	Rel PH	RI	Status
Phaseolus vulgaris L. var. *vulgaris*, Fabaceae (H 1930 MCNS)	poroto amarillo, p. blanco, p. negro, p. negro guillador	2	0.18	2	0.06	12.0	NA
Polygonum sp., Polygonaceae (H&Lo 996 MCNS)	picantilla	2	0.18	2	0.06	12.0	
Solanum sp., Solanaceae (H 2519 MCNS)	yerba mora	2	0.18	2	0.06	12.0	
Theobroma cacao L., Sterculiaceae	chocolate	2	0.18	2	0.06	12.0	EX
Tipuana tipu (Benth.) Kuntze, Fabaceae (H 2109 MCNS)	tipa	2	0.18	2	0.06	12.0	NA
Tunilla soherensii (Britton et Rose) Hunt& Illiff var. *soherensii*, Cactaceae (H 1637 M-MCNS)	airampo	2	0.18	2	0.06	12.0	NA
Ullucus tuberosus Lozano, Basellaceae (H 1305 M-MCNS)	papa verde	2	0.18	2	0.06	12.0	NA
Vriesea friburgensis Mez var. *tucumanensis* (Mez.) L. B. Sm., Bromeliaceae (H 2290 MCNS)	payo	2	0.18	2	0.06	12.0	NA
Petroselimun crispum (Mill.) A. W. Hill, Apiaceae (H 1959 MCNS)	perejil	1	0.09	3	0.10	9.5	EX
Aechmea distichantha Lem. var. *distichanta*, Bromeliaceae (H&A 1517 MCNS)	taraca	1	0.09	2	0.06	7.5	NA
Aloysia citriodora Palau, Verbenaceae (H 2574 MCNS)	cedrón	1	0.09	2	0.06	7.5	NA
Celtis iguanaea (Jac.) Sarg., Celtidaceae (H 2148 MCNS)	tala	1	0.09	2	0.06	7.5	NA
Citrus reticulata Blanco, Rutaceae	mandarina	1	0.09	2	0.06	7.5	EX
Commelina erecta L., Commelinaceae (H&A 1496 M-MCNS)	santa lucía	1	0.09	2	0.06	7.5	NA
Lagenaria siceraria (Molina) Standl., Cucurbitaceae (H 1343 MCNS)	porongo	1	0.09	2	0.06	7.5	AD
Minthostachys mollis Griseb., Lamiaceae (H 2489 MCNS)	toronjil cerreño	1	0.09	2	0.06	7.5	NA
Not identified (H 2464 MCNS)	flor de tierra, huaji	1	0.09	2	0.06	7.5	
Not identified (H 2473 M-MCNS)	siete vueltas	1	0.09	2	0.06	7.5	
Psidium aff guineense Swartz, Myrtaceae (H 2639 MCNS)	arazay	1	0.09	2	0.06	7.5	NA

Table 2. Continued.

Species, family (Herbarium number according to collector)	Vernacular name	#BS	Rel BS	#PH	Rel PH	RI	Status
Tabebuia lapacho (Schum.) Sandw., Bignoniaceae (H 2003 MCNS)	lapacho amarillo	1	0.09	2	0.06	7.5	NA
Tillandsia australis Mez, Bromeliaceae (H&A 1523 MCNS)	payo	1	0.09	2	0.06	7.5	NA
Adiantopsis chlorophylla (Sw.) Fée, Pteridaceae (H 2448 MCNS)	ala de cuervo	1	0.09	1	0.03	6.0	NA
Allium cepa L., Liliaceae (N 1577 M-MCNS)	cebolla	1	0.09	1	0.03	6.0	EX
Anethum graveolens L., Apiaceae (H 2538 MCNS)	eneldo	1	0.09	1	0.03	6.0	EX
Asclepias flava Lillo, Asclepiadaceae (H 1052 MCNS)	leche tres	1	0.09	1	0.03	6.0	NA
Azorella compacta Phil., Apiaceae (H&G 1044 MCNS)	yareta	1	0.09	1	0.03	6.0	NA
Bougainvillea stipitata Griseb., Nyctaginaceae (H 1015 MCNS)	huancar	1	0.09	1	0.03	6.0	NA
Brassica sp., Brassicaceae	mostaza	1	0.09	1	0.03	6.0	EX
Camellia sinensis (L.) Kuntze, Teaceae	té	1	0.09	1	0.03	6.0	EX
Capsicum frutescens L., Solanaceae (H 1373 MCNS)	ají amarillo	1	0.09	1	0.03	6.0	EX
Senna spectabilis (DC.) H. S. Irwin & Barneby, Fabaceae (H 2102 MCNS)	carnaval	1	0.09	1	0.03	6.0	EX
Senna crassiramea (Benth) H. S. Irwin & Barneby, Fabaceae (H 2466 M-MCNS)	sumalagua	1	0.09	1	0.03	6.0	NA
Chenopodium quinoa Willd., Chenopodiaceae (H 1893 M-MCNS)	quiuna, quinoa	1	0.09	1	0.03	6.0	NA
Chrysophyllum gonocarpum (M. & E.) Engler, Sapotaceae (H 2638 MCNS)	aguaí	1	0.09	1	0.03	6.0	NA
Tanacetum parthenium (L.) Sch. Bip., Asteraceae (H 2482 M-MCNS)	ajenco	1	0.09	1	0.03	6.0	AD
Cissampelos pareira L., Menispermaceae	níspero	1	0.09	1	0.03	6.0	EX
Citrus paradisi Macf., Rutaceae (H 2105 MCNS)	pomelo	1	0.09	1	0.03	6.0	EX
Cucurbita maxima Duchesne, Cucurbitaceae (H 1573 MCNS)	guinea	1	0.09	1	0.03	6.0	NA
Cyclanthera pedata (L.) Schrad., Cucurbitaceae (H 1338 MCNS)	achoscha	1	0.09	1	0.03	6.0	NA

Table 2. Continued.

Species, family (Herbarium number according to collector)	Vernacular name	#BS	Rel BS	#PH	Rel PH	RI	Status
Cymbopogon citratus (DC) Stapf., Poaceae (H 2043 M-MCNS)	cedrón paja	1	0.09	1	0.03	6.0	EX
Cynara scolymus L., Asteraceae (H 2470 M-MCNS)	alcachofa	1	0.09	1	0.03	6.0	EX
Datura feroz L., Solanaceae (H 2285 MCNS)	chamico	1	0.09	1	0.03	6.0	EX
Erythrina falcata Benth., Fabaceae (H 1795 MCNS)	ceiba	1	0.09	1	0.03	6.0	NA
Escallonia resinosa (Ruiz et Pav.) Pers., Saxifragaceae (HG&M 1212 MCNS)	chachacoma	1	0.09	1	0.03	6.0	NA
Eupatorium sp., Asteraceae (H 2498 MCNS)	borrajilla	1	0.09	1	0.03	6.0	
Gorgonidium vermicidum (Speg.) Bogner & Nicolson, Araceae (H 1924 MCNS)	papa de víbora	1	0.09	1	0.03	6.0	NA
Gunnera schindleri L. E. Mora, Gunneraceae	querusilla blanca	1	0.09	1	0.03	6.0	NA
Hypolepis repens (L.) C. Presl., Dennstaedtiaceae (H&Lo 960 MCNS)	ala de cuervo	1	0.09	1	0.03	6.0	NA
Hyptis mutabilis (Rich.) Briq., Lamiaceae (H 2520 MCNS)	salvia mora	1	0.09	1	0.03	6.0	NA
Illicium verum Hook. f., Illiciaceas	anís estrellado	1	0.09	1	0.03	6.0	EX
Inga sp., Fabaceae	pacay	1	0.09	1	0.03	6.0	
Juglans australis Griseb., Juglandaceae (H 1107[a] MCNS)	nogal	1	0.09	1	0.03	6.0	NA
Juglans regia L., Juglandaceae	nogal castillo	1	0.09	1	0.03	6.0	EX
Krameria lappacea (Dombey) Burdet et Simpson, Krameriaceae (H 2300 M-MCNS)	chipichape	1	0.09	1	0.03	6.0	NA
Leonurus sibiricus L., Lamiaceae (H 2573 MCNS)	papa de paloma	1	0.09	1	0.03	6.0	AD
Lepidium meyenii Walp., Brassicaceae (GS 165 SI)	papa macaia, macaia	1	0.09	1	0.03	6.0	NA
Lippia alba (Mil.) N. E. Br., Verbenaceae (H 2632 MCNS)	cedrón árbol	1	0.09	1	0.03	6.0	NA
Malva sp., Malvaceae (H&A 1483 M-MCNS)	malva loca	1	0.09	1	0.03	6.0	
Not identified	carallanta	1	0.09	1	0.03	6.0	
Not identified	c'uru	1	0.09	1	0.03	6.0	
Not identified	yurito malva	1	0.09	1	0.03	6.0	
Not identified	zacatera	1	0.09	1	0.03	6.0	
Oryza sativa L., Poaceae (H 1582 M-MCNS)	arroz	1	0.09	1	0.03	6.0	EX

Table 2. Continued.

Species, family (Herbarium number according to collector)	Vernacular name	#BS	Rel BS	#PH	Rel PH	RI	Status
Passiflora tenuifila Killip, Passifloraceae (H&A 1515 MCNS)	granadilla	1	0.09	1	0.03	6.0	NA
Peumus boldus (Molina), Monimiaceae	boldo	1	0.09	1	0.03	6.0	EX
Pimpinella anisum L., Apiaceae (H 1624 M-MCNS)	anís castillo	1	0.09	1	0.03	6.0	EX
Piper aduncum L., Piperaceae (H 2564 MCNS)	matico	1	0.09	1	0.03	6.0	NA
Pisum sativum L., Fabaceae (H 1450 M-MCNS)	arveja	1	0.09	1	0.03	6.0	EX
Pleopeltis macrocarpa (Bory ex Willd) Kaulf., Polypodiaceae (H 2451 MCNS)	pori pori, poli poli, canchalagua	1	0.09	1	0.03	6.0	NA
Polylepis australis Bitter, Rosaceae	queñua	1	0.09	1	0.03	6.0	EN
Smallanthus macrosyphus (Baker) A. Grau, Asteraceae (H 1250a MCNS)	pucunillo	1	0.09	1	0.03	6.0	NA
Prosopis nigra (Griseb.) Hieron., Fabaceae (H&G 1038 MCNS)	algarroba	1	0.09	1	0.03	6.0	NA
Ricinus communis L., Euphorbiaceae	tártago	1	0.09	1	0.03	6.0	E
Salix humboldtiana Willd., Salicaceae (Zul. 2782 SI)	sauce	1	0.09	1	0.03	6.0	NA
Scoparia plebeja Cham. Et. Schltdl., Scrophulariaceae (H 1067 MCNS)	yerba de víbora	1	0.09	1	0.03	6.0	NA
Senecio bomanii R. E. Fries, Asteraceae (H 2009 MCNS)	cosillo	1	0.09	1	0.03	6.0	NA
Sida poeppigiana (K. Schum.) Frytell, Malvaceae (H 1982 MCNS)	afata	1	0.09	1	0.03	6.0	NA
Sida rhombifolia L., Malvaceae (H 2505 MCNS)	afata	1	0.09	1	0.03	6.0	NA
Smallanthus sonchifolia (Popp. Et Endl.) Robinson, Asteraceae (H 1903 M-MCNS)	yacón	1	0.09	1	0.03	6.0	EX
Solanum tucumanense Griseb., Solanaceae (H&G 2406 MCNS)	hediondilla	1	0.09	1	0.03	6.0	NA
Tagetes terniflora H. B. K., Asteraceae (H&L 1689)	suico	1	0.09	1	0.03	6.0	NA
Tanacetum vulgare L., Asteraceae (H 2260 MCNS)	santa maría	1	0.09	1	0.03	6.0	AD
Valeriana officinalis L., Valerianaceae	valeriana	1	0.09	1	0.03	6.0	EX

Table 2. Continued.

Species, family (Herbarium number according to collector)	Vernacular name	#BS	Rel BS	#PH	Rel PH	RI	Status
Vanilla mexicana Mill., Orchidiaceae	vainilla	1	0.09	1	0.03	6.0	EX
Vicia faba L., Fabaceae (H 2263 MCNS)	haba	1	0.09	1	0.03	6.0	EX

BS – number of body systems treated; Rel BS – relative number of body systems treated (normalized to maximum value of 1); PH – number of pharmacological properties; Rel PH – relative number of pharmacological properties (normalized to maximum value of 1); RI – relative importance (Rel PH + Rel BS) 2×100(CTES) – Herbario del Instituto de Botánica del Nordeste, Corrientes; (MCNS) – Herbario del Museo de Ciencias Naturales Salta, Universidad Nacional de Salta; (M-MCNS) – Herbario del Museo de Ciencias Naturales Salta, Universidad Nacional de Salta. Sample section; (SI) – Herbario del Instituto Darwinion, San Isidro; GS – Gómez Sosa, E. V.; H&A – Hilgert, N. I. & Arenas, P.; H&G – Hilgert, N. I. & Gil, G. E.; H & L – Hilgert, N. I. & Lamas, M. L.; H&Lo – Hilgert, N. I. & Lomáscolo S.; H – Hilgert, N. I.; HG&M – Hilgert, N. I., Gil, G. E. & Marino, G.; Jörg. – Jörgensen, P.; Krap. – Krapovickas, A.; Zul. – Zuloaga, F. O.; NA – native; EN – endemic; EX – exotic; AD – naturalized adventitious.

avoid the shock of any remedy of opposite condition. These affections are considered to be of natural origin and they can promote other diseases. In these situation usually the *rural doctor* should help the patient.

Species diversity and relative importance

To estimate the theoretical total number of species used medicinally in the locations of the National Park the curve of species accumulation that best fits the Clench Model ($R = 0.999$) gives an asymptotic value of 266, that is to say the amount found (188) represents 71% of the stated total, whereas the estimators yield the following results: Chao2: 227, Jacknife1: 240, Jacknife2: 257, i.e. the observed species are between 73 and 83% of the estimated totals. For the neighboring villages the Clench model ($R = 0.998$) was also smoothed, giving an asymptote in 290. Consequently, the 230 observed species correspond to 79% of this total. The estimators gave the following values: Chao2: 288, Jacknife1: 295, Jacknife2: 323, consequently, the resultant percentage was found to be between 71 and 80% of these calculations.

The neighboring populations to the Baritú National Park (that is to say, those with a lower grade of isolation) resulted in having a greater species richness of medicinally used plants than Abra de Minas, Lipeo and Baritú, as also predicted by the estimators and species accumulation curves. The difference found represents 18.3% whilst the final estimates are between 9.3 and 21.2%.

According to the present results all local populations use at least 259 ethnospecies for medicines, comprising of 230 plants and 2 mushrooms (in addition to 16 species which have been identified by Genera, 4 by Family and 7 unidentified species purchased as fragments). The known species include 69 families of flowering plants and 5 Pteridophyta families. Ten families (Asteraceae, Fabaceae, Lamiaceae, Rutaceae, Solanaceae, Poaceae, Malvaceae, Apiaceae, Piperaceae and Verbenaceae) comprise nearly half of the total. These medicinal plants encompass 53 pharmacological properties; analgesic agents, antibiotic agents, gastrointestinal agents and respiratory agents are especially common. One species has been assigned 30 pharmacological properties (*Coronopus didymus*), 5 species (*Erythroxylum coca* var. *coca*, *Citrus limon*, *Sambucus nigra* subsp. *peruviana*, *Malva parviflora*, *Acacia macracantha*) have 14 or more properties and 65 species have only one pharmacological property (Table 2).

The values of RI vary between 6 and 100, being highest for *Coronopus didymus* (Table 2). No correlations were found between the RI and the methods of administration or the recipes.

Methods of use

In Table 3 can be seen how many species were cited for known illnesses in the 11 body systems or the systemic affections (BS) considered in the area, how many references were reported, and the method of administration. At the same time is shown the amount of possible affections in each body system (BS). It can be seen that the hot and cold syndrome, digestive and reproductive BS's contribute to more than half (55.6%) of the total reported affections and that these represent the treatments which involve the greatest diversity of species.

In relation to the method of administration, there is practically no difference in the reported totals, 50.2% are for external use and 49.8% for internal use. For external administration the use of combined species is predominant (53.5%) followed by the use of individual species (36.5%). For internal administration the use of one species only (63.8%) for recipes predominates, followed by the use of combinations of plants (29.3%). In both cases, mixtures with minerals, excrements or other elements are given in lower proportions (10% and 6.9% respectively). The method for internal administration was correlated with recipes of an individual species (Coef.: 0.654, Sig. < 0.001), although this type of recipe also correlates with the method of external administration (Coef.: 0.364, Sig. < 0.001). In any case, the predominance of each type of use changes according to the affection being treated. In both types of application the parts of the plant 'above ground' represent the parts most used, followed by the reproductive organs. For external use, and in third place, is the use of bark and wood, and for internal use are roots (Table 3).

The comparison between the administration methods and the recipes of the *rural doctors* with the rest of the informants gave significantly different results ($\chi^2 = 10.36$, DF $= 4$, $\alpha = 0.05$). In this case the *rural doctors* apply more external and less internal recipes than expected and more recipes of combined species and less of individual species than expected (Table 4). Discriminant analysis, based on the type of informant, correctly classified 91.9% of the

Table 3. Number of genera, families and medicinal species referred to and the method of administration for each body system or systemic affection (BS).

Body systems or systemic affections	Number of illnesses	Number of family	Number of genera	Number of species	Number of event	Use																			
						External										Internal									
						T	#1	#2	#3	#A	#B	#C	#D	#E	#F	T	#1	#2	#3	#A	#B	#C	#D	#E	#F
Hot and cold syndrome	3	54	110	144	743	536	176	341	19	40	47	66	344	38	1	207	150	43	14	14	8	67	110	7	1
Digestive	10	48	110	134	553	35	13	19	3	4	1	6	24	0	0	518	367	124	27	52	24	126	291	18	7
Reproductive	16	49	87	97	391	115	47	62	6	8	13	12	73	8	1	276	164	76	36	32	13	52	149	29	1
Skeletal-muscular system	11	40	71	81	237	219	61	136	22	16	29	24	139	9	2	18	16	2	0	3	3	2	6	4	0
Respiratory	8	25	45	54	210	72	12	43	17	7	8	23	34	0	0	138	69	60	9	8	0	49	76	3	2
Socio-cultural or supernatural	7	33	61	67	203	117	50	55	12	9	3	15	81	5	4	86	49	32	5	1	1	26	50	5	3
Nervous system	12	35	62	73	201	164	100	51	13	18	5	55	74	5	7	37	17	17	3	1	1	10	24	1	0
Urinary	3	37	63	69	185	45	11	22	7	2	6	11	20	5	1	140	73	65	2	34	6	28	69	3	0
Dermatological	6	25	38	44	159	149	63	49	37	5	33	17	80	10	4	10	9	0	1	1	3	2	3	1	0
Infections	10	19	25	26	67	51	16	26	9	8	18	7	14	3	1	16	13	0	3	0	4	5	5	0	2
Cardiovascular	5	17	19	20	47	2	2	0	0	0	1	0	1	0	0	45	33	11	1	7	6	11	18	2	1
Fiber	1	12	20	22	35	17	6	11	0	1	1	12	1	0	2	18	3	13	2	2	1	3	10	1	1
Total					3031	1522	557	815	145	118	165	248	885	83	23	1509	963	443	103	155	70	381	811	74	18

Internal – Inhalations, enemas, smoke, ingestion, aromatherapy; External – vapors, bathing, oral, local application, compresses y vapors, gargling, lavages, 'limpias,' 'compostura,' magic, tourniquets; T – total; 1 – plants used alone; 2 – plants combined with other species; 3 – plants combined with resins, ashes, salt, oil, human urine, bicarbonate, alcohol, sugar, human milk, human or chicken excrement, pig fat, kerosene, alum or earth; A – roots, rhizomes, bulbs, tubers, pseudo bulbs, and their derivatives, ashes o starch; B – bark and woods; C – reproductive organs and derivatives (fruits, flowers, nectar, petals, placenta, juice, spores); D – aerial parts (leaves and shoots and their modifications); E – complete plant; F – others (gum, oil, water accumulated in bracts, sap, etc.).

registered cases according to the frequency of use of the species by the method of administration and the type of recipe.

On the other hand, no relation was noted between the specializations of the individuals who apply medicinal plants and the body systems or systemic affections most mentioned, or that more species were involved in their cures. This includes not only sicknesses treated exclusively by consultation and participation of the *rural doctor* (the hot and cold syndrome) but also those assisted by domestic methods or with the help of an herbal doctor (digestive and reproductive diseases).

The medicinal plants include 8 life forms with herbs predominating (48.2%) followed by trees (26.6%), shrubs (14.3%), epiphytes (6.5%), vines (1.3%), saprophytes (0.8%) and hemi parasitic (0.4%). Of all the medicinal species found, 91 species are exotic, 17 of which are naturalized adventitious, and 146 are native, 5 of which are endemics of Argentina. On comparing the use of native and exotic species significance differences were found ($\chi^2 = 11$, DF = 11, $\alpha = 0.05$). A greater than expected use of native species was recorded in the treatment for the hot and cold syndrome, the skeletal-muscular system and for dermatological disorders, meanwhile exotic species were used at a higher than anticipated level for the treatment of the respiratory and digestive systems (Table 5). Discriminant analysis based on the origin of the species correctly classifies 67.14% of the observed cases according to the frequency of use of the species per body system.

Discussion

The practices observed in the area coincide in the main with those described for Northwest Argentina by Palma (1978) and Hilgert (2001). With respect to medicine practiced within the family context, no evidence was seen of the

Table 4. Comparison between the use of species for distinct body systems between *rural doctors* and the remainder of the informants.

	Number of events observed in rural doctors	Number of events expected in rural doctors	Number of events observed in common people	Number of events expected in common people	Totals
Internal	111	129.91	1186	1167.09	1297
External	142	123.10	1087	1105.90	1229
1	112	126.30	1149	1134.70	1261
2	121	106.27	940	954.73	1061
3	20	20.43	184	183.57	204
Totals	506	506.00	4546	4546.00	5052

Contingency table for the Chi squared test.

1 – Plants used alone; 2 – plants combined with other species; 3 – plants combined with resins, ashes, salt, oil, human urine, bicarbonate, alcohol, sugar, human milk, human or chicken excrement, pig fat, kerosene, alum or earth.

Table 5. Comparison of the use of native and exotic medicinal plants and exotic in the distinct body systems.

	Number of native species observed	Number of native species expected	Number of exotics species observed	Number of exotics species expected	Totals
Socio-cultural or supernatural	47	46	29	29	76
Hot and cold syndrome	97	9	57	5	154
Respiratory	31	4	36	25	67
Cardiovascular	19	18	11	11	30
Digestive	86	8	60	5	146
Fiber	11	11	8	7	19
Nervous system	50	52	36	3	86
Skeletal-muscular system	61	53	27	3	88
Reproductive	64	6	41	40	105
Urinary	50	47	28		78
Infections	19	18	11	11	30
Dermatological	39	34	18	2	57
Totals	574	5	362	3	936

Contingency table for the Chi squared test.

inseparable relation between the use of prayer and the use of wild plants, in difference to the proposal of Hurrel (1995). On the other hand, this relation is evident in treatments applied by *rural doctors* where prayer and the magic-religious factor is the principal agent for curing, using the plant only as a vehicle; concurring with Pérez de Nucci (1988). The hot and cold theory involves similar concepts to those described for the inhabitants of the Zenta River Basin situated to the south (Hilgert 2001).

The estimation of the total of medicinal species for each group of localities (villages of the National Park and neighbors of the same) is restricted to the spatial scale of the samples and is not open to extrapolation (Moreno 2000). Consequently, in the case of Abra de Minas, Lipeo and Baritú, it can be considered that the total number of medicinal species used would be very close to the value found in this present work; as to the rest, even though we have a better number of surveyed individuals this is not representative of the total of these populations. The difference between the medicinal species detected in the locations within the Baritú National Park and the total estimated may in part result from the addition of new species from the surveys of the neighboring villages (85).

No positive relation was found between the level of isolation and the species richness, in agreement with the statements of Levy et al. (1997). The neighboring localities (less isolated) resulted in having greater species richness. This is probably due to the better possibilities of access by these villagers to consultation with Bolivian *rural doctors* and the herbal markets of the country, within which the villages maintain a strong hereditary herbal tradition of the Kallawayas (Madrid de Zito Fontan and Palma 1997).

Of the 10 botanical families with the most widely used species, 8 coincide with references by Hilgert (2001) for rural populations which inhabit the Yungas area to the south of the area studied. Additionally, 6 families show as pointers in a ranking carried out by Moerman (1996) to analyze the botanical families in relation to the therapeutic categories in which the native flora of North America are used and also in an analysis of the botanical families most used for medicinal purposes in distinct regions of the world (Moerman et al. 1999).

Phillips and Gentry (1993) proposed an index of value of use (UV) for the species. The UV assists in the consensus of the informants in function of the proportion of individuals who independently make reference to a determinate use of a certain form. On the other hand, the RI used in this work reflects the total usages and does not attempt to quantify the relative importance of each use (Phillips 1996). The UV and RI indexes do not respond in a similar way for the same species with the same base data due to the fact that they are based on and correspond to distinct variables, belonging to two differing approximations. It is considered that the RI better reflects the importance of use of the species as it coincides to a greater part with the order in which the informants mention the species. This order, according to the proposal of some sampling techniques, reflects the value that each species has for the informant (Bernard 2000).

The order of importance found in the present study does not coincide with that found previously by Hilgert (2001) in which digestive and reproductive illnesses were the most important.

The correlation found between recipes of an individual species and the internal method of use, which is higher than external use, could be an indicator of a common understanding based on traditional practice and observation.

Considering that hardly any herbs have been found to be useful in ways which had not already been recognized by traditional phytotherapists (Barsh 1997), the differential use of the same species for distinct sicknesses (high RI, Table 2) is valuable data for those interested in finding new active substances.

The proportions found between external and internal use do not coincide with that cited for medicinal plants of North America, where species for internal use predominate (Moerman 1996). We suppose that these differences are based on cultural aspects that define the perception of the sickness and, with this, the way to treat it, or, as proposed by Ososki et al. (2002), they could be based on the preferences of *rural doctors*. Nevertheless, as with the references made by Ososki et al. (2002) there is an agreement between the method of administration of the treatments and the relative location of the affected BS. For example, for 'external' problems (skeletal-muscular system, dermatological) there are external uses and for 'internal' sicknesses (urinary or respiratory system) the uses are internal. Although it is possible to demonstrate that the majority of ailments considered within the nervous system are treated by external means, coincidently the greater parts of these are considered as a consequence of complications of socio-cultural or supernatural illnesses.

On comparing the use of medicinal plants by the layperson and by *rural doctors* differences were found in the method of administration and the type of recipes. This could be explained by the specialization in treating sicknesses that require 'limpias' (ritual cleansing), 'composturas' (ritual accommodation of organs, bones, etc), bathing, or a whole range of therapeutic treatment, that involve the use of ointments and potions of complex preparation. The use of the same species for distinct affections, combined with distinct plants, occasionally is due to increase in or canceling out of a certain bioactive substance according to the mixtures used. In consequence, we can assume that the *rural doctor* prepares remedies in ways which isolate their most bioactive compounds or remove toxic ones, combining plants in ways they create medically significant synergistic effects, as proposed by Barsh (1997).

On the other hand, it is important to emphasize that in the cures effected by rural doctors, the vegetable element provides the medium to create the suitable conditions, but the rituals and prayers are considered the true elements that make possible the cure, in agreement with the statements by Pérez de Nucci (1988).

In agreement with Bennet and Prance (2000), some exotic species such as *Saccharum officinarum* or *Cymbopogon citratus* are included as flavoring; however, these in turn possess bioactive substances.

In the local populations, the unique distinction that is made between the exotic species and native ones is that the major part of the first ones are 'castillas' (home-grown) which according to explications only survive after having been cultivated locally and do not really allude in the majority of cases to their introduction by Spaniards.

According to Voeks (1996) the predominance in the use of herbs and the none differential use between exotic species and native ones can be interpreted a result of the cultural adaptation to the use of those species with a greater availability in peridomestic surroundings, frequently in disturbed areas. According to the same author, this can also reflect the difficulty in finding areas of pristine vegetation or is a product of cultural changes and in the long term, the destruction of basic knowledge about the medicinal properties of the primary forests. Given the good conditions of environment conservation in the study area it is considered that an acceptable explication for the region can be found in the first conclusion. On the other hand, *Myroxylon peruiferum* is very rare in the region and *Cinchona ledgeriana* does not grow at all there, despite which, both possesses an elevated RI.

Conclusion

The populations studied live in an Argentine region of great botanical diversity that can be a source of many phytotherapeutic elements. Although the population has access to health centers and some industrial medicines the use of traditional alternative medicines is very common. The species registered represent a high percentage (between 70–80%, according our calculations) of the estimated total of herbalist medicines of the area studied. The species with the greater RI are *Coronopus didymus*, *Rosa* sp., *Citrus limon, Sambucus nigra* L. subsp. *peruviana, Citrus sinensis, Malva parviflora y Erythroxylum coca* Lam. var. *coca*, all of which are readily accessible within the region as they grow wild, they are cultivated, are ruderal or they are bought in markets or stores.

Taking into account Cox's (1990) proposal, which states that a group that has lived a long time in an environment and has a conservative 'medical tradition', it could be an interesting site to look for new drugs, the RI value and the method of use of the species are important tools for the selection of plants to be studied more exhaustively. In our study, the results can be interpreted as a reflex of the cultural syncretism, because it is possible to find both native and exotic species sharing the high scores of RI.

Native species and exotic species are used differently according to the body system to which they are applied. It could be interesting to investigate the origin of the introduction of the exotic species, as mentioned by Bennet and Prance (2000) it is very probable that some have been introduced as foodstuffs, others as ornaments and only some as therapeutics.

The rural doctors use different administration methods and recipes compared to the rest of the population, although this does not necessarily signify a greater understanding of the medicinal properties of the plants, rather a different role in the traditional medical system.

There remains the future task of evaluating the differences in the local herbalist knowledge, with deeper investigation of the capabilities of the population to recognize useful species and their application. Upon deeper investigation of those aspects that are considered in choosing the plant to be used (the state of the plant, the suitable phenological moment for harvesting, the quality of the environment where the plant grows, etc.) the quality and the depth of the herbal knowledge of all the population may be estimated since errors in the selection or the preparation can result in a non effective or a lethal potion.

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References

Ankili A., Sticher O. and Heinrich M. 1999. Medical ethnobotany of the Yucatec Maya: healers'consensus as quantitative criterion. Economic Botany 53: 144–160.

Balick M.J. 1996. Transforming ethnobotany for the new millennium. Annals of the Missouri Botanical Garden 83: 58–66.

Barsh R. 1997. The epistemology of traditional healing systems. Human Organizations 56: 28–37.

Bennet B.C. and Prance G.T. 2000. Introduced plants in the indigenous pharmacopoeia of Northern South America. Economic Botany 54: 90–102.

Bernard H.R. 2000. Social Research Methods. Thousand Oaks, SAGE.

Bianchi A.R. and Yánez C.E. 1992. Las precipitaciones del noroeste argentino. Instituto Nacional de Tecnología Agropecuaria, Salta, Argentina.

Brown A.D. 1995. Las selvas de montaña del noroeste de Argentina: problemas ambientales e importancia de su conservación. In: Brown A.D. and Grau H.R. (eds), Investigación, Conservación y Desarrollo en Selvas Subtropicales de Montaña. Proyecto de Desarrollo Agroforestal, LIEY, pp. 9–18.

Brown A.D., Grau H.R., Malizia L.R. and Grau A. 2001. Argentina. In: Kappelle M. and Brown A.D. (eds), Bosques nublados del neotrópico. INBio, Costa Rica,pp. 623–659.

Cabrera A.L. 1976. Regiones fitogeográficas argentinas. Enciclopedia Agricultura y Jardinería 2, Editorial ACME, S.A. Buenos Aires, Argentina.

Caniago I. and Siebert S.F. 1998. Medicinal plant ecology, knowledge and conservation in Kalimantan, Indonesia. Economic Botany 52: 229–250.

Colwell R.K. 2000. EstimateS. Statistical Estimation of Species Richness and Shared Species from Samples. Version 6.0b1. University of Connecticut. http://viceroy.eeb.econn.edu/estimates.

Cox P.A. 1990. Ethnopharmacology and the search for new drugs. In: Chadwick D.J. and Marsh J. (eds), Bioactive Compounds from Plants. John Wiley and Sons, New York, pp. 40–47.

Ellen R. and Harris H. 2000. Introduction. In: Ellen R., Parkes P. and Bicker A. (eds), Indigenous Environmental Knowledge and its Transformations. Critical Anthropological Perspectives. Routledge, Taylor & Francis Group, London and New York, pp. 1–29.

Frei B., Balisberger M., Sticher O and Heinrich M. 1998. Medical ethnobotany of the Zapotecs of the Isthmus-Sierra (Oaxaca, México): documentation and assessment of indigenous uses. Journal of Ethnopharmacology 62: 149–165.

Frei B., Sticher O. and Heinrich M. 2000. Zapotec and mixe use of tropical habitats for securing medicinal plants in Mexico. Economic Botany 54: 73–81.

Gadgil M., Brekes F. and Folke C. 1993. Indigenous knowledge for biodiversity conservation. Ambio 22: 151–156.

Hersh-Martínez P. 2002. La doble subordinación de la Etnobotánica Latinoamericana en el descubrimiento y desarrollo de medicamentos: algunas perspectivas. Etnobiología 2: 103–119.

Hilgert N.I. 2001. Plants used in home medicine in the Zenta River basin, Northwest Argentina. Journal of Ethnopharmacology 76: 11–34.

Hunzinger H. 1995. La precipitación horizontal: su importancia para el bosque a nivel de cuencas en la Sierra de San Javier, Tucumán, Argentina. In: Brown A.D. and Grau H.R. (eds), Investigación, Conservación y Desarrollo en Selvas Subtropicales de Montaña. Proyecto de Desarrollo Agroforestal, LIEY, pp. 53–58.

Hurrell J.A. 1990. Interpretaciones de Relaciones en Ecología a partir de la Noción de Sistema, para el referente empírico Santa Victoria e Iruya (Salta, Argentina). Tesis Doctoral 548, Tomo III. Museo de Ciencias Naturales, Universidad Nacional de La Plata, La Plata, Buenos Aires, Argentina.

Hurrel J.A. 1991. Etnomedicina: Enfermedad y Adaptación en Iruya y Santa Victoria (Salta, Argentina). Revista del Museo de La Plata Antropología 9: 111–124.

Hurrel J.A. 1995. Ecología biocultural: etnomedicina y adaptación en Santa Victoria e Iruya (Salta, Argentina. In: Brown A.D. and Grau H.R. (eds), Investigación, Conservación y Desarrollo en Selvas Subtropicales de Montaña. Proyecto de Desarrollo Agroforestal, LIEY, pp. 223–230.

Hurrell J.A. and de la Sota E.R. 1996. Etnobotánica de las Pteridófitas de los pastizales de altura de Santa Victoria (Salta, Argentina). Revista del Museo de La Plata Botánica XIV: 353–364.

Iharlegui L. and Hurrell J.A. 1992. Asteraceae de Interés Etnobotánico de los Departamentos Santa Victoria e Iruya (Salta, Argentina). Ecognicion 3: 3–18.

Kalland A. 2000. Indigenous knowledge: prospects and limitations. In: Ellen R., Parkes P. and Bicker A. (eds), Indigenous Environmental Knowledge and its Transformations Critical Anthropological Perspectives. Routledge Taylor & Francis Group, London and New York, pp. 319–335.

Levy A., Brown A.D., Grau H.R. and Grau A. 1997. Local knowledge and the use of plants in rural communities in the montane forests of Northwestern Argentina. Mountain Research an Development 17: 263–271.

Lupo C. and Echenique M.R. 1997. Etnobotánica en la comunidad puneña de Yavi, Jujuy, Argentina. Parte I. Parodiana 10: 9–34.

Madrid de Zito Fontan L. and Palma N.H. 1997. La imagen reflejada: una ida y vuelta de la medicina científica a la medicina tradicional (a propósito de la Medicina Kallawaya). Kallawaya (n.s.) 4: 31–48.

Martinez M.R. and Pochettino M.I. 1992. The "Farmacia Casera" (Household pharmacy): a source of ethnopharmacobotanical information. Fitoterapia 63: 209–216.

Moerman D.E. 1996. An analysis of the food plants and drug plant of native North America. Journal of Ethnopharmacology 52: 1–22.

Moerman D.E., Pemberton R.W., Kiefer D. and Berlin B. 1999. A comparative analysis of five medicinal floras. Journal of Ethnobiology 19: 49–67.

Moreno C.E. 2000. Manual de métodos para medir la biodiversidad. Textos Universitarios. Universidad Veracruzana. Xalapa, Veracruz, México.

Osseweijer M. 2000. "We wander in our ancestor's yard": sea cucumber gathering in Aru, Eastern Indonesia. In: Ellen R., Parkes P. and Bicker A. (eds), Indigenous Environmental Knowledge and its Transformations Critical Anthropological Perspectives. Routledge Taylor & Francis Group, London and New York, pp. 55–76.

Ososki A.L., Lohr P., Reiff M., Balick M.J., Kronenberg F., Fugh-Berman A. and O'Connor B. 2002. Ethnobotanical literature survey of medicinal plants in the Dominican Republic used for women's health conditions. Journal of Ethnopharmacology 79: 285–298.

Palma N.H. 1978. La medicina popular del noroeste argentino (sus implicancias médico-sanitarias). Editorial Huemul, Buenos Aires, Argentina.

Palma N.H. 1994. La medicina y el hombre que los médicos deben conocer. Kallawaya (n.s.) 1: 21–49.

Pérez de Nucci A.M. 1988. La Medicina Tradicional del Noroeste Argentino. Historia y Presente. Serie Antropológica. Ediciones del Sol, Buenos Aires, Argentina.

Phillips O.L. 1996. Some quantitative methods for analyzing ethnobotanical knowledge. In: Alexiades M.N. and Wood Sheldon J. (eds), Selected Guidelines for Ethnobotanical Research: A Field Manual. Bronx, The New York Botanical Garden, pp. 171–197.

Phillips O. and Gentry A.H. 1993. The useful plants of Tambopata, Peru: II. Additional hypothesis testing in quantitative ethnobotany. Economic Botany 47: 33–43.

SPSS Inc. 2000. SPSS Windows. Versión 10.1.4 (16 March 2001).

StatSoft Inc. 1998. STATISTICA for Windows [Computer program manual]. Tulsa, OK: StatSoft, Inc., 2300 East 14th Street, Tulsa, OK 74104, phone: (918) 749–1119, fax: (918) 749–2217, email: info@statsoft.com, WEB: http://www.statsoft.com.

Torres G. 1982. Curanderismo y Brujería en el área de la selva Tucumano-Oranense. Programa de Investigaciones sobre Epidemiología Psiquiátrica (PEPSI-CONICET) Buenos Aires, Argentina Documenta Laboris 2: 1–38.

Voeks R.A. 1996. Tropical forest healers and habitat preference. Economic Botany 50: 381–400.

Zuloaga F.O. and Morrone O. (eds), 1996. Catálogo de las plantas vasculares de la República Argentina. I. Pteridophyta, Gymnospermae y Angiospermae (Monocotyledoneae). Monograph in Systematic Botany Missouri Botanical Garden 60: 1–323.

Zuloaga F.O. and Morrone O. (eds), 1999. Catálogo de las plantas vasculares de la República Argentina. II. Angiospermae (Dicotyledoneae). Monograph in Systematic Botany Missouri Botanical Garden 74: 1–1269.

Zuloaga F.O., Nicora E.G., de Agrasar Z.E., Morrone O., Pensiero J. and Cialdella A.M. 1994. Catálogo de la familia Poaceae en la República Argentina. Monograph in Systematic Botany Missouri Botanical Garden 47: 1–178.

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Hedges and green lanes: vegetation composition and structure

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Abstract. In this paper the vegetation of 20 green lanes, defined as tracks bounded by hedgerows, is examined in terms of composition and structure and compared with that of 20 matched single hedgerows. For analysis the vegetation of the lanes was separated into three areas; central track, verges inside of hedgerows and verges outside of hedgerows. The vegetation of these areas was found to differ in species richness, community structure, plant strategies and environmental traits. When compared with verges of the matched single hedgerows, the inside verges and central track were greatly different whereas the outside verge appeared broadly similar. Green lanes contained significantly more plant species than matched single hedgerows, differences being most pronounced when compared as landscape units, rather than as a mean of the constituent parts. The potential effect of surrounding land use on green lane floral diversity is discussed as well as the importance of maintaining the structural diversity of green lanes for farmland biodiversity.

Introduction

Hedges are known to be valuable habitats for wildlife, especially so within landscapes subject to intensive farming practices (Dover and Sparks 2000; Hinsley and Bellamy 2000; Maudsley 2000; McCollin et al. 2000). During the latter half of the 20 th century the UK's stock of hedges declined substantially in response to the need for larger fields to optimise the efficiency of farm machinery and also due to neglect (Barr et al. 1993). Data collected in the Countryside Survey 1990 (Barr et al. 1993) showed a 17% decline in UK hedgerow length between 1984 and 1990, however the most recent survey of UK hedgerow stocks (Haines-Young et al. 2000) indicated a stable stock with a balance between hedgerow loss and creation. However, as newly created hedges will take time to develop their ecological potential, a simple equivalence in length between survey dates actually represents a degradation of the UKs hedgerow stocks.

Intensive farming practices continue to be detrimental to many species of non-pest flora and fauna in many countries throughout the World (Stoate 1996; Boutin and Jobin, 1998; Benton et al. 2002; Aude et al. 2003), despite the mitigating effects of agri-environment schemes (Carey et al. 2002), and hedgerows are seen as one of the last strongholds for many species in intensive farmland (Parish et al. 1994; Sparks et al. 1996; Boutin and Jobin, 1998). A third of Britain's plant species have been found in hedgerows (Barr et al. 1995) and although these are not restricted to hedgerows, many of their other habitats have been so reduced that hedges have become a valuable refuge. Diversity in hedgerow ground flora has declined in recent years (Barr et al. 1993) not only affecting the plant species themselves, but also the wildlife that relies upon them.

The structure of green lanes varies (Dover et al. 2000), but here are defined as two parallel hedges separated by an unmetalled (non-sealed) track. Recent work has shown them to be valuable habitat for butterflies (Dover, Sparks and Greatorex-Davies 1997; Dover et al. 2000; Dover and Sparks 2001), bumblebees and plants (Dover and Sparks 2001; Croxton et al. 2002; Croxton et al. 2005). Dover et al. (2000) showed that both the 'inside' of green lanes, the area enclosed by the two hedges, and the 'outside' of green lanes, the field sides of the boundary hedges to be superior to single hedges in butterfly species richness and abundance. Explanations proposed for differences between green lanes and hedges include modified microclimate, including enhanced shelter, lower agricultural inputs and less intensive management regimes, and higher structural diversity (Dover and Sparks 2001). Croxton et al. (2002) showed the inside of green lanes to be superior to the outside of green lanes in bumblebee abundance and richness and in plant species richness. Croxton et al. (2002) also showed that the inside, outside and 'central track' of green lanes had different plant communities. Croxton et al. (2005) extended this to show the tracks of green lanes had different communities to tracks and verges running alongside single hedgerows. Croxton et al. (2002) argued that the outside of green lanes could be used to represent the environment experienced by field boundary hedges, although this has been shown to not be the case for butterflies (Dover et al. 2000). In this paper, we revisit the vegetation of green lanes and compare it with nearby matched single hedges. The study area was located in a northern mixed farming area of England.

Methods

Selection of sites

Twenty sections of green lanes were identified from farmland within a 10 km radius of Chester 53 ° 11′ N 02° 53′ W (Figure 1). Green lanes, in this study, were defined as tracks bordered on each side by a hedgerow running through farmland and used by farm vehicles, livestock or horses. Lanes were only chosen where the width between hedges was more than 2 m and, with one exception, the track unmetalled. The one metalled lane used had become almost entirely covered in grass and moss. Each green lane was matched with a single hedgerow, paired for similar orientation, surrounding land use and

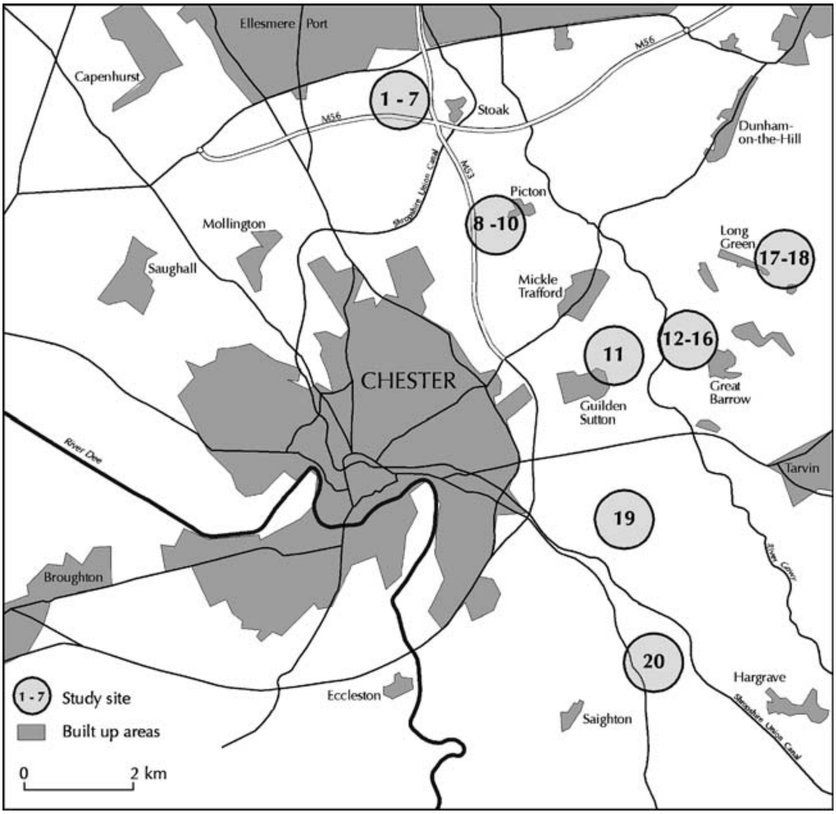

Figure 1. Map showing the positions of the 20 green lane and matched single hedgerow study sites used in this research.

height. All pairs of lane/matched single hedge were of the same length, and within the same 1 km^2grid square. In most cases one lane was matched with one hedge; however, due to difficulty in finding lanes it was necessary to split very long lanes into subsections which were then compared with different hedges. Subsections were only used if noticeably different in character, and each section was separated by a minimum of 100 m – the mean being 250 m.

Data collection

Green lanes

Five locations were selected at random on each lane. At each location the percentage cover of each plant species was recorded using a 50 × 100 cm quadrat from both outside verges, both inside verges and the central track, a verge being defined as the strip of vegetation either between the central track and the hedge (inside verge), or between the hedge and the crop of the

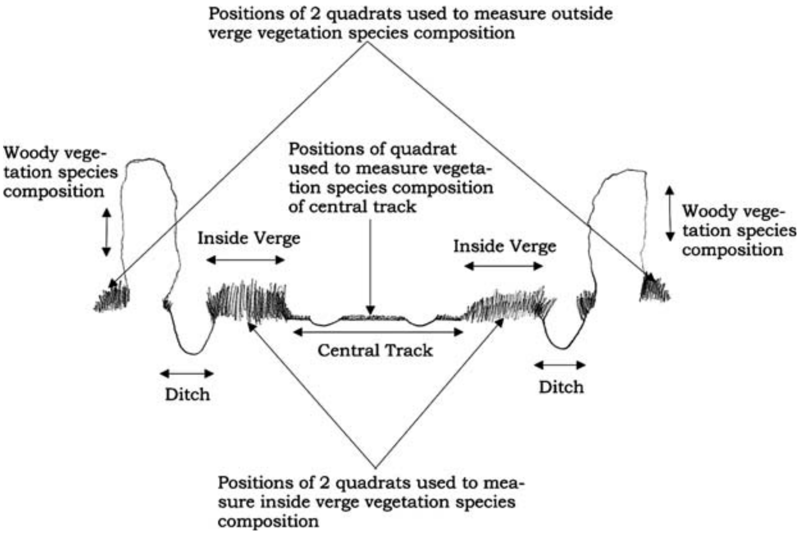

Figure 2. Diagram representing cross-section of green lane indicating positions of quadrats on inside verges, outside verges, and the central track.

bordering field (outside verge). The number and percentage composition of woody plant species forming the hedgerows was counted in a 5 m section at each location. A diagram of the positions of samples taken on green lanes is shown in Figure 2.

Hedgerows

Measurements on the matched single hedges were recorded as for the green lane, except for those features not present on a single hedge.

Analysis of data

A green lane may be compared with a matched single hedgerow by using two, quite different approaches. One approach compares the two on a like-for-like basis e.g. the two verges of a matched single hedgerow compared with two outside verges on a green lane. To take into account the green lane's more complex structure, a second approach is also used where green lane and matched single hedgerow are compared as different field boundary types or 'landscape elements'. This approach looks at a green lane as a unit consisting of a central track bordered by two inner verges, two hedgerows, and two outer verges, and compares its vegetation with that of the matched single hedgerow and the two verges either side.

Species richness

Ground vegetation: The number of species in the different parts of green lanes (outside verges, inside verges and central track), were compared with each other, and matched single hedgerows using two-way ANOVA.

Hedges and green lanes are clearly structurally different. We have used three approaches in analysing species richness. Firstly, equivalent sub-components of green lanes were compared to look at species richness differences within a lane (Figure 3a–c). Secondly the vegetation of a hedge (Figure 3d) was compared with the insides (e) and outsides (f) of a green lane. We were also interested in comparing hedges and green lanes as complete landscape elements and so thirdly, we have compared the vegetation of hedges with a sampling strategy which represents the entire range of subcomponents of green lanes (Figure 3d and g).

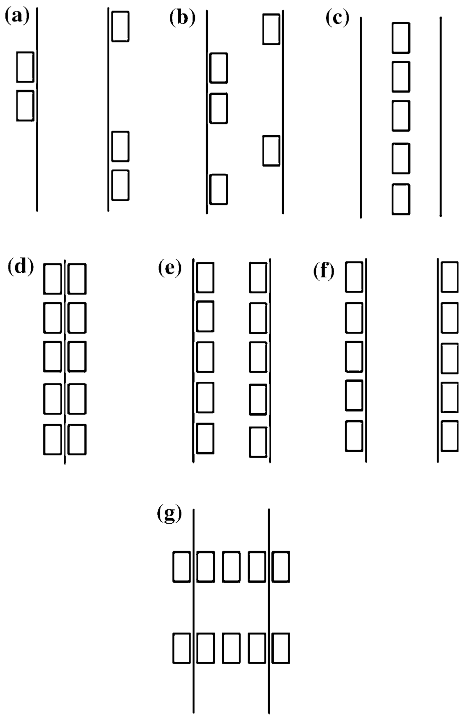

Figure 3. Diagrams representing various positions of quadrat samples used to calculate species richness. Diagrams a, b and c represent sampling strategies used to compare structural components of a lane with each other. These are (a) the outside verges, (b) the inside verges, and (c) the central track. Diagrams d, e and f represent sampling strategies used to compare various sub-components of green lanes with the equivalent on a single hedgerow, where (d) single matched hedgerow, (e) inside verges, (f) outside verges. Diagram g represents the sampling strategy used to represent a green lane as a landscape unit. (▯) Quadrat position, (|) hedge.

For the first method of analysis comparing green lane sub-components, species richness was calculated as the total combined species number in five quadrats per lane. For the inside and outside verges (Figure 3a and b) the five quadrats were randomly selected from the 10 sampled.

For both the second and third method of analysis, species richness was calculated as the sum of 10 quadrats per lane or hedgerow. For the sampling strategy representing the entire range of subcomponents of green lanes (Figure 3g) the positions of the two cross-sections were randomly selected for each lane.

Woody vegetation: The mean species richness of woody hedgerow plants per 5 m section was calculated. For green lanes the mean of the two hedgerows was used.

Individual species

The mean percentage cover for each plant species recorded was calculated for the inside verge, outside verge and central track of a lane, and the verge of a matched single hedgerow. Due to the data not meeting assumptions of normality, the nonparametric Friedman's two-way ANOVA was used for significance testing between these areas for all species with a mean value of 1% or more in any of the four areas. All significance testing in this study was performed using the Minitab 13 statistical package.

Ellenberg indicator and CSR values

Weighted mean indicator values for the ground flora (Hill et al. 1999) were calculated for each area of lane and hedge using mean percentage cover as weighting factors. Indices used were for L (light), M (moisture), R (reaction – an indicator of soil acidity, related to pH) and N (nitrogen). Weighted CSR values (Competitor, Stress-tolerator, Ruderal) were also calculated (Grime et al. 1988) using the same approach. The Kruskal–Wallis one-way ANOVA was used to test significance between areas for both Ellenberg and CSR values, followed, where appropriate, by multiple comparison testing (Siegel and Castellan 1988). A correlation matrix was constructed between Ellenberg and CSR values to check for inter-correlation between variables.

Plant communities

Plant community differences between the central track, both inside and outside verges of the lanes and the verges of the matched single hedgerows were assessed using Correspondence Analysis (CA) on mean percentage species cover on all 20 lanes and 20 hedgerows using down-weighting of rare species. This analysis was performed on all species using the Canoco package. The 'site effect' (variation caused by differences between the 20 sites) was eliminated using a series of 19 binary variables as covariables in the analysis. One-way ANOVA tests to examine for differences between the areas of green lanes and single hedgerows were performed on the first CA axis. To ascertain which species were most responsible for the positioning of sites along axis1, Pearson correlations were performed between the first axis and each plant species.

Results

Species richness

The inside verges appear to be the most species rich areas of a green lane, more so than either the central track or the outside verges (Table 1a). However it is when a green lane is treated as a whole landscape unit that the greatest difference in species richness compared with a matched single hedgerow is seen, the species richness of the lane being significantly greater ($p < 0.001$) (Table 1b). When the various sub-components of green lanes were compared with hedgerows (Table 1c) only the inside verge sub-component (Figure 3e) had significantly greater species richness ($p < 0.001$).

Woody vegetation

The species richness of woody hedgerow vegetation (Table 1d) for both green lanes and matched hedgerows was not significantly different ($p > 0.05$).

Ellenberg indicators and CSR

The Ellenberg indicator values for light (L), moisture (M), reaction (R) and nitrogen (N) for each area of green lanes and matched single hedgerows are given in Table 2. The significantly greater L-value indicates that more light is

Table 1. Mean herbaceous vegetation species richness values ± standard error (a) comparing structural components of green lanes, (b) using a landscape element approach to compare lanes and matched hedgerows, (c) comparing structural sub-components of green lanes with matched hedgerows, and (d) comparing mean woody species richness per hedgerow of green lane and per matched hedgerow.

	Mean ± SE
(a) Structural components of green lanes	
Inside verges	$15.45^{b} \pm 0.65$
Outside verges	$12.15^{a} \pm 0.79$
Central track	$12.65^{a} \pm 1.18$
(b) Landscape element approach	
Green lane	$23.50^{a} \pm 1.20$
Matched hedgerow	$15.75^{b} \pm 0.92$
(c) Hedgerow vs. structural components of green lanes	
Matched hedgerow	$15.75^{a} \pm 0.92$
Inside lane verges	$20.95^{b} \pm 0.92$
Outside lane verges	$17.55^{a} \pm 0.83$
(d) Hedge species	
Green lanes	$1.88^{a} \pm 0.11$
Matched hedgerows	$1.68^{a} \pm 0.11$

Values that share the same superscript letter are not significantly different ($p > 0.05$). No adjustment was made for multiple comparison testing.

Table 2. Ellenberg and CSR values ± standard error for the inside verges, outside verges and central track of green lanes, and the verges of matched single hedgerows.

	Light	Moisture	Reaction	Nitrogen
Inside verge	$6.28^{c} \pm 0.06$	$5.80^{a} \pm 0.08$	$6.56^{a} \pm 0.05$	$6.59^{b} \pm 0.10$
Outside verge	$6.70^{ab} \pm 0.05$	$5.53^{a} \pm 0.05$	$6.38^{a} \pm 0.09$	$6.27^{ab} \pm 0.11$
Central track	$6.91^{a} \pm 0.06$	$5.72^{a} \pm 0.09$	$6.35^{a} \pm 0.07$	$6.10^{a} \pm 0.07$
Single hedgerow	$6.53^{bc} \pm 0.05$	$5.72^{a} \pm 0.08$	$6.45^{a} \pm 0.07$	$6.37^{ab} \pm 0.11$
	C	S	R	
Inside verge	$0.66^{b} \pm 0.02$	$0.18^{b} \pm 0.02$	$0.16^{a} \pm 0.01$	
Outside verge	$0.60^{b} \pm 0.01$	$0.16^{b} \pm 0.01$	$0.25^{b} \pm 0.02$	
Central track	$0.44^{a} \pm 0.03$	$0.10^{a} \pm 0.01$	$0.45^{c} \pm 0.03$	
Single hedgerow	$0.63^{b} \pm 0.02$	$0.15^{ab} \pm 0.01$	$0.25^{b} \pm 0.02$	

Values that share the same superscript letter are not significantly different ($p > 0.05$). See text for levels of significant differences between pairs.

received in the central track than the inside verges of green lanes ($p < 0.001$). The N values indicate that the highest fertility of soil is found on the inside verges and the lowest on the central track. For L, R and N the values for the outside of the green lane hedge and the matched single hedgerow verge are similar, with no significant difference between them ($p > 0.05$).

CSR values (Table 2) indicate that plant species occurring on the central track of green lanes have the lowest value for Competitors and Stress-tolerators, and the highest value for Ruderals, indicating a higher amount of disturbance than the other parts of the lanes. For both Competitor and Ruderal values the differences between the central track and the other areas of the lane is highly significantly different ($p < 0.001$).

The inside verges of green lanes exhibit a higher Competitor, and Stress-tolerator value than all other areas of lanes and matched single hedgerows, whereas they have the lowest Ruderal value – significantly lower than all other lane areas ($p < 0.05$) indicating that the 'inside' species are subject to lower disturbance than elsewhere.

The verges 'outside' the hedges of the green lanes and the matched single hedgerow verges have intermediate levels of stress and disturbance. As was shown for the Ellenberg values, the CSR values for these two areas are very similar, and are not significantly different ($p > 0.05$).

The correlation matrix between Ellenberg and CSR values (Table 3) reveals that many of the indicator values are significantly inter-correlated. Caution is therefore required in using these values to interpret the results.

Individual floral species

Of the 30 species which had > 1% cover in green lanes and hedgerows (Table 4), 10 species were most abundant in the inside verges of green lanes, with six of these significantly so; in particular *Urtica dioica, Rubus fruticosus*

Table 3. Correlation matrix between Ellenberg (L, M, R, N) and CSR (C, S, Rud) values for inside verges (IS), outside verges (OS) and central track (Mid) of green lanes, and the verges of matched single hedgerows (Hedge).

	L	M	R	N	C	S
M	−0.253*					
R	−0.115	−0.063				
N	−0.358**	−0.005	0.703***			
C	−0.596***	0.124	0.414***	0.544***		
S	−0.264*	−0.15	−0.333**	−0.397***	0.115	
Rud	0.629***	−0.035	−0.214	−0.282*	−0.828***	−0.467

*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$.

and *Hedera helix* were most abundant. In contrast four species were recorded as most abundant on the outside of the lane, these being grasses characteristic of farmland such as *Dactylis glomerata*, *Deschampsia flexuosa*, *Arrhenatherum elatius*, and *Lolium perenne*; only the latter two species showed significant differences between the four areas.

Of the eight species recorded as most abundant in single hedgerow verges, most abundant were farmland grasses such as *Elymus repens* and *Holcus mollis*, and the woody hedge species *Prunus spinosa*. The forb *Cirsium arvense* was equally as abundant in both the green lane outside verges and single hedgerow verges. All except *Elymus repens* showed significant differences in occurrence between the four areas.

Eight species were recorded as most abundant on the central track, six of these species showing significant differences in occurrence between the four areas. Of these the perennial grass species *Agrostis stolonifera* had the highest central track abundance, followed by the forbs *Ranunculus repens* and *Trifolium repens*.

Plant communities

The Correspondence Analysis reveals differences between the communities of ground vegetation occurring in these areas of the green lanes and the hedgerows (Figure 4). The plot reveals broad separation between vegetation communities from the three sampled areas of green lanes, the most prominent separation being with the central track. Outside verge communities appear similar to the communities of the matched single hedgerow verge, indicated by the broad overlap of points, whereas both inside verge and central track are mostly separated from the matched single hedgerow indicating a difference in communities between these areas. One-way ANOVA revealed all areas to be significantly different on the first axis of variation ($p < 0.001$) (Table 5) apart from the outside verge of the green lane and the matched single hedgerow verges, which were not significantly different from one another ($p > 0.05$). All the plant species significantly correlated ($p < 0.05$) with the first axis of

Table 4. Percentage cover values ± standard error for vegetation species found to occur on the inside verges, outside verges and central track of green lanes, and the verges of matched single hedgerows at a level $> 1\%$ for one or more of these areas.

Species	Inside verges	Outside verges	Central track	Single hedgerow	*p*
Grasses and rushes					
Agrostis stolonifera	3.9 ± 0.8	9.5 ± 3.0	20.0 ± 3.1	9.1 ± 2.4	**
Arrhenatherum elatius	8.5 ± 2.9	11.0 ± 1.7	1.0 ± 0.7	10.2 ± 2.5	***
Dactylis glomerata	3.8 ± 0.7	8.5 ± 1.7	7.6 ± 2.3	7.1 ± 1.7	ns
Deschampsia flexuosa	0.5 ± 0.5	2.5 ± 1.1	1.2 ± 0.6	1.6 ± 0.6	ns
Elymus repens	3.0 ± 1.0	3.6 ± 0.9	0.9 ± 0.3	4.3 ± 1.3	ns
Festuca gigantea	0.3 ± 0.2	0.3 ± 0.3	0.0	1.7 ± 1.2	ns
Festuca rubra	0.0	0.0	1.1 ± 1.1	0.0	ns
Holcus lanatus	1.8 ± 0.6	1.4 ± 0.6	4.8 ± 1.6	0.7 ± 0.4	ns
Holcus mollis	1.3 ± 0.5	4.1 ± 1.2	1.3 ± 1.0	5.5 ± 1.6	**
Juncus bufonius	0.0	0.0	1.3 ± 0.8	0.0	**
Lolium perenne	0.4 ± 0.2	11.5 ± 2.2	6.4 ± 2.8	9.8 ± 2.5	***
Poa annua	0.0 ± 0.0	0.5 ± 0.3	4.1 ± 1.9	0.1 ± 0.1	*
Broadleaved species					
Ballota nigra	0.1 ± 0.1	0.1 ± 0.1	0.0	1.0 ± 1.0	ns
Cirsium arvense	1.7 ± 0.4	2.3 ± 0.7	0.2 ± 0.1	2.3 ± 0.6	**
Conopodium majus	0.9 ± 0.3	0.5 ± 0.2	0.4 ± 0.3	1.1 ± 0.6	ns
Epilobium hirsutum	1.3 ± 0.7	0.4 ± 0.4	0.1 ± 0.1	0.2 ± 0.1	ns
Filipendula ulmaria	2.5 ± 1.5	0.0 ± 0.0	0.7 ± 0.6	0.8 ± 0.5	ns
Galium aparine	1.2 ± 0.3	0.5 ± 0.4	0.0 ± 0.0	0.5 ± 0.2	***
Heracleum sphondylium	2.0 ± 0.5	1.0 ± 0.3	1.0 ± 0.5	1.4 ± 0.8	ns
Plantago major	0.0 ± 0.0	0.5 ± 0.4	4.0 ± 1.4	0.0 ± 0.0	***
Ranunculus repens	3.8 ± 0.9	1.9 ± 0.7	9.6 ± 2.4	3.3 ± 1.5	*
Rumex obtusifolium	1.3 ± 0.3	0.7 ± 0.4	1.2 ± 0.4	0.7 ± 0.2	ns
Stachys sylvatica	2.4 ± 0.6	0.3 ± 0.2	0.2 ± 0.2	0.1 ± 0.0	***
Trifolium repens	0.1 ± 0.1	0.0 ± 0.0	6.4 ± 1.7	0.0 ± 0.0	***
Urtica dioica	21.7 ± 3.7	12.7 ± 2.7	1.5 ± 0.4	17.2 ± 4.2	***
Woody species					
Hedera helix	4.5 ± 1.4	2.9 ± 1.1	0.0 ± 0.0	0.6 ± 0.2	***
Prunus spinosa	1.5 ± 0.5	1.3 ± 0.4	0.0	2.4 ± 0.8	**
Rosa canina	1.5 ± 0.5	0.7 ± 0.2	0.2 ± 0.2	0.7 ± 0.3	**
Rubus fruticosus	13.7 ± 2.3	5.3 ± 0.9	1.0 ± 0.6	3.8 ± 0.7	***
Ulex europaeus	0.1 ± 0.1	0.3 ± 0.2	0.0	1.0 ± 1.0	ns

ns = $p > 0.05$; *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$.

variation are shown in Table 6. This revealed that the grass species *Arrhenatherum elatius*, *Lolium perenne* and *Poa annua*, as well as the forbs *Plantago major* and *Trifolium repens* were most correlated with this axis and so strongly contributed to the positioning of the different sites along it.

Discussion

The green lanes surveyed in this study clearly contained a greater diversity of plant species than their matched single hedgerow counterparts. The difference

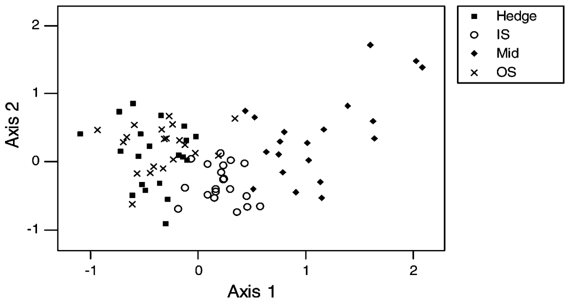

Figure 4. CA analysis plots for herbaceous vegetation taken from 3 positions on each of 20 green lanes (IS = inside verge, OS = outside verge, Mid = central track) and on 20 matched single hedgerow verges. Log-transformations have been performed on both *x* and *y* axes.

Table 5. Significance results for 2-way ANOVA tests between inside verges (IS), outside verges (OS) and central track (Mid) of green lanes, and the verges of matched single hedgerows (Hedge) for the first axis of variation obtained from CA analysis.

Axis 1	OS	Mid	Hedge
IS	***	***	***
OS		***	ns
Mid			***

ns = $p > 0.05$; ***$p < 0.001$.

Table 6. Plant species found to be significantly correlated ($p < 0.05$) with the first axis of variation obtained from CA analysis.

Species	*r*	*p*
Grasses		
Agrostis stolonifera	−0.34	**
Arrhenatherum elatius	−0.40	***
Elymus repens	−0.35	**
Lolium perenne	−0.41	***
Poa annua	0.39	***
Broadleaved species		
Cirsium arvense	−0.34	**
Cirsium vulgare	−0.24	*
Persicaria maculosa	0.27	*
Plantago major	0.40	***
Polygonum aviculare	−0.24	*
Trifolium repens	0.44	***
Urtica dioica	−0.34	**
Woody species		
Prunus spinosa	−0.33	**

Pearson correlation coefficients (*r*) and associated *p* values are shown.
ns = $p > 0.05$; *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$.

is most pronounced when the effect of the structure of the green lane is taken into account by comparing the green lane on a landscape element basis with the matched single hedgerow, i.e. a green lane consists of two parallel hedges with two inside verges, two outside verges and a track running down its centre, whereas a single hedgerow consists simply of a hedge with a verge on either side. An increased vegetation diversity of green lanes when treated as a landscape unit is partly a result of the differing environmental factors provided by the various parts of green lane structure as implied by the work of Dover et al. (2000) for butterflies, and Croxton et al. (2002) for both bumblebees and vegetation.

The results here show, that in terms of vegetation species, the inside verge of the lane is significantly more diverse than the outside verge. Pesticide drift is known to reduce plant species richness in hedgerow verges (Kleijn and Snoeijing, 1997). The verge species richness difference across a green lane hedge shown here may be a result of the buffering effect of hedges to pesticide drift as suggested by Tsiouris and Marshall (1998). The CA also indicates that the vegetation communities occurring in these two areas are substantially different from each other in the majority of green lanes studied. The Ellenberg values indicate which environmental conditions are reflected by these plant communities; plants found in the inside verge are more shade tolerant than those in the outside and also prefer greater levels of moisture. The abundance of the species *Stachys sylvatica* on the inside verges emphasises this relationship. These results are supported by those obtained by Croxton et al. (2002). The greater shade on the inside verges of the lanes could result from the parallel nature of the hedgerows, especially on the narrowest lanes, where both hedgerows may shade each verge for part of the day. The faces of hedgerows bordering the inside edges of the green lanes used in this study only received irregular cutting, perhaps once every 3 or 4 years whereas the outside faces of the hedges tended to receive annual cuts (Personal comm. landowners). This lower level of management results in bushier, overhanging hedges on the inside of lanes that may provide more shade.

The Ellenberg N-Value, indicates higher fertility ‘inside’ the lanes than outside. Croxton et al. (2002) suggested this might result from the leaching of fertilisers from adjacent field applications into green lane ditches, a build up of humus from fallen leaves and other vegetative material, and defecation from birds and other animals in overhanging hedges and trees as possible contributors to this. For the majority of lanes surveyed in this study, all of these suggestions still apply. However, for a quarter of grasslands bordering the lanes, no fertilizer application or muck-spreading was recorded in the study year. In these cases grass was grazed by cattle and so their defecation would be a likely source of nutrient leaching in a similar way to inorganic fertilisers. Caution must be taken in interpreting Ellenberg values due to a strong correlation between Ellenberg N-values and CSR Competitor values. As Competitor values and Ruderal values are strongly negatively correlated, it may be that disturbance rather than nutrient levels are the factors most heavily influencing the plant species found in these areas.

The CSR values indicate how these plant communities differ in their life history traits and the inside verges of lanes appears to present a less disturbed environment than the outside, although only the Ruderal value is significantly different. A greater level of disturbance would be expected on the outside from grazing livestock and occasional ploughing on the outside edges of the verges bordering arable fields.

The central track of the green lanes harbours a plant community different to the other areas of the lanes. The lanes studied by Croxton et al. (2002) were in a fully arable landscape, where the central track was found to consist more of a grassland community than the other areas. This study shows that the same is true for green lanes in a mixed arable and grassland landscape with the perennial grass species *Agrostis stolonifera* and *Lolium perenne* and the forb *Ranunculus repens* most abundant in both cases. Ellenberg values reveal that the plant communities of the central track have a significantly higher light score than the inside verges, indicating that this area is less shaded. Our data confirms the findings of Croxton et al. (2002) in that the central track appears to be damper and have lower soil fertility than the outside of the hedge.

Lower nutrient levels are likely to be due to the distance from the ditch, and the buffering effect of the hedge (Tsiouris and Marshall 1998) from applications of artificial fertilisers and muck-spreading in bordering fields, but some nutrient inputs are likely from defecation of farm animals when moved from field to field along the lanes. The ruts in green lanes may also act as temporary linear water storage ponds creating damper conditions around the central track compared to the freer draining and ditched inner verges.

The high Ruderal, and low Stress-tolerator and Competitor values indicate that the central track is more disturbed than the other areas of the lane. This is probably as a result of trampling by livestock, horses and people, mowing and flattening by vehicles, resulting in an abundance of trampling-tolerant species such as *Plantago major*. Again, inter-correlations need to be taken into account, and the strong correlation found between CSR Ruderal and Ellenberg L-values suggests that it may be disturbance rather than light largely influencing these results. Disturbance may also contribute more to the results than nutrient levels, as discussed above.

Unlike Croxton et al. (2002) this study directly compared the vegetation of the outside verge of a green lane with that of a matched single hedgerow. The results of this study shows that the outsides of these two field boundaries are in fact broadly similar in both vegetation community structure and species diversity and in Ellenberg and values for light, pH and fertility as well as stress and disturbance represented by CSR values. Both communities are made up chiefly of *Urtica dioica* as well as agricultural weeds such as *Arrhenatherum elatius* and *Elymus repens* and grasses commonly sown for fodder such as *Lolium perenne* and *Dactylis glomerata*. The only difference in these field boundaries lies in the level of moisture indicated by the Ellenberg M-value. Although not significant, the trend suggests that the moisture content of the soil is higher alongside a matched single hedgerow than along the outside of a green lane. Higher levels of soil moisture in matched single hedgerows may, as with green lanes, also be heavily influenced by the presence of ditches, with 14 out of 20 matched single hedgerows having a ditch alongside them. Croxton et al. (2002) assumed that the outside of a green lane was analogous to matched hedgerows in both bee and vegetation component. We confirm their assumption for vegetation but urge caution in their assumption of this for bumblebees as Dover et al. (2000) found that the outside of green lane contained more species and a greater abundance of butterflies than single hedgerows.

This research confirms that green lanes are reservoirs of biodiversity in the impoverished modern agricultural landscape. It also underlines the importance of the structure of green lanes and the need to maintain its various components. The two outside verges of green lanes resemble matched single hedgerows in terms of their floral composition, however, when the areas inside the hedges of a green lane are also included the species diversity greatly increases and far exceeds that of a matched single hedgerow. A green lane should therefore be recognised as a single landscape unit, for if one hedgerow of a green lane is lost, many aspects of its vegetation diversity may rapidly decline. To maintain the diversity of vegetation inside green lanes requires continued usage of green lanes by farm vehicles, livestock, horses and people to prevent lanes from becoming overgrown and eventually strips of linear woodland, which, although valuable in their own right would be unlikely to maintain the structural and plant community diversity found in green lanes. The vegetation of the outside verges of green lanes are likely to benefit from management found to be beneficial to the flora of single hedgerow verges such as wildflower/grass strip planting (Moonen and Marshall 2001). The richness of the herbaceous flora of green lanes appears to be derived from the heterogeneous abiotic conditions resulting from the size, structure and use of green lanes. The surfacing of green lanes for improved accessibility usually with tarmac or concrete is clearly a real threat to biodiversity.

Dover et al. (2000) commented that green lanes were not recognised as a specific landscape element in the Countryside Survey 1990 (Barr et al. 1993) and indeed they are still not recognised as a linear landscape feature in the most recent Countryside Survey (Haines-Young et al. 2000). Loss/gain statistics for green lanes are therefore still unknown limiting the recognition of the need to protect them. A continued effort needs to be placed into researching the usage of green lanes by other groups of organisms, and also into beneficial methods of managing, maintaining, restoring and creating new green lanes.

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References

Aude E., Tybirk K. and Bruus Pederson M. 2003. Vegetation diversity of conventional and organic hedgerows in Denmark. Agriculture, Ecosystems and Environment 99: 135–147.

Barr C.J., Britt C.P. and Sparks T.H. 1995. Hedgerow Management and Wildlife: A Review of Research on the Effects of Hedgerow Management and Adjacent Land on Biodiversity. ITE/ADAS.

Barr C.J., Bunce R.G.H., Clarke R.T., Fuller R.M., Furse M.T., Gillespie M.K., Groom G.B., Hallam C.J., Hornung M., Howard D.C. and Ness M.J. 1993. Countryside Survey 1990. Department of the Environment, Main Report.

Benton T.G., Bryant D.M., Cole L. and Crick H.Q.P. 2002. Linking agricultural practice to insect and bird populations: a historical study over three decades. Journal of Applied Ecology 39: 673–687.

Boutin C. and Jobin B. 1998. Intensity of agricultural practices and effects on adjacent habitats. Ecological Applications 8: 544–557.

Carey P.D., Barnett C.L., Greenslade P.D., Hulmes S., Garbutt R.A., Warman E.A., Myhill D., Scott R.J., Smart S.M., Manchester H.J., Robinson J., Walker K.J., Howard D.C. and Firbank L.G. 2002. A comparison of the ecological quality of land between an English agri-environment scheme and the countryside as a whole. Biological Conservation 108: 183–197.

Croxton P.J., Carvell C., Mountford J.O. and Sparks T.H. 2002. A comparison of green lanes and field margins as bumblebee habitat in an arable landscape. Biological Conservation 107: 365–374.

Croxton P.J., Hann J.P., Greatorex-Davies J.N. and Sparks T.H. 2005. Linear hotspots? The floral diversity of green lanes. Biological Conservation 121: 579–584.

Dover J.W., Sparks T.H. and Greatorex-Davies J.N. 1997. The importance of shelter for butterflies in open landscapes. Journal of Insect Conservation 1: 89–97.

Dover J.W., Sparks T., Clarke S., Gobbett K. and Glossop S. 2000. Linear features and butterflies: the importance of green lanes. Agriculture, Ecosystems and Environment 80: 227–242.

Dover J. and Sparks T. 2000. A review of the ecology of butterflies in British hedgerows. Journal of Environmental Management 60: 51–63.

Dover J.W. and Sparks T.H. 2001. Green lanes: biodiversity reservoirs in farmland?. In: Barr C.J. and Petit S. (eds), Hedgerows of the World: Their Ecological Functions in different landscapes. IALE (UK), Lymm, pp. 241–250.

Grime J.P., Hodgson J.G. and Hunt R. 1988. Comparative Plant Ecology: A Functional Approach to Common British Species. Unwin Hyman, London.

Haines-Young R.H., Barr C.J., Black H.I.J., Briggs D.J., Bunce R.G.H., Clarke R.T., Cooper A., Dawson F.H., Firbank L.G., Fuller R.M., Furse M.T., Gillespie M.K., Hill R., Hornung M., Howard D.C., McCann T., Morecroft M.D., Petit S., Sier A.R.J., Smart S.M., Smith G.M., Stott A.P., Stuart R.C. and Watkins J.W. 2000. Accounting for Nature: Assessing Habitats in the UK Countryside. DETR, London.

Hill M.O., Mountford J.O., Roy D.B. and Bunce R.G.H. 1999. Ellenberg's Indicator Values for British Plants. HMSO, Norwich.

Hinsley S.A. and Bellamy P.E. 2000. The influence of hedge structure, management and landscape context on the value of hedgerows to birds: a review. Journal of Environmental Management 60: 33–49.

Kleijn D. and Snoeijing G.I.J. 1997. Field boundary vegetation and the effects of agrochemical drift: Botanical change caused by low levels of herbicide and fertilizer. Journal of Applied Ecology 34: 1413–1425.

Maudsley M. 2000. A review of the ecology and conservation of hedgerow invertebrates in Britain. Journal of Environmental Management 60: 65–76.

McCollin D., Jackson J.I., Bunce R.G.H., Barr C.J. and Stuart R. 2000. Hedgerows as habitat for woodland plants. Journal of Environmental Management 60: 77–90.

Moonen A.C. and Marshall E.J.P. 2001. The influence of sown margin strips, management and boundary structure on herbaceous field margin vegetation in two neighbouring farms in southern England. Agriculture Ecosystems and Environment 86: 187–202.

Parish T., Lakhani K.H. and Sparks T.H. 1994. Modelling the relationship between bird population variables and hedgerow and other field margin attributes. I. Species richness of winter, summer and breeding birds. Journal of Applied Ecology 31: 764–775.

Siegel S. and Castellan N.J. 1988. Non-parametric Statistics for the Behavioural Sciences. McGraw-Hill, New York.

Sparks T.H., Parish T. and Hinsley S.A. 1996. Breeding birds in field boundaries in an agricultural landscape. Agriculture, Ecosystems and Environment 60: 1–8.

Stoate C. 1996. The changing face of lowland farming and wildlife Part 2 1945–1995. British Wildlife 7: 162–172.

Tsiouris S. and Marshall E.P.J. 1998. Observations on patterns of granular fertiliser deposition beside hedges and its likely effects on the botanical composition of field margins. Annals of Applied Biology 132: 115–127.

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Biodiversity and land use change on the Causse Méjan, France

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Abstract. This paper argues that due to the co-evolution of biological and cultural diversity, a meaningful study of biodiversity must be positioned within complex social-ecological systems. A complex systems framework is proposed for conceptualising the study of social-ecological systems. A case study approach is adopted whereby changes in biodiversity on the Causse Méjan, France, are linked with changes in society, land use, agricultural practices and policies. We argue that ecological and social resilience is linked through the dependence on ecosystems of communities, and in turn by the influence of institutional structures, including market forces, on the use of natural resources. Within a non-equilibrium evolutionary perspective, we highlight the difficulty of choosing a landscape and biodiversity of reference and postulating that it is in equilibrium with a type of social organisation. We conclude by exploring an 'adaptive management' approach to the management of the biodiverse landscape studied.

Introduction

Biodiversity refers to the biological variability either at the level of species richness, ecosystem diversity or genetic variation. Since the signing of the Convention on Biological Diversity in 1992, biodiversity has become almost a household word, and its conservation has become the stated objective of national governments and the scientific community (cf. Takacs 1996). However, the assessment of biodiversity remains problematic, because neither the process involved, nor the evaluation of biodiversity change are fully understood, and as yet no widely accepted indicators of biodiversity have been developed. The relationship between diversity, complexity, stability and ecosystem function are among the most fundamental questions in the history of ecology, and around which no general ecological concensus has emerged (May 1972, 1973; Bengtsson 1998). The measurement of biodiversity is also strongly dependent on the chosen spatio-temporal scale of assessment. Today the relationship between species richness and ecological function is at the centre of biodiversity research (cf. Pimm 1984; Lawton 1994; Naeem et al. 1994; Tilman 1997). Species richness, which is the most commonly used indicator of biodiversity, suggests that all species are equal with respect to function. However, it is increasingly recognised that a limited number of species, which Lawton (1994) refer to as ‘ecosystem engineers’, seem to control the critical processes necessary for ecosystem function. As Walker (1992, p. 20) puts it some species are determinants or ‘drivers’ of the ecosystem, where as others can be likened more to ‘passengers’, whose loss leads to little change in the rest of the ecosystem. This is why Walker and other ecologists have called for a shift from focusing on species in biodiversity and conservation circles, to emphasis on maintaining the integrity of ecosystem functions (Walker 1992). The problem with the ecological redundancy argument is that we cannot hypothesise about the potential future role of species currently not seen as critical to ecosystem function, nor can we know the importance of ecosystem functions that remain undiscovered or not understood (Stanley 1995). Folke et al. (1996) argue that the critical question is whether more diverse ecosystems are more resistant or resilient when environmental conditions change. One must also acknowledge the ethical argument that all species have intrinsic value independent of their usefulness to humans (Dietz and Stern 1998; Wilson 2001).

This paper is concerned with the relationship between biodiversity and land use change, and by implication the association between biological and cultural diversity. Much evidence suggests that the decline in farmland biodiversity is related to changing farming practices (MacDonald 2000; Benton et al. 2003). Neither can that change always be interpreted in unambiguously positive or negative terms in relation to biological and other environmental variables. A study by Baudry and Bunce (1991) of successional processes associated with abandoned grassland ecosystems, found that biodiversity at field level may decline in the short term, as aggressive pioneer species colonize, but may increase over longer time periods as ecological complexities increase, and once more decline as the woodland canopy closes. A consideration of land use change, means that humans, their culture, values, policies and economies need to be incorporated as an integral part of the biodiversity debate (Gômez-Pompa and Kaus 1992). Lévêque and Mounolou (2003, p. 5) argued that, “biodiversity is a framework for considering the whole range of questions raised by human relationships with other species and the environment, – a kind of ‘mediator’ between ecological and social systems”. Consequently, the question of biodiversity conservation, does not concern only nature, but also culture. In fact biological and cultural diversity are increasingly seen to be mutually reinforcing. As stated by Bridgewater (2002, p. 9), “we cannot understand and manage the ‘natural’ environment unless we understand the human culture that shaped it". The realisation that social and ecological systems are in fact linked my seem obvious, but in scientific terms this is very profound, and raises the major theoretical and methodological issue of overcoming the artificial boundaries of academic disciplines, that are no where more entrenched than between the natural and social sciences (cf. Berkes and Folke 1998; Holling et al. 1998; Gunderson 2003). In the following case study of the Causse Méjan, we find that the biodiversity associated with its high value continental grasslands, are intimately linked with its farming system, past and present.

The argument of this paper is that any meaningful study of biodiversity and its conservation has to be positioned within a complex social-ecological framework. The term social-ecological systems refer to the integrated concept of humans in nature, humans as part of the ecosystem (Berkes 2004). The first section of the paper proposes a conceptual framework for the study of social-ecological systems. The second section presents a case study of the co-evolved biological and cultural diversity on the Biosphere reserve of the Causse Méjan, in the French Massif Central.

Complex systems

As yet there is little agreement as to how linkages between natural and social systems can be accommodated conceptually or methodologically. Since complexity lies at the root of social-ecological interaction, I argue that complex systems theory may hold some interesting pointers in terms of a working conceptual framework. Complexity theory first emerged in the realm of physics, in particular the work of Nicolis and Prigogine (1977, 1989), but has subsequently permeated many other disciplines, including ecology and the social sciences. Kauffman (1993) makes an important distinction between complexity and complication. For example, one can describe a clock as complicated, in the sense that it has many linkages, but once we understand the mechanism it will work in a predictable manner. Fioretti (1996) suggests that if a phenomenon can be described by more than one logical model, then it is complex, i.e. it is our difficulty in understanding that is at issue. A complex system is described as one that has more than one possible future, it is a non-deterministic system, whose future cannot be determined in advance. This is because complex, non-linear systems far from equilibrium demonstrate self-organisation and emergent properties (Nicolis and Prigogine 1977). Emergent properties are defined as properties of the whole that cannot be predicted from an understanding of the individual parts. The whole is more than the sum of its parts, just as a painting is more than the individual strokes of paint used by the artist to create it. The non-linear behaviour of complex systems means that one cannot predict the outcome of large interventions based on an understanding of smaller parts, in contrast to the linear cause and effect deterministic model. Non-linearity results in unpredictable behaviour, and the spontaneous emergence of structure in situations far from equilibrium. Holling et al. (1998, p. 352) explains that this occurs, ‘‘either because periodically small changes can propagate dramatically, and flip the system into another development path, as in chaos theory, or because stability regions collapse as slow processes accumulate and move the system from one set of controlling mechanisms and processes to another as in catastrophe theory’’. Thus, the evolution of complex systems is characterised by movement from order through instability to new order. It is the non-linear property of social-ecological systems that generate Holling’s (1986), four stage cycle of exploitation, conservation, renewal and re-organisation. This cycle describes the slow accumulation of capital, natural or social, interspersed with rapid phases of reorganisation, where novelty can emerge and become incorporated into another cycle (Holling and Gunderson 2002). One of the insights from complexity thinking is that a multiplicity of scales, prevents there being one ‘correct’ perspective in a complex system (Berkes 2004). Phenomena at each level of the scale tend to have their own emergent properties. Consequently the system must be analysed simultaneously at different scales.

As a consequence of the emerging non-equilibrium theoretical perspective, which essentially views ecosystems as ‘moving targets’ (Holling 1993), with multiple potential futures, there has been a shift in focus away from notions of sustainability, which assumes that there is only one fixed point equilibrium, to an interest in ecosystem resilience. Resilience, as used here, is defined as the ability of ecosystems to absorb and utilise change, whilst maintaining its structure in the face of disturbance, i.e. the magnitude of disturbance an ecosystem can absorb or buffer before it re-defines itself within another meta-stable domain (Holling 1973, 1986) [1]. This is often likened to the analogy of a ball moving between a series of hills and valleys, once the resilience boundary of the valley has been surpassed, the ball moves over the hill and into another meta-stable domain. It is also increasingly acknowledged that ecological and social resilience is linked, through the dependence on ecosystems of communities and their economic activities, which in turn impact on ecological resources (Norgaard 1994; Adger 2000). Resilience therefore depends on the diversity of ecosystems as well as the institutional and community rules which govern social systems (Adger 2000). If ecosystems are ‘moving targets’ and if humans are necessarily a part of nature, the management challenge of today is seen as the understanding of social-ecological systems, in particular the adjusting of social structures and processes to match the ecological complexities under study (Olsson 2003). The resilience idea has been applied to linked social and ecological systems, in the Adaptive Management approach, which I shall return to later.

In conclusion, reductionism may have mastered the ‘science of the parts’, but complexity theory insists that the ‘science of the integration of the parts’ is equally important and far more complicated to achieve. In the next section of the paper, the above ideas inform a case study example of the co-evolving biological and cultural diversity on the Causse Méjan.

Co-evolution of nature, culture and biodiversity on the Causse Méjan

The Méjan is an elevated limestone plateau, of approximately 33,000 ha, which form part of the Grands Causses of the South of France (see Figure 1). It was essentially due to the quality of its open continental steppe landscape, and

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[1] Other definitions of resilience emphasise the speed of recovery from disturbance.

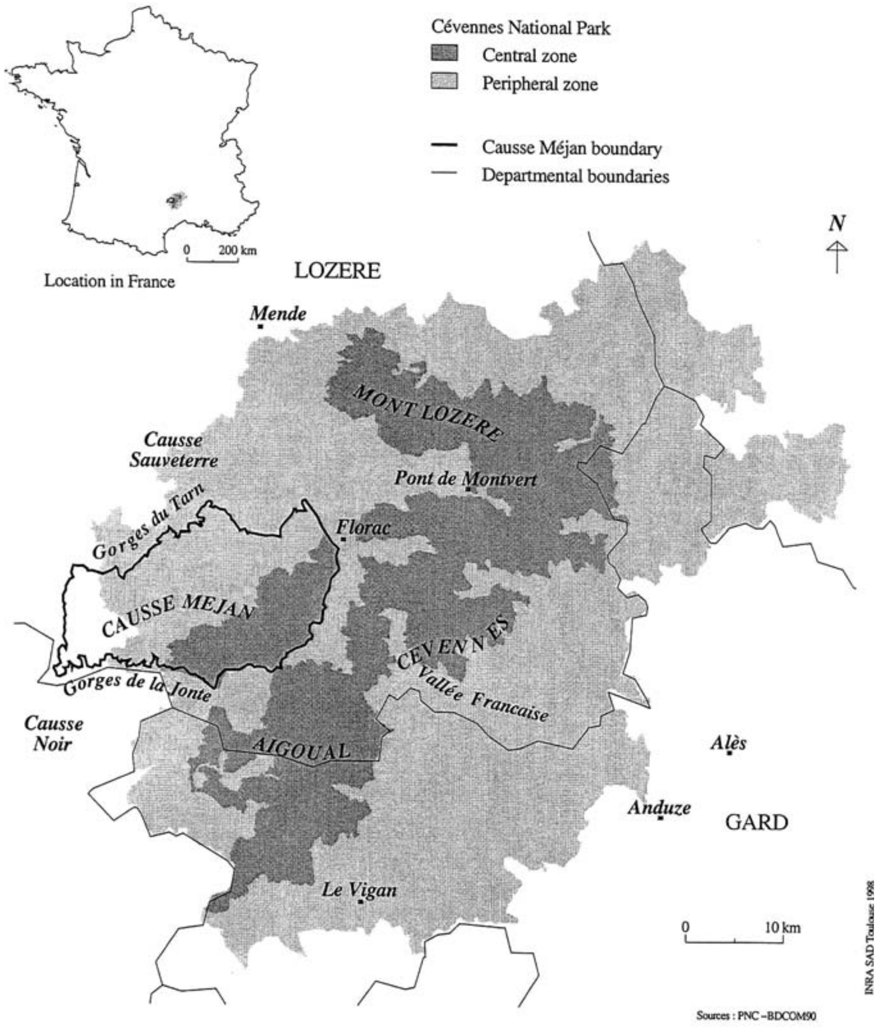

Figure 1. Location of the Causse Méjan, the Cévennes and the Mont Lozère within the Cévennes National Park.

associated rare biodiversity that the Méjan was included within the lived-in Cévennes National Park (CNP) when it was created in 1970. The steppe grasslands are dominated by S*tipa pennata*, but *Festuca duriuscula, Festuca ovina, Festuca brometalia, Aphyllantes monspelliensis, and Brachypodium pinnatum*, are also common. Spring flowers include various species of orchids, anemones and mountain aster. Its original fauna, especially its butterfly's are also of major interest to naturalists. The national park introduced vultures (*Gyps fulvus*) and a herd of Przewalski horses (*Equus przewalski*) on to the Causse. In 1984, the Méjan along with the rest of the Cévennes national park was classified as a UNESCO Biosphere reserve. Bridgewater (2002) reminds us that Biosphere reserves are examples of blending biological and cultural diversity *par excellence*. The landscape and biodiversity of the Méjan is an expression of the age old dialogue between its people and its nature. Two-thirds of the Cévennes national park is currently forested, including the majority of the Cévennes, Aigoual and Mont Lozère landscapes (Benoit and Valéro 1997). Consequently, the open Méjan steppe occupies a privileged position within the park, both aesthetically and in terms of its biodiversity. The perceived major ecological threat to the Méjan today is the closing in of its landscape, in particular the colonisation of the denuded elevated causse by woody shrubs, especially juniper (*Juniperus communis*) and boxwood (*Buxus sempervirens*). An examination of the evolution of the Méjan's landscape, along with the role played by humans and their farming systems in the fashioning of both its landscape and biodiversity, provided us with a typical example of a co-evolving social-ecological systems. It also raises questions as to what is 'traditional'.

Forest or steppe

In the biohistory of the Méjan one finds much discussion as to whether its natural vocation is that of a closed forested biotope or an open steppe landscape and its associated biodiversity. The well known naturalist Flahault (1933), proposed that forestry was the natural vocation (climax vegetation) for the Méjan, in keeping with its climate and soils. He concluded that humans were degrading the forest, with pastoralism being the major source of erosion and degradation. Flahault along with other naturalists, such as Braun-Blanquet and Braun-Blanquet (1971) stresses the importance of reforestation projects, in order to conserve the natural environment of the plateau. This message was shared by many prominent foresters whose voices were especially vocal back in the early 20th century, when the whole area experienced severe depopulation and land abandonment (cf. Bieau 1963). This stands in stark contrast to the ecological endeavours of today, including those of the national park, which are centred around maintaining the denuded steppe, and keeping the regenerating forest at bay (Collins 1990; PNC 1998). As noted by Lepart et al. (2000), we have over a short period of time seen a complete reversal in expert's advocacy of ecosystem's management, in relation to the Méjan.

The paleoecology and biohistory of the Méjan indicates that the open steppe of today is indeed an antrophic creation, brought about by a series of land clearances since the Gallo-Roman period, and maintained by various agro-pastoral systems (Vernet 1995; Crosnier 1996; Friedberg et al. 2000). Within equilibrium centred, Clementsian ecology the current re-colonisation of the Causse would be interpreted as a natural succession towards a *Pinus sylvestris* forest climax, in equilibrium with the soils and climate of the area. However, from a biodiversity (plus aesthetic and cultural patrimony) point of view the anthropic steppe of the last few centuries is richer and rarer than that associated with the more common regenerating European forests. What the ecologists of today are trying to protect and re-create is essentially a form of agri-biodiversity, most closely associated with late 19th century labour intensive farming practices (O'Rourke 1999, 2000, 2005). Along similar lines, MacDonald et al. (2000, p. 57) found that the reduction in labour intensive traditional farming practices in European uplands, is as valid a threat to their biodiversity as physical land abandonment. The low intensive farming systems that created important semi-natural habitats, such as on the Méjan, have been referred to by Baldock et al. (1996), as High Nature Value Farming. Such areas of high conservation value associated with farming have been created indirectly, rather than purposefully by certain types of agricultural systems. Today, with the retreat of traditional farming from much of Europe, there are calls for European policies and conscious management to protect such high value sites (Beaufory et al. 1994; Bignall and McCracken 1996). The current interest in high nature value farming begs the question as to how agri-biodiversity can be disassociated from how we farm the land, and ultimately societies relationship with nature.

Changing farming systems

Paul Marres (1935) pioneering work on the Méjan indicates that prior to the early 20th century its economy was based on a subsistence agro-pastoral system, centred around cereal production. The cereal was grown in the deeper soils of the arable land, known as '*dolines*', and which constituted approximately 10% of the plateau's surface area. At this time rustic caussenard breed of sheep were essentially kept as a source of manure for the cereal plots, and to a lesser extent for their wool, which was transformed in the local cottage textile industry. Demographic pressure between the 17th and 19th century saw an acceleration in land clearance and the temporary cultivation of cereal on poor rangelands, often resulting in accelerated erosion. By the late 19th century there was practically no forest on the Méjan, and it was at this period that the plateau assumed its most typical barren steppe landscape (Petit 1978)[2]. Rural exodus, from the late 19th century on meant that the Méjan and the surrounding area lost over 80% of its population, and much of its agriculture and textile industry. When humans retreated, the forest, the metronome of this society and landscape, advanced.

In the early 20th century, the old agro-pastoral system on the Méjan gave way to the production of sheep milk for the Roquefort cheese dairies. Today

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[2] The Méjan reached its demographic peak around the mid 19th century, reflected in a population density of approximately 13 people per km^2, as opposed to its current desertified state of less than 1.4 people per km^2.

the greatly expanded, modernised and mechanised, approximately 55 sheep farmers on the Méjan, can be almost equally divided between sheep milk producers and those orientated towards mutton production. Due to a combination of economies of scale, quota systems, labour shortages and market demands, the sheep farming system on the Méjan (especially the milk producers) was transformed into a highly mechanised, intensive system, where the animals are increasingly kept in doors (*hors sol*) and concentrated feedstuffs (such as hay, lucerne and meal concentrates) are brought in from outside. Changes in the farming systems, in particular grazing practices, and allied changes in the social and economic system, have had a direct impact on the biodiversity and landscape of the Méjan (cf. Friedberg et al. 2000).

Among the most important changes to the technical farming system were changes in sheep races from the rustic caussenard breed to the more selected and better performing Blanc du Massif Central for meat production, and the Lacaune for milk production. The nutritional needs of these more demanding feeders and the associated technical changes in the sheep rearing system, has led to more intensive use of the arable land for both cereal and fodder production, and less frequent use of the rangelands. It is the decrease in outdoor grazing, which is seen to be responsible for the regenerating scrub (especially boxwood and juniper). In the case of the milking sheep the decrease in time they spend grazing outdoors, is also linked to changes in the lambing season to coincide with the Roquefort milk collection period, which on the Méjan is from January to July (cf. Osty 1978; Osty and Lardon 1994; O'Rourke 1999). The consequential advancing of the lambing period into winter rather than the traditional spring time, reduced the possibility of outdoor grazing of high performance sheep during the harsh Méjan winters, and necessitates large stocks of both locally produces and bought-in high quality fodder. Outdoor grazing is restricted to off-milking autumnal maintenance period (Osty and Lardon 1994). In the past, the hardy caussenard breed of sheep grazed outdoors from March to December. There is more diversity in the mutton production system, but the dominant type of lamb produced on the Méjan today, is an indoor raised lamb, geared towards an 'out of season' market niche, along with simplifying shepherding and the management of naturally poor rangelands.

Impact of grazing on scrub control

Controversy surrounds the control of regenerating scrub (boxwood and juniper) via grazing (cf. Hubert 1978; Dutoit and Allord 1995; Gibson et al. 1987). Research by Rousset (1998) and Rousset and Lepart (1999) on the impact of grazing and stamping on boxwood and juniper scrub in the Grands Causses of the South of France, found that once the scrub is established, sheep grazing has very limited impact on it. However, grazing can contribute to slowing down the installation of the above woody shrubs, but it cannot stop it. What appears to be critical is grazing at the time of seed dispersal (Noy-Meir et al. 1989). Rousset (1998) found that spring grazing has a significant impact on the survival of boxwood during the first 4–10 years of its long life cycle. Sheep will not eat the toxic adult boxwood. According to local knowledge it was only during winter grazing, which no longer exists, that the sheep agreed to eat the small juniper shrubs, as there was nothing else to eat. Spring grazing is effective for the control of conifer in the east of the plateau, since the young shrubs are edible. Lepart et al. (2000) concluded that pasturage on its own cannot maintain the open steppe biotope of the Mejan. They point out that in the past the caussenard society along with grazing, used other methods, such as manually clearing the scrub. For example, boxwood and juniper were seen as valuable sources of firewood, and boxwood leaves were used as a source of green fertiliser and for animal litter. Similarly the conifer on the east of the causse, were traditionally maintained by controlled burning, (*écobuage*), which the sheep farmers of today no longer feel competent in, with some more recent fires burning out of control. It has also come to light that different types of grazers (even within the same species, age and teeth size can make a difference) produce different types of biodiversity. For example, Cohen and Lardon (1996) detected biodiversity differences in Méjan pasturelands that were grazed by horses as opposed to sheep in the past. Consequently the biodiversity of today is also a function of the gastronomical preferences of the grazers of the past.

In conclusion, the modernisation of the sheep farming system on the Méjan, and the adoption of an essentially productionist model, has brought a substantial raise in the local farmers standard of living and quality of life, along with leaving its mark on the landscape and biodiversity of the plateau. Today a clash has emerged between conservation objectives and development objectives. The agrarian developmental objective of the Méjan are tied-in with a subsidy and market oriented, relatively intensive farming system. Whereas the conservationists and naturalists, in direct opposition to their colleagues of a few decades ago, are calling for the preservation of the unique biodiversity and cultural patrimony of the denuded 19th century agro-pastoral steppe. The way the conservationists, including the national park, propose to maintain or 're-create' the open steppe landscape and its associated biodiversity, is essentially by appeals to 'traditional' farming practices, especially outdoor grazing, in the name of sustainable development. Grazing along with the mechanical removal of scrub, forms the basis of agri-environmental policies (EU Regulation 2078/92), recently implemented on the plateau[3]. Parts of the Méjan are also a designated Natura 2000 site, under the Habitats and Species Directive (92/43/EEC).

Grazing along with the mechanical removal of scrub were also the methods applied under the European Life-Nature project, entitled 'Re-creating nature'. Along similar lines the national park launched a new mutton label, 'L'Agneau

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[3] The annual EU budget for agri-environmental measures is only 4% of the overall EU agricultural budget.

de Parcours', which is marketed as a traditional spring lamb, raised outdoors and fattened at grass (Benoit and Valéro 1997). However, the 'Agneau de Parcours', is perceived by the local sheep farmers to be labour intensive, involves shepherding, and the lamb takes longer to finish (6 months as opposed to 3–4 months for indoor lambs). Outdoor grazing on the poor rangelands of the Méjan would also involve a reduction in stocking densities and subsidies, which account for 100% of the sheep farmers available income. Neither does the 'Agneau de Parcours' have a secure market niche, or the ability to command a substantially higher market price to compensate for the above inconveniences. The problem with the various extensification incentives on offer is that the local sheep farmers perceive them as a step backwards, involving time consuming shepherding, which is no longer socially acceptable, and the management of poor rangelands. They are also seen to be out of kilter with market forces and many agricultural subsidies, which up to now were based on high stocking densities. Co-evolution implies the evolution of two entities due to mutual influence. Changes in the Méjan society, its inhabitants perceived needs and images of success, along with changes in land use practices and market forces, have inevitably brought about changes in the Causse's biodiversity. Once more testimony to the close links between cultural and biological diversity.

Discussion

The Causse Méjan case study indicate that current biodiversity is not just a natural dimension, rather it is due to a long-term co-evolution of natural and anthropogenic factors. One can clearly see how different farming systems, economic incentives and social values, favour one type of land use, and consequently one type of biodiversity, over another. The biodiversity of the high value cultural landscape studied, is as much about people and their changing farming systems as it is about species, habitats and ecosystems. Given the long term socio-natural history of the Méjan how, as Lepart et al. (2000, p. 23) asks, can one choose a landscape and biodiversity of reference, and postulate that it is in equilibrium with a type of social organisation? Similarly, the idea of 'tradition' or 'traditional farming practices' is a time related concept. Traditional practices and knowledge cannot be isolated from the world views, social, economic and belief systems, which give them their sense. Neither are traditions static, they evolve adapt and redefine themselves. The recent re-aligning of nature with traditional, (and both their oppositions to modernity), has permeated European agri-environmental policies, as if 'traditional' farming practices, were a means of putting nature and culture back together again. But, because of the close links between biological and cultural diversity, attempts to hold the landscape and its biodiversity still at a particular moment in time, will also have to address the 'freezing' of the societies with which they co-evolved, or else purposefully 're-create' artificial landscapes. Hence, the eco-museum and Disneyland analogy. A number of agri-environmental policies and projects aimed at 're-creating nature', have been accused of a nostalgic attempt to aestheticise the countryside, rather than address the human, biological and natural resource issue in question. They also beg the question as to why we seek to preserve that, which must change? The question remains as to whose nature, and of which epoch, we are to prioritise, can its essence and biodiversity be captured by scientifically defined botanical inventories? Should the land managers and inhabitants of the habitats concerned, have some say in defining their version of local natural and cultural patrimony, along with how it should be managed? The critical question posed by Larrère and Larrère 1997, p. 15) is, if equilibrium is no longer the principal regulator of ecological systems, and if nature necessarily has a history, and if biodiversity is not positive in all contexts, how can we distinguish favourable evolution's and co-evolutions from less favourable one? On what rules can environmental or biodiversity policy be based?

In complex systems terms, when one examines the socio-natural co-evolution on the Méjan, we observe that its landscape, biodiversity and society are in constant transition, and temporarily self-organise around different meta-stable points. The cereal based economy of the 19th century along with the associated abundant cheap labour to be found in the local society, partly gave way to a forest vocation in the late 19th century, and to agro-pastoralism in the 20th century. The factors which push the cycles in the system to change from one phase to another, or in Holling's (1986) terms, from conservation to release, reorganisation and exploitation are to be found in the social-ecological resilience of the different epochs, and the corresponding different demands made on the landscape. Policy changes along with market forces are among the recent drivers of the release and reorganisation phase, characterised by rapid conversion. We note that changes in key social mechanisms, such as policy change or life style change, could affect the ecosystem state as much as changes in key structuring ecological variables. We also note the importance of emergent properties, whose impacts could not have been foreseen in advance, such as the establishment of the national park, the Roquefort dairies, changes in the common agricultural policy (CAP), and the social re-awakening attributed to the establishment of the 'Association Méjan', which is attributed with creating a strong agrarian local identity and turning the tide on the abandonment of the Méjan in the bleak days of the 1950s and 1960s.

Van der Leeuw (2000), reminds us that in a co-evolutionary process, human, social and economic systems shape and are shaped by the ecological endowments of the region, and such processes are occurring at a variety of scales from local to global. Humans are an integral part of the Méjan's ecosystem, and the maintenance of its ecological resilience is strongly linked to and dependent on social mechanisms. Within such a complex system, management needs to be adaptive, inclusive and sensitive to the various scales impacting on the system.

Given the complex, non-linear, poorly understood and inherently unpredictable nature of social-ecological systems, along with what is increasingly seen as the failure of ‘command and control’ approaches to conservation management, the ideas of ‘Adaptive Management’ have gained in importance in recent years (cf. Holling and Meffe 1996; Berkes and Folke 1998; Olsson and Folke 2001; Gunderson 2003; Berkes 2004). Folke (2002, p. 20) defined adaptive comanagement as a process by which institutional arrangements and ecological knowledge are tested and revised in an ongoing process of trial and error. Adaptive management was designed to integrate uncertainty into the decision making process and to ensure that policy makers and managers could learn from their successes as well as from their failures (Berkes 2002). Essentially policies are treated as hypothesis and management as experimental from which managers can learn. The barrier between research, management and end users breaks down. It recognises that information will never be perfect, and stresses ‘learning by doing’, by testing different hypothesis and policies and monitoring the feedback, which once more feeds into policy and management recommendations within an iterative process. As Holling and Meffe (1996, p. 332) put it, because ecosystems are unpredictable, management has to be flexible, adaptive and experimental at scales compatible with the scale of the critical ecosystem function. For example, in the Méjan case study, the farming systems that directly impact on local biodiversity, are essentially responding to regional European agricultural policies and globalised markets. Once more confirming that ecosystem resilience depends not only on the diversity of ecosystems, but also on the institutional rules which govern social systems. Institutions and communities being a central component linking social and ecological resilience. More research needs to be done in this area.

Conclusions

The emerging theoretical framework for social-ecological systems recognises that ecosystems co-evolve with ever changing societal values, and their economic, technological, and political systems. They are also complex systems characterised by uncertainty and imperfect knowledge, which needs to be acknowledged within the policy and decision making environment. Ecological management should concentrate on building resilience in social-ecological systems, rather than universally applying rigid top-down policies. In cultural landscapes, which today cover most of the Earth’s terrestrial systems, biological diversity cannot be divorced from cultural diversity. We need to develop a consistent theory of biological and cultural co-evolution in order to understand the biosphere and humans place in it. Given the complexity and uncertainty inherent in such a task, I argued in this paper that a complex systems framework, along with an adaptive management approach to resource management may provide us with a useful starting point. Since the biodiversity of terrestrial ecosystems is expected to be mainly affected by land use change within the next 100 years, we need to focus on land use management for the preservation of biological diversity (cf. Sala et al. 2000; Waldhardt 2003). Can we purposefully manage landscapes for ‘biodiversity’, while at the same time disassociate the land from the cultural systems that co-created the biodiversity in question? Or should equal emphasis be given to the cultural and biological aspects of ecosystems in their management? One is reminded of (Belshaw’s 2001, p. 278) observation:

“A countryside managed to look good, ... could only be unsettlingly artificial, with both sheep and their farmers playing roles, like actors at Disneyland, while to make this the opportunity to ‘rationalise’ farming and food production could only dehumanise, denature us further”.

We also need to address our schizophrenic concern for biodiversity and nature conservation in a fraction of our territory, whereas outside the boundaries of these generally ‘disadvantaged areas’, the exploitation of natural resources by industrialised societies is not in question? Here we continue to maintain the dualism between nature and culture. Biodiversity is after all about how we live and how we manage the land.

References

Adger W.N. 2000. Social and Ecological Resilience; are they linked?. Progress in Human Geography 24(3): 347–364.

Baldock D., Beaufoy G., Brouwer F. and Godeschalk F. 1996. Farming at the Margins: Abandonment or Redevelopment of Agricultural Lands in Europe. Institut for European Environmental Policy Agricultural Economics Research Institute, London/The Hague.

Baudry J. and Bunce R.G.H. (eds) 1991. Land Abandonment and its Role in Conservation. Options Méditerranéennes – Seminar Series A-No. 15: CIHEAM Centre International de Hautes Etudes Agronomiques Méditerranéennes, Zaragoza, Spain.

Beaufory G., Baldock D. and Clark J. 1994. The Nature of Farming: Low Intensity Farming Systems in Nine European Countries. Institute for European Environmental Policy (IEEP), London.

Belshaw C. 2001. Environmental Philosophy: Reason, Nature and Human Concern. Acumen, Chesham, Bucks.

Bengtsson J. 1998. Which Species? What kind of diversity? Which ecosystem function? Some problems in studies of relations between biodiversity and ecosystem function Applied Soil Ecology 10: 191–199.

Benoit G. and Valéro G. 1997. Agriculture et environnement dans le Parc National des Cévennes: le lancement de l’operation ‘Agneon de Parcours’. Bulletin de la Societé Languedocienne de Géographie 3–4: 101–121.

Benton T.G., Vickery J.A and Wilson J.D. 2003. Farmland Biodiversity: Is Habitat Heterogeneity the Key. Trends in Ecology and Evolution 18(4): 182–188.

Berkes F. 2002. Cross-scale Institutional Linkages: Perspectives from the bottom up. In: Ostrom E., Dietz T., Dolsak N., Stern P., Stonich S. and Weber E. (eds), The Drama of the Commons. National Academy Press, Washington, DC.

Berkes F. 2004. Rethinking Community-Based Conservation. Conservation Biology 18(3): 621–630.

Berkes F. and Folke C. (eds) 1998. Linking Social and Ecological Systems. Cambridge University Press, Cambridge.

Bignall E.M. and McCracken D.I. 1996. Low intensity Farming Systems in the Conservation of the Countryside. Journal of Applied Ecology 33: 416–424.

Bieau C. 1963. Le Parc et la Forêt. Cévennes et Mont Lozère,Vol. 33, pp. 4–8.

Braun-Blanquet J. and Braun-Blanquet G. 1971. Les pelouses steppiques des Causses méridionaux. Vegetatio 22(4–5): 201–247.

Bridgewater P.B. 2002. Biosphere Reserves: Special Places for People and Nature. Environmental Science and Policy 5: 9–12.

Collin G. 1990. Rural Society and Protected Areas: Which Dialogue? The Case Study of Cevennes National Park and Biosphere Reserve (France). Landscape and Urban Planning 19: 173–180.

Cohen M. and Lardon S. (eds) 1996. Usage des Sols, Pratiques d'Eleveurs, Représentations de la Nature et Dynamique des Milieux et des Ressources. Rapport final de recherche du PIR EnvironnementVie et Sociétés du CNRS, Laboratoire de Géographie Physique, Paris.

Crosnier C. 1996. Administrer la Nature: enjeux biologiques et sociaux dans le Parc National des Cévennes. In: Baudot P. et al. (eds), Impact de l'Homme sur les Milieux Naturels: Perceptions et Mesures. Editions de Bergier, Grasse.

Dietz T. and Stern P. 1998. Science, Values and Biodiversity. BioScience 48: 441–444.

Dutoit T. and Allard D. 1995. Biodiversité et valeur agronomique des pelouse calcaires : effet du paturage ovin. Fourrage 142: 145–158.

Fioretti G. 1996. A Concept of Complexity for the Social Sciences. International Institute for Applied Systems Analysis. Laxenburg, Austria.

Flahault C. 1933. La vocation forestiére des grands Causses du Massif Central de France. Bulletin de la Société Botanique Suisse 42: 681–698.

Folke C. 2002. Resilience for Sustainable Development: Building Adaptive Capacity in a World of Transformations. Rainbow Series 3. International Council for Scientific Unions (ICSU), Paris.

Folke C., Holling C.S. and Perrings C. 1996. Biological Diversity, Ecosystems and the Human Scale. Ecological Applications 6: 1018–1024.

Friedberg C., Cohen M. and Mathieu N. 2000. Faut-il du'un paysage soit ouvert ou fermé? L'exemple de la pelouse séche du causse Méjan Natures, Sciences, Sociétés 8(4): 26–42.

Gibson C., Watt T. and Brown V. 1987. The use of sheep grazing to recreate species-rich grasslands from abandoned arable land. Biodiversity Conservation 42: 165–183.

Gômez-Pompa A. and Kaus A. 1992. Taming the Wilderness Myth. BioScience 42: 271–279.

Gunderson L.H. 2003. Adaptive Dancing: interactions between social resilience and ecological crisis. In: Berkes F., Coding J. and Folke C. (eds), Navigating Social-Ecological Systems: Building Resilience for Complexity and Change. Cambridge University press, Cambridge, pp. 33–52.

Holling C.S., Berkes F. and Folke C. 1998. Science, Sustainability and Resource Management. In: Berkes F. and Folke C. (eds), Linking Social and Ecological Systems. Cambridge University Press, Camnbridge, pp. 342–362.

Holling C.S. 1973. Resilience and Stability of Ecological Systems. Annual Review of Ecology and Systematics 4: 1–23.

Holling C.S. 1986. The Resilience of Terrestrial Ecosystems: local surprise and global change. In: Clark W.C. and Munn R.E. (eds), Sustainable Development of the Biosphere. Cambridge University Press, Cambridge, pp. 292–317.

Holling C.S. 1993. Investing in Research for Sustainability. Ecological Applications 3: 552–555.

Holling C.S. and Gunderson L.H. 2002. Resilience and Adaptive Cycles. In: Holling C.S. (ed.), Panarchy. Island press, Washington DC.

Holling C.S. and Meffe G.K. 1996. Command and Control and the Pathology of Natural Resource Management. Conservation Bioloy 10(2): 328–337.

Hubert D. 1978. Evaluation du role de la végétation dans le bilan écologique et agro-économique des Causses. These de l'Université des Sciences et Techniques du Languedoc, 240 pp.

Kauffman S. 1993. At Home in the Universe: The Search for Laws of Complexity. Oxford, Oxford University Press.

Larrère C. and Larrère R. 1997. La Crise Environnementale et ses Enjeux: Ethique, Science et Politique. In: Larrère C. and Larrére R. (eds), La Crise Environnementale, Les Colloques, No. 80, INRA Editions, Paris.

Lawton J.H. 1994. What do species do in ecosystems? Oikos 71: 367–374.

Lepart J., Marty P. and Rousset O. 2000. Les conceptions normatives du paysage. Le cas des Grands Causses. Natures, Sciences, Sociétiés 8(4): 16–25.

Lévêque C. and Mounolou J-C. 2003. Biodiversity. Wiley and Sons, Chichester.

MacDonald D., Crabtree J.R., Wiesinger G., Dax T., Stamou N., Fleury P., Gutierrez Lazpita J. and Gibon A. 2000. Agricultural abandonment in mountain areas of Europe: Environmental consequences and policy response. Journal of Environmental Management 59: 47–69.

Marres P. 1935. Les Grands Causses. Étude de Géographie Physique et Humaine, Tome I et II. Arrault et Cie, Tours.

May R.M. 1972. Will a large complex ecosystem be stable? Nature 128: 413–414.

May R.M. 1973. Stability and Complexity in Model Ecosystems. Princeton University Press, Princeton, NJ.

Naemm S., Thompson I.J., Lawler S.P., Lawton J.H. and Woodfin R.M. 1994. Declining biodiversity can alter the performance of ecosystems. Nature 368: 734–737.

Nicolis G. and Prigogine I. 1977. Self-Organisation in Non-Equilibrium Systems: From Dissipative Structures to Order through Fluctuations. Wiley International, New York.

Nicolis G. and Prigogine I. 1989. Exploring Complexity. Freeman, New York.

Norgaard R.B. 1994. Development Betrayed: The End of Progress and a Coevolutionary Revisioning of the Future. Routledge, London.

Noy-Meir I., Gutman M. and Kaplan Y. 1989. Responses of Mediterranean grassland plants to grazing and protection. Journal of Ecology 77: 290–310.

Olsson P. 2003. Building Capacity for Resilience in Social-Ecological Systems. Unpublished Ph.D Dissertation, Department of Systems Ecology, Stockholm University, Sweden.

Olsson P. and Folke C. 2001. Local Ecological Knowledge and Institutional Dynamics for Ecosystem Management: A study of lake Racken watershed, Sweden. Ecosystems 4: 85–104.

O'Rourke E. 1999. The Causse Méjan: changing relationships between agriculture, environment and society within a French National Park. Landscape Research 24(2): 141–165.

O'Rourke E. 2000. The Reintroduction and Reinterpretation of the Wild. Journal of Agricultural and Environmental Ethics 13: 145–165.

O'Rourke E. 2005. Socio-natural Interaction and Landscape Dynamics in the Burren, Ireland. Landscape and Urban Planning 70: 69–83.

Osty P.-L. 1978. Le Causse Méjan. 4. Elevages et Eleveurs en 1978. INRA, Paris.

Osty P.-L. and Lardon S. 1994. Systemes Techniques et gestion de l'espace: quelle qualité de l'organisation spatiale. Les éleveurs ovins du Causse Méjan. Etude et Recherches sur les Systémes Agraires et le Développement 28: 211–218.

Petit F. 1978. Le Causse Méjan, 2 : Exode Rural et Utilisation du Territoire (de 1850 á nos Jours). Institut National de la Recherche Agronomique (INRA), Paris.

Pimm S.L. 1984. The Complexity and Stability of Ecosystems. Nature 307: 321–326.

PNC – Parc National des Cévennes 1998. Plan de Gestion, Antenne Causses et Gorges. Parc National des Cévennes, Florac.

Rousset O. 1998. Impact des pratiques pastorales "Article 19" sur la dynamique d'enfrichement des milieux caussenard. Rapport de fin de contrat (programme européen pastel), CNRS, INRA.

Rousset O. and Lepart J. 1999. Évaluer l'impact du paturage sur le maintien des milieux ouvert. Le cas des pelouse séches. Fourrages 159: 223–235.

Sala O.E., Chapin F.S., Armesto J.J., Berlow E., Bloomfield J. and Dirzo R. 2000. Biodiversity-Global Biodiversity Scenarios for the Year 2100. Science 287: 1770–1774.

Stanley T.R. 1995. Ecosystem Management and the Arrogance of Humans. Conservation Biology 9: 363–365.

Takacs D. 1996. The Idea of Biodiversity: Philosophies of Paradise. John Hopkins University Press, Baltimore.

Tilman D. 1997. Biodiversity and ecosystem functioning. In: Daly G.C. (ed.), Nature's Services: Societal Dependence on Natural Ecosystems. Island Press, Washington, DC, pp. 93–112.

Van der Leeuw S. 2000. Lland Degradation as a Socionatural Process. In: McIntosh R.J., Tainter J.A. and McIntosh S.K. (eds), The Way the Wind Blows: Climate, History and Human Action. Columbia University Press, New York.

Vernet J.-L. 1995. Végétation et Paléoécologie des Grands Causses. In: Bonniol J. and Saussol A. (eds), Grands Causses: nouveaux enjeu, nouveaux regard. Féderation pour la Vie et la Sauvegarde du Pays des Grands Causses, Mileau, pp. 91–105.

Waldhardt R. 2003. Biodiversity and Landscape – summary, conclusions and perspectives. Agriculture, Ecosystems and Environment 98: 305–309.

Walker B. 1992. Biodiversity and Ecological Redundancy. Conservation Biology 6(1): 18–23.

Wilson E.O. 2001. The Diversity of Life. Penguin Books, New York and London.

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Impact of game hunting by the Kayapó of south-eastern Amazonia: implications for wildlife conservation in tropical forest indigenous reserves

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Abstract. Indigenous forest reserves represent approximately one fifth of Brazilian Amazonia and pose enormous challenges for sustainable natural resource management by native Amazonians. In collaboration with the Kayapó Indians of A'Ukre of southeastern Amazonia, we obtained a game harvest profile of over 1360 forest vertebrates consumed at this village over a 20-month period, including 743 mammals, 361 forest tortoises and 256 birds from a minimum of 42 game species. This amounted to a total of 13,775 kg of game animals harvested over the entire study (mean = 26.2 kg d^{-1}). We also obtained some 450 km of line transect census data of midsized to large-bodied vertebrates within the core hunting catchment of this village and in an unhunted but otherwise comparable site upriver of A'Ukre. Population density estimates of 16 of the 18 species censused were significantly depressed by hunting by central place foragers within the village catchment, and a number of harvest-sensitive prey species showed clear evidence of local depletion. For the time being, however, we can conclude that hunting was sustainable at the landscape scale largely because source-sink dynamics in the context of low village catchment density is made possible by large surrounding tracts of primary forest that remain unharvested or underharvested.

Introduction

Most Amazonian indigenous peoples have been officially conferred land tenure status over large territories under varying degrees of legal implementation. A total of 401 indigenous reserves have been legally designated in Brazilian Amazonia, accounting for a combined acreage of 104.3 million ha (=20.8% of the region) or five times the area currently designated as strictly protected on paper (ISA 2004). Although over 99% of the native Indian population of Brazilian Amazonia (~180,000) inhabit these Indian Lands, they account for relatively low human densities (mean = 0.17 person km^{-2}), providing encouraging prospects for sustainable management of natural resources, including game vertebrates.

The impact of rapidly changing patterns of resource extraction by indigenous peoples has become central to discussions on the long-term integrity of remaining tracts of tropical forests. While native Amazonians can be seen as legitimate allies of conservationists as legally empowered guardians of many biologically important wildlands (Schwartzman et al. 2000; Zimmerman et al. 2001), they can profoundly change forest structure and composition in the long run (Peres 1994; Terborgh 1999). This debate is particularly relevant to low-density animal populations that are selectively harvested over large areas, raising growing concerns over the role of indigenous reserves in biodiversity conservation.

Protein acquisition by indigenous peoples in lowland Amazonia relies heavily on wild meat from forest vertebrates (Redford and Robinson 1987; Jerozolimski and Peres 2003). Subsistence hunting becomes even more important in unflooded (*terra firme*) forest areas where aquatic sources of animal protein are often scarce. Subsistence hunters have access to most areas of Amazonia, affecting even the core of many nature and indigenous reserves (Peres and Lake 2003). Indeed, populations of many large-bodied tropical forest vertebrates have declined precipitously even in structurally undisturbed forests (Peres 2000a), a phenomenon that has become increasingly recognized at a pantropical scale (Fa and Peres 2001; Milner-Gulland et al. 2003).

The demographic viability of many game vertebrate populations depends on the rate at which different target species are harvested per unit time, the total hunting area exploited (hereafter, catchment area), and the site-specific annual productivity of different target species. In this paper, we examine the patterns of game harvest by the Kayapó Indians of southeastern Amazonia, and the extent to which these can be defined as sustainable. We focus on the Kayapó Indians because their impact as game hunters has been framed as a central issue in a prominent debate over the long-term role of indigenous reserves in tropical biodiversity conservation (Schwartzman et al. 2000; Terborgh 2000; Peres and Zimmerman 2001). We rely on a detailed game harvest profile obtained from Kayapó villagers at A'Ukre, with whom we have been working continuously over the past 11 years (Zimmerman et al. 2001). Game population densities were derived from wildlife surveys conducted in both an unhunted and a persistently hunted site, and then compared with sustainable harvest estimates for different game species. We then provide a general discussion on how the impact of subsistence hunting in Amazonian indigenous reserves can be mitigated.

The Kayapó of A'Ukre

The Kayapó are traditionally semi-nomadic hunter-gatherers who historically occupied the vegetation transitions between the central Brazilian scrublands (*cerrado*) and the seasonal forests of southeastern Amazonia (Vidal 1977). However, the Kayapó were gradually pushed by frontier expansion into their present closed-canopy forest domain, and they currently number some 3900 Indians scattered among 15 villages (Zimmerman et al. 2001). These are

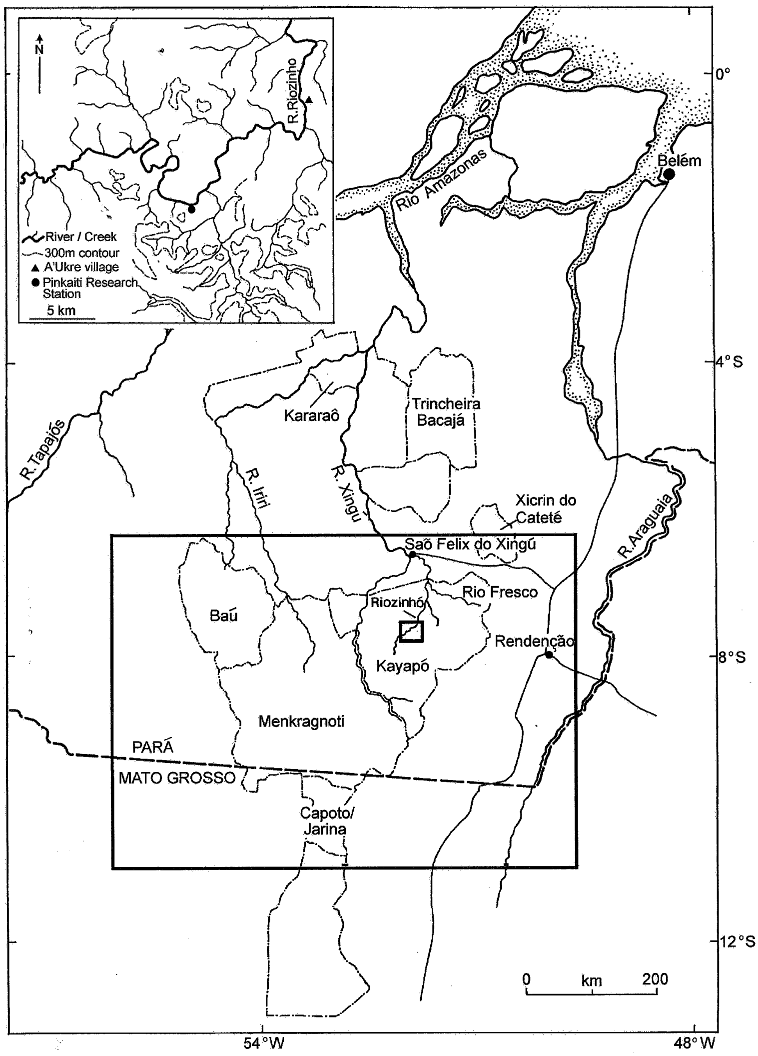

Figure 1. Location of the study area (upper left inset map) along the Riozinho river, within the Kayapó Indian Land. Larger map shows the extent and distribution of indigenous territories in southeastern Brazilian Amazonia, including all officially recognized Indian Lands of southern Pará and northern Mato Grosso inhabited by the Kayapó.

distributed over six officially recognized Indian Lands of southern Pará and northern Mato Grosso, and comprise a combined acreage of 11,346,326 ha (Figure 1). This study was conducted at A'Ukre (7°41′15″ S; 51°52′25″ W), an average-sized Kayapó village located 220 km west of the nearest town (Redenção), and along the Rio Riozinho, a second-order tributary of the upper Rio Xingú. A'Ukre is one of six Indian villages located within the Kayapó

Indian Land, a territory of 3.3 million ha inhabited by some 1946 Kayapó. During the study period, A'Ukre consisted of 133 villagers (mean density = 0.04 person km^{-2}) belonging to 17 family units (mean = 7.9 people per family) distributed around a circular arrangement of family households. Children and dependent young represented 62.4% of the village population, which included 21 male hunters.

The Kayapó of A'Ukre territory is closed to outside hunters and forest extractors; river access is lengthy and treacherous because of rapids, waterfalls and lack of paved roads, and the village is accessible only by small aircrafts stationed at Redenção. Hunting at A'Ukre dates from the late 1970s and early 1980s when the village was formed by migrant families from the neighboring village of Kuben-Krã-Kein, located 5 days upriver by canoe. A'Ukre villagers control some 300,000 ha of the Kayapó Indian Reserve, which is unofficially bounded by three neighboring village territories (Moikarako, Kuben-Krã-Kein and Gorotire). The extent to which these areas are controlled by different communities became an issue only during the past two decades when communities began to vie for ownership of broadleaf mahogany trees (*Swietenia macrophylla*, Meliaceae), the most valuable forest resource in this region (Zimmerman et al. 2001).

Methods

Field sites

The study sites consisted primarily of highly seasonal transitional evergreen forests sustained primarily by clay soils. Canopy cover in this region is highly heterogeneous including more open forests dominated by *Attalea maripa* palms and large numbers of woody lianas; high *terra firme* forests, where large emergents such as Brazil-nut trees (*Bertholletia excelsa*, Lecythidaceae) were common; and small *cerrado* enclaves in areas of shallow soils that often expose the surface bedrock (Brasil 1974). Approximately, 70% of the A'Ukre territory is covered in forest, the remaining consisting of *cerrados* that are largely restricted to upland plateaus and rocky ridges (100–200 m a.s.l.). The *cerrados* are largely undisturbed and remain ungrazed by domestic livestock, whereas forest areas are largely undisturbed except for highly selective logging of mahogany trees along valley bottoms. Mean rainfall averages 1640 mm (N = 10 years) with a clearly demarcated dry season (June–September) that typically include 100 consecutive days without rain.

Game harvest profile

Game harvest at A'Ukre was examined during 542 days spread over a period of 20 consecutive months (November 1994–July 1996; Figure 2). This includes a more intensive sampling period of 324 days over 14 months (June 1995–July 1996). All village households were visited on a daily basis and cooperation from villagers was facilitated by our long term working relationship with the Kayapó of A'Ukre (Zimmerman et al. 2001). In total, data on 1360 prey items were obtained. All terrestrial vertebrate kills brought into A'Ukre were identified, sexed, and weighed with a size-graded set of *Pesola*© scales (accurate to 10, 50 and 100 g). Additional information was obtained directly from hunters using a standard questionnaire, including hunter identity, the approximate location of the site where a given prey item was encountered, and weapon used. Kayapó hunters have an excellent cognitive map of the areas they hunt, and positional data on reported kill sites were verified in August 2000 when the entire A'Ukre catchment was mapped using GPS fixes of all main hunting sites. All 21 hunters living at A'Ukre during the study took part in data collection. A body weight survey of all inhabitants of A'Ukre was carried out in August 1996.

The number of animals of each species consumed at A'Ukre over the entire study was corrected to a full year (365 days) to provide an annualized observed harvest (OH) rate. The annual harvest rate per unit area within the core catchment (117 km^2; see below) was also estimated. Estimates of the biomass harvested (kg km^{-2}) were also calculated by multiplying the number of animals harvested by the species-specific mean body mass obtained from fresh, whole

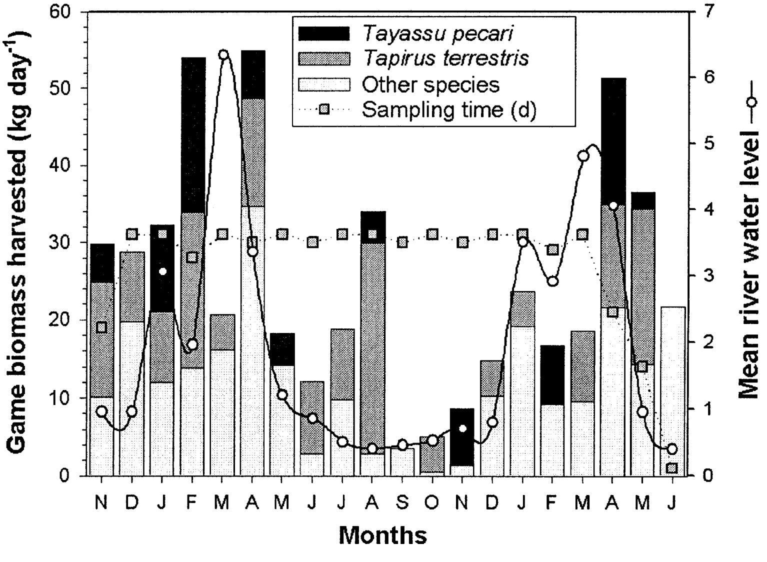

Figure 2. Monthly variation in daily game biomass harvested at A'Ukre between November 1994 and June 1996. Two ungulate species – tapir and white-lipped peccary – accounted for a disproportionately large contribution to the overall harvest. Shaded squares and open circles indicate the sampling effort allocated to the harvest profile (in days) and mean monthly river water-level at the Pinkaití field station, respectively.

carcasses weighed during the entire study. Sample sizes for body mass data exceeded 10 weighed kills for 26 of the 42 vertebrate species in the harvest profile.

We also examined patterns of hunter selectivity considering the body mass of all target species for which both observed harvest and population density estimates were available. This was calculated using the Ivlev's selectivity index (S_i), which ranges from -1.0 to $+1.0$ and compares availability (A) with utilization (U) as in $S_i = (U - A)/(U + A)$ (Bodmer 1995).

Hunting catchment area

The A'Ukre core catchment area was mapped with the aid of a GPS receiver and included (i) the forest area covered during single-day hunting forays within a radius of 8 km from A'Ukre and the Riozinho river for the most frequently hunted areas; and (ii) an additional 1-km wide forest strip of 8 km up and down from the village along the west bank of the river, where hunting was consistently restricted to shorter inland incursions. This resulted in an estimated core catchment area of 117 km^2. Data on kill locations obtained from A'Ukre hunters during daily interviews indicated that 68% of all animals captured (or 79% of the aggregate game biomass consumed at A'Ukre) were harvested within this core catchment. Hunting treks into more distant forest areas accounted for 210 kills (15.9%) taken during only 15 of the last 324 days of study, and were treated separately in the analysis. These data were thus excluded from calculations of sustainable harvest rates within the core catchment, but included in the total number of kills and game biomass consumed at A'Ukre.

Population density estimates

Line-transect surveys were conducted along several transects of 4–5 km in length, placed at two study sites with different histories of hunting pressure: (1) Pinkaití, a virtually unhunted area located 12–18 km upriver of A'Ukre, and (2) A'Ukre, a persistently hunted area in the vicinities of, and up to 5.5 km from, the center of this village (Figure 1). Although Pinkaití had been occasionally visited by A'Ukre hunters for as long as 20 years, hunting at this site had been discontinued 5 years prior to censuses when Pinkaití became a research station with continuous investigator presence (Zimmerman et al. 2001). Our total census effort amounted to a cumulative walking distance of 248.5 km at Pinkaití, conducted over four consecutive years (1994–1997), and 199.4 km at A'Ukre conducted over two years (1997–1999). Density estimates at these sites were then compared to examine the abundance responses of vertebrate species to persistent game harvest within the A'Ukre catchment area. This assumes that game density estimates were primarily a function of hunting pressure rather than differences in forest structure and composition. This assumption appears to be valid because the Pinkaití and A'Ukre census areas were similar in terms bird, mammal and tree species composition, canopy gap structure, and distances from the river (Baider 2000, H. Nascimento and C. Peres, unpubl. data).

To avoid detection biases along hunting trails, all censuses were carried out on purpose-cut transacts which had been measured and marked every 50 m with the help of a *Hip – Chain*® to aid mapping of animal locations. Census walks were carried out on rainless days at a mean velocity of ca. 1250 m h^{-1}, with brief stops every 50–100 m to maximize detection of all acoustic or visual cues. During each encounter with a prey species (groups or individuals), we noted the time of day, species identity, group size, perpendicular distance (PD) to the trackline (with the aid of a Range Finder®), and distance along the transect. Observations were terminated within 12 min of each detection event and, in the case of social species, only accurate group counts were used to estimate mean group size. Census walks were conducted in the morning (0700–1100 h) and in the afternoon (1400–1800 h), corresponding to intervals of maximum activity for diurnal game species. Further details on survey methodology can be found in Peres (1999).

Population density estimates (ind. km^{-2}) at each area were derived using the Distance software, v. 3.5 (Laake et al. 1994) for all species that met the recommended minimum number of independent sightings (25–30) for reasonably robust model fits (Buckland et al. 1993; S. Buckland, pers. comm.). Because modeling independent detection events becomes increasingly difficult for smaller samples, we used the most effective strip-width method (Whitesides et al. 1988) for a few uncommon species by determining the fall-off point in the PD histograms. This consisted of the PD interval where the sighting frequency was equal to or less than 50% of the preceding level, and was used to calculate the effective strip-width (Whitesides et al. 1988). The species-specific census area was then used to estimate the overall density of each species on the basis of their detection frequencies.

Detection data for red brocket deer (*Mazama americana*) and grey brocket deer (*M. gouazoupira*) were pooled because identifications to species level during censuses were not always possible. The same was applied to both species of curassows (*Mitu tuberosa* and *Crax fasciolata*) and the two sympatric congeners of common guans (*Penelope pileata* and *P. superciliaris*) occurring in both census areas.

Sustainable harvest estimates

For a set of 24 game species (consisting of a single species or functionally equivalent congeners), observed harvest rates per km^2 (OH) were compared with maximum sustainable harvest (MSH) estimates derived from estimates of maximum production rates (P_{max}) using the Robinson and Redford (1991) model. $P_{\max}$ was calculated on the basis of the maximum finite rate of increase ($\lambda_{\max}$) and the local population density of each species. For the two most important ungulate species harvested by the Kayapó, these $P_{\max}$ estimates were marginally higher than those estimated using the Bodmer (1994) method (i.e. tapir: 0.082 vs. 0.074 ind. km^{-2} year^{-1}; white-lipped peccary: 4.67 vs. 3.59, ind. km^{-2} year^{-1}). Here we assume that density estimates obtained from field censuses at the unhunted site serve as a baseline for the A'Ukre village catchment. These best-available density estimates sidestep the use of 'predicted densities', as recommended by Robinson and Redford (1991) when no other density estimates are available, which in Amazonian *terra firme* forests tend to overestimate the MSH of game species (Peres 2000b).

Maximum intrinsic rates of increase ($r_{\max}$) for mammal and some gamebird species were obtained from Robinson and Redford (1986) and Begazo and Bodmer (1998), respectively. Because $r_{\max}$ values were not available for a few game species, we considered approximate values from a closely related species.

Results

Kayapó game hunting

Hunting is arguably the most important subsistence activity for the Kayapó providing the bulk of their protein requirements. Hunting was carried out primarily by married men and throughout the year, although alternative aquatic sources of animal protein became very important during the dry season when the low water-level facilitates fishing (Figure 2). Although both traditional and modern hunting technology was used, most game vertebrates were killed with fire weapons (16- to 44-gauge shotguns), with the most frequently used weapon (20-gauge shotguns) accounting for 53% of all kills. However, tortoises were hand-captured and stored for later consumption, and three armadillo species were killed primarily with the aid of iron diggers. The use of bow-and-arrows was not recorded during the study, although white-lipped peccaries swimming across rivers were killed with traditional hardwood clubs. Hunting and feeding taboos against any given game species or body parts were rarely reported, but were related to special contexts such as newborn babies, illnesses in the family, and elderly persons.

Most Kayapó hunts consist of single-day incursions on foot into forest trails fanning out from the village, but some forays were aided by motorized dugout canoes that were largely restricted to areas near the village, usually due to fuel shortages. In single-day hunts, hunters (alone or in small groups) leave the village at 0600-0800 h and return just before dusk, thus limiting their effective range to distances that can be covered on foot within at most 12 h of daylight. On average, hunters went out on single-day hunts twice weekly and covered a maximum radius of 8–10 km from the village. In addition, Kayapó hunters also go on occasional hunting treks into more remote areas well outside the core village catchment, usually prior to traditional village feasts that required large amounts of meat. During these treks, most A'Ukre adult and adolescent males collectively move to a temporary base camp set up far from the village (12–26 km), from which they repeatedly disperse alone or in pairs, typically over a period of 3–28 days (mean = 7 days).

Patterns of game harvest

A total of 1360 forest vertebrates were consumed by the Kayapó of A'Ukre during the study, including 743 mammals (54.6% of all kills), 361 testudine reptiles (26.5%) and 256 birds (18.8%). These included 21 mammal, at least 19 bird, and two tortoise species (Table 1). Prey items obtained by Kayapó hunters weighed an average of 11.41 kg (±24.29 kg, $N = 1096$), but ranged widely from Crested Oropendula (*Psarocolius decumanus*) weighing less than 0.3 kg to lowland tapir weighing over 175 kg. As shown in the overall distribution of prey body mass (Figure 3), however, potential prey items smaller than 1 kg were rarely taken by hunters who were able to concentrate primarily on a few species of large mammals, and two species of forest tortoises (*Geochelone* spp.) that were consumed primarily during ceremonial feasts involving all village members (Figure 4).

Kayapó hunters clearly exhibited a bias towards large-bodied target species as shown by an abrupt step transition from negative to positive Ivlev's indices of selectivity as the size of prey species increased. Prey body mass alone explained more than half of the overall variation in prey selectivity ($r = 51.7\%$, $F_{1,22} = 23.5$, $N = 24$, $p < 0.001$), and mammal species larger than 30 kg

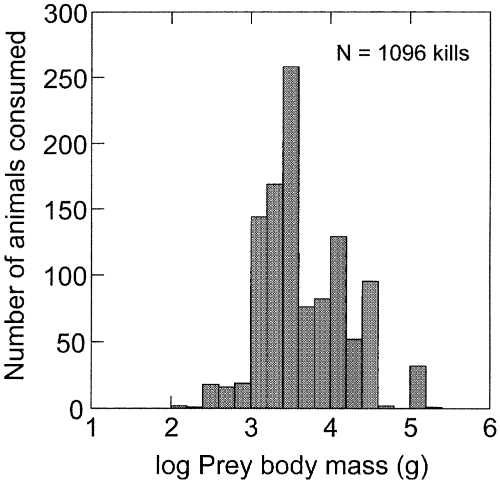

Figure 3. Size distribution of forest vertebrate kills consumed by the Kayapó of A'Ukre, in terms of the ($\log_{10}$-transformed) body mass of all whole carcasses (adults and juveniles) individually weighed at the village.

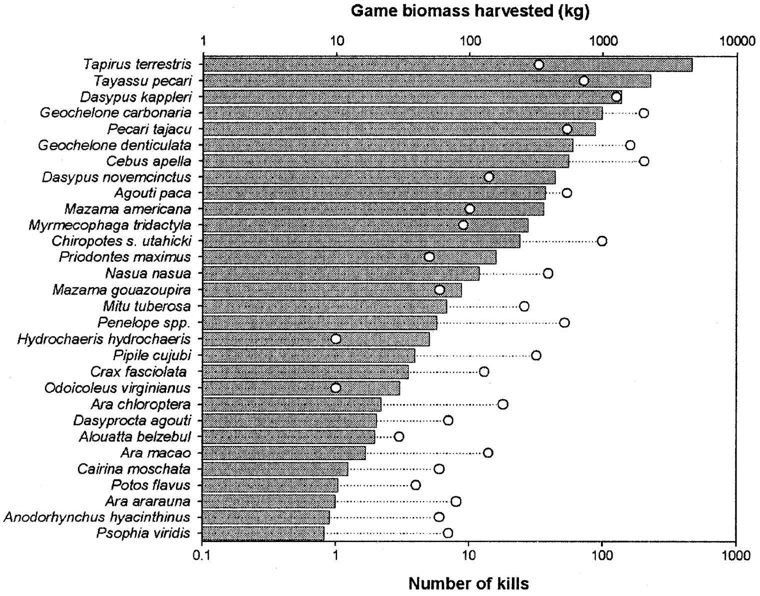

Figure 4. Total number of kills (open circles) and prey biomass (shaded bars) harvested at A'Ukre during this study. Species are ranked according to their overall biomass contribution to the village offtake.

(giant armadillo, tapir and white-lipped peccary) were associated with highly positive selectivity values on the basis of their local population density. Red brocket deer comprised the only large-bodied forest prey species that was selected against. In contrast, small-bodied species (< 3 kg) were always associated with negative selectivity values, and were often deliberately bypassed during hunting forays.

Brown capuchin monkeys, both tortoise species, and great long-nosed armadillos were the numerically dominant prey items, although large ungulates accounted for most of the biomass consumed (Figure 4). Primates, tapirs, peccaries, xenarthrans and large caviomorph rodents comprised the most important mammalian prey. In contrast, agoutis and all three species of cervids, including the white-tailed deer that was restricted to the cerrado plateaus of the A'Ukre territory, contributed with only a small number of kills. Capture of small rodents, marsupials, bats, canids, felids and mustelids were never reported or observed, although large cats such as puma and jaguar were perceived as a threat and occasionally killed. A'Ukre hunters also killed a number of bird species for food, including cracids, trumpeters, macaws and oropendulas, although gamebirds accounted for a modest contribution to the total biomass harvested. A small number of toucans, parrots, and oropendulas were also killed primarily for their feathers which were traditionally used in ornamental handcraft.

In terms of biomass, 86.3%, 11.5% and 2.3% of the total game offtake was derived from mammal, reptile, and bird species, respectively (Table 1). Primates comprised the most important mammalian order in numeric terms accounting for 22.4% of all kills. Three ungulate species – lowland tapir, white-lipped peccary and collared peccary – comprised 11.7% of all kills and 56.2% of the total biomass harvested, and tapirs alone contributed with a staggering one third of the total game biomass consumed at A'Ukre (Figure 2). The monthly white-lipped peccary harvest, which provided the second highest contribution in terms of biomass (16.4%), was relatively erratic (Figure 2), and coincided with episodic hunting treks preceding ceremonial feasts or the occasional appearance of large herds moving through the village catchment.

A total of 13,775 kg of game animals were harvested over the entire study (mean = 26.2 kg day^{-1}), including 6323 kg harvested during the last 324 days of sampling (mean = 19.5 kg day^{-1}). Given that approximately 30% of this crude biomass is non-edible (Townsend 2000), we estimate that some 9642 kg of fresh game meat was actually consumed by the 133 Kayapó living in A'Ukre, resulting in a mean daily per capita rate of 138 g of game meat consumed. The number of animals killed within the A'Ukre catchment area accessed during single-day hunts represented 67.8% of the total harvest or 3.8 animals km^{-2}. This corresponded to 42.4 kg km^{-2} or 78.5% of the total game biomass consumed at the village.

Effects of hunting on local game stocks

The aggregate game stock in the A'Ukre catchment within 6 km of the village (94 ind. km^{-2}) was less than half of that at the unhunted Pinkaití site (223 ind. km^{-2}). Population density estimates for 16 of 18 game species censused at both forest sites were significantly higher at Pinkaití (paired *t*-test, $t = 3.38$, P_{adj}, = 0.003, $N = 18$; Table 2). Surveys at A'Ukre failed to detect four game species (or signs of their presence) – tapir, white-lipped peccary, giant armadillo, and giant ant-eater – and this is consistent with information provided by Kayapó hunters. For most group-living target species, the smaller populations censused at A'Ukre were a combined effect of both smaller mean group sizes and lower group densities (Table 2). Consequently, the standing aggregate game biomass density at A'Ukre (232 kg km^{-2}) was only 21% of that at Pinkaití (1098 kg km^{-2}), reflecting a substantial overall difference in game biomass density of −59% from the unhunted to the hunted site.

Harvest-sensitive species including all midsized to large-bodied primates, tapir, white-lipped peccary, giant armadillo, razor-billed curassow, red-throated piping guan and tortoises showed the largest relative differences between Pinkaití and A'Ukre (Table 2 and Figure 5). On the other hand, coatis (*Nasua nasua*) and small tinamous (*Crypturellus* spp.) were actually more abundant in the heavily hunted area. However, small gamebirds such as small tinamous and marbled wood-quail (*Odontophorus gujanensis*) were not

Table 1. Number of individuals, aggregate biomass and percentage of game species removed by the Kayapó of A'Ukre over 525 days of sampling (12 November 1994–June 1996).

Species	English name	Body mass (g)^a	No. of kills	% of kills	Total biomass (kg)	% of biomass
Mammals						
Primates						
Cebus apella	Brown capuchin monkey	2711	203	14.9	550.24	4.0
Chiropotes satanas utahicki	Bearded saki monkey	2412	99	7.3	238.75	1.7
Alouatta belzebul	Red-handed howler monkey	6533	3	0.2	19.60	0.1
Perissodactyls						
Tapirus terrestris	Lowland tapir	139,600	33	2.4	4606.80	33.4
Artiodactyls						
Tayassu pecari	White-lipped peccary	31,400	72	5.3	2260.80	16.4
Pecari tajacu	Collared peccary	16,237	54	4.0	876.83	6.4
Mazama americana	Red brocket deer	36,000	10	0.7	360.00	2.6
Mazama gouazoupira	Gray brocket deer	14,500	6	0.4	87.00	0.6
Odoicoleus virginianus	White-tailed deer	30,000	1	0.1	30.00	0.2
Xenarthrans						
Dasypus kappleri	Great long-nosed armadillo	10,907	126	9.3	1374.30	10.0
Dasypus novemcinctus	Nine-banded armadillo	3140	14	1.0	439.60	3.2
Pridodontes maximus	Giant armadillo	31,500	5	0.4	157.50	1.1
Myrmecophaga tridactyla	Giant anteater	30,500	9	0.7	274.50	2.0
Tamandua tetradactyla	Collared anteater	3100	1	0.1	3.10	0.0
Rodents						
Agouti paca	Paca	6820	54	4.0	368.28	2.7
Dasyprocta agouti	Red-rumped agouti	2875	7	0.5	20.13	0.1
Hydrochaeris hydrochaeris	Capybara	50,000	1	0.1	50.00	0.4
Lagomorphs						
Sylvilagus brasiliensis	Brazilian rabbit	1200	1	0.1	1.20	0.0
Carnivores						
Nasua nasua	South American coati	3047	39	2.9	118.82	0.9
Potos flavus	Kinkajou	2600	4	0.3	10.40	0.1

Panthera onca	Jaguar	35,000	1	0.1	35.00	0.3
Total (mammals)			743	54.6	11,882.85	86.3
Birds						
Cracids						
Mitu tuberosa	Razor-billed Curassow	2611	26	1.9	67.89	0.5
Crax fasciolata	Bare-faced Curassow	2678	13	1.0	34.81	0.3
Penelope superciliaris and *P .pileata*	Rusty-margined and White-crested Guan	1097	52	3.8	57.02	0.4
Pipile cujubi	Red-throated Piping-Guan	1222	32	2.4	39.11	0.3
Trumpeters						
Psophia viridis	Dark-winged Trumpeter	1167	7	0.5	8.17	0.1
Psittacids						
Ara ararauna	Blue-and-yellow Macaw	1233	8	0.6	9.87	0.1
Ara chloroptera	Red-and-green Macaw	1218	18	1.3	21.93	0.2
Ara macao	Scarlet Macaw	1187	14	1.0	16.62	0.1
Anodorhynchus hyacinthinus	Hyacinth Macaw	1500	6	0.4	9.00	0.1
Aratinga spp., *Pyrrhura* spp. and *Amazona* spp.	Parakeets and parrots	–	57	4.2	30.75	0.2
Ramphastids						
Ramphastos vitellinus and *R. tucanus*	Channel-billed and Red-billed Toucan	400	5	0.4	2.00	0.0
Icterids						
Psarocolius decumanus and *Gynnnostinops bifasciatus*	Crested and Amazonian Oropendula	267	12	0.9	3.20	0.0
Anatids						
Cairina moschata	Muscovy Duck	2067	6	0.4	12.40	0.1
Total (birds)			256	18.8	312.77	2.3
Reptiles						
Testudines						
Geochelone carbonaria	Red-footed tortoise	4913	201	14.8	987.51	7.2
Geochelone denticulata	Yellow-footed tortoise	3698	160	11.8	591.88	4.3
Total (reptiles)			361	26.5	1579.39	11.5
Overall total		–	1360	100.0	13,775.01	100.0

[a] Mean body mass (g) of all carcasses (or live captures in the case of tortoises) weighed at A'Ukre.

Table 2. Population density and biomass of forest vertebrates censued at the Kayapó Reserve, based on a total effort of 248.5 km at Pinkaití and 199.4 km at A'Ukre.

Species	No. of detection events		Mean group size		ESW (m)		Group density (Groups km^{-2})		Population density (ind. km^{-2})		Population biomass[a](kg km^{-2})		%Change[b]
	Pinkaití	A'Ukre	Pinkaití	A'Ukre	Pinkaití	A'Ukre	Pinkaití	A'Ukre	Pinkaití	A'Ukre	Pinkaití	A'Ukre	
Cebus apella	66	18	7.3	5.2	24.0	20.0	5.0	2.3	36.6	11.7	99.2	31.7	−68.1
Chiropotes s. utahicki	16	3	23.5	6.3	35.0	35.0	0.92	0.21	16.5	1.3	39.8	3.2	−91.9
Alouatta belzebul	18	2	7.8	3.0	35.0	35.0	1.03	0.14	8.0	0.4	52.3	2.7	−94.8
Tapirus terrestris	9	0	1.0	1.0	38.0	–	0.62	0.00	0.62	0.0	86.6	0.0	−100.0
Tayarsu pecari	1	0	150	–	45.0	–	0.04	0.00	5.9	0.0	185.3	0.0	−100.0
Pecari tajacu	10	2	4.0	3.0	14.0	14.0	1.2	0.36	8.5	1.1	137.7	17.5	−87.3
Mazama spp.	37	9	1.0	1.0	20.0	13.0	3.2	1.7	4.5	1.7	129.7	50.2	−61.3
Nasua nasua	2	9	12.5	3.5	9.0	9.0	0.45	2.5	5.7	8.9	17.4	27.2	56.8
Dasyprocta agouti	274	68	1.05	1.0	13.0	13.6	41.2	12.5	43.3	12.5	124.5	35.9	−71.2
Agouti paca[c]	7	1	1.0	1.0	1.0	1.0	4.5	0.5	4.5	0.5	30.7	3.4	−88.9
Priodontes maximus[d]	5	0	1.0	–	5.0	–	1.6	–	1.6	0.0	50.4	0.0	−100.0
Crax fasciolata and *Mitu tuberosa*	55	5	2.0	1.8	15.6	15.6	7.1	0.8	9.0	1.44	23.8	3.8	−84.0
Penelope spp.	64	36	2.8	1.7	17.4	10.3	8.0	8.3	22.3	14.2	24.5	15.6	−36.3
Pipile cujubi	18	3	2.0	1.6	24.6	24.6	1.5	0.31	2.8	0.52	3.4	0.6	−81.4
Psophia viridis	40	12	6.4	4.7	14.8	12.0	4.4	2.5	33.1	11.8	38.6	13.8	−64.4
Tinamus spp.	61	20	1.05	1.07	23.5	23.5	14.4	10.8	15.1	11.6	18.1	13.9	−23.2
Crypturellus spp.	34	19	1.06	1.2	12.5	12.5	9.8	14.6	10.4	17.5	4.0	6.7	68.3
Geochelone spp.	9	2	1.0	1.0	3.5	3.5	7.5	1.4	7.5	1.43	32.3	6.2	−80.9
Total	–	–	–	–	–	–	–	–	223.3	93.6	1098.1	232.4	−58.1

[a] Population biomass density was calculated on the basis of mean (male and female) weights of carcases obtained at A'Ukre.

[b] Relative shift in population density (or biomass) from Pinkaití to A'Ukre.

[c] Density estimate based on the number of fresh tracks (<24 h) recorded within 5 m of all transects.

[d] Density estimate based on the number of recently dug holes (<24 h) recorded within 5 m of all transects.

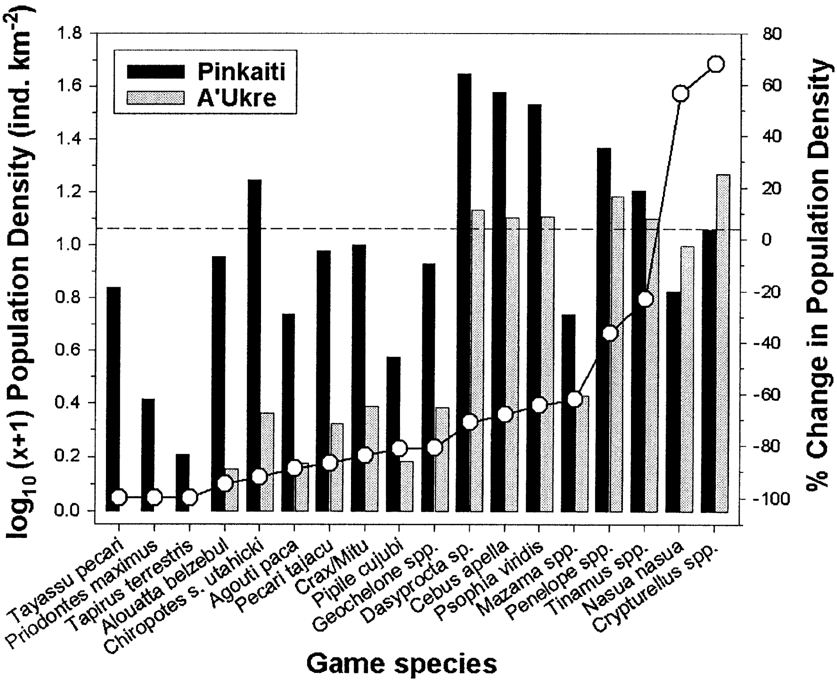

Figure 5. Population density estimates ($\log_{10} x + 1$) for game species in an unhunted (Pinkaití) and a persistently hunted forest site (A'Ukre). Species are ranked from the most negative to the most positive abundance differences (open circles) between the unhunted and hunted sites. Only 2 of the 18 game vertebrate taxa censused were more abundant in the A'Ukre catchment area.

harvested at A'Ukre, which suggests that populations of most target species had been moderately to severely reduced by hunting in the A'Ukre catchment area. Furthermore, body size of game species (expressed as $\log_{10}$ mean body mass) explained most of the variation in the direction and magnitude of differences in both population density ($r^2 = 0.53$, $F_{1,22} = 24.8$, $p < 0.001$) and biomass between Pinkaití and A'Ukre ($r^2 = 0.59$, $F_{1,22} = 31.9$, $p < 0.001$). The intrinsic rates of natural increase ($r_{\max}$), on the other hand, had no apparent effect on these differences in abundance (density shifts: $r^2 = 0.001$, $F_{1,22} = 0.02, p = 0.878$; biomass shifts: $r^2 = 0.003$, $F_{1,22} = 0.08, p = 0.784$).

Game yield in relation to distance from A'Ukre

On the basis of 822 carcasses obtained during day-hunts and hunting treks for which the location of the kill was known, we estimate that game vertebrates consumed at A'Ukre were brought down at an average distance of 10.2 km (SD = 8.6 km; range = 1–25 km) from the village, and for many important species, game yields were substantially higher in hunting zones that were increasingly farther from the village. This is illustrated for four desirable and

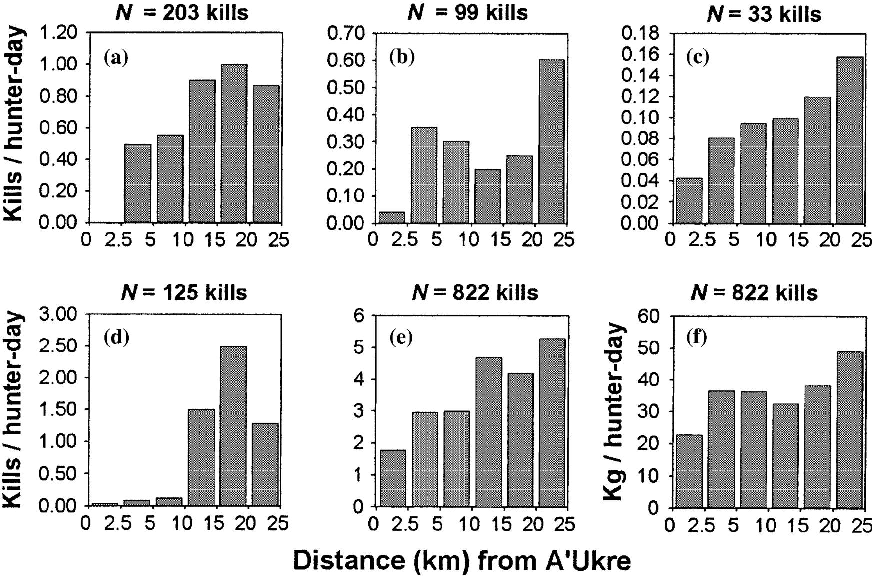

Figure 6. Relationship between prey capture efficiency (expressed as kills obtained per day spent hunting) and physical accessibility to different hunting zones, defined as their straight-line distance from the village of A'Ukre, for (a) brown capuchin monkey, (b) bearded saki monkey, (c) lowland tapir, (d) both species of forest tortoises, and (e) all game species combined. The total prey biomass captured (f) as a function of distance from the village is also shown using the same metric.

frequently harvested species by the variation in prey capture success (defined as the number or biomass of kills obtained per unit of hunting time) as a function of the straight-line distance between kill sites and the village. In these terms, locally depleted prey species such as brown capuchin monkey, bearded saki monkey, tapir, and *Geochelone* tortoises—which contributed with 50.6% of the total game biomass harvested—were most cost-effectively harvested in the most distant hunting sites (Figure 6a–d). The same relationship applies to most target species for which we have data on kill location, whether we consider the total number of kills retrieved (Figure 6e) or the aggregate biomass they represented (Figure 6f). Furthermore, prey body size explained a significant proportion of the species variance in mean linear distance between A'Ukre and kill sites (r^2 = 15.4%, $F_{1,26}$ = 4.75, p = 0.039, N = 28). In other words, large-bodied species were more likely to be captured by these central-foragers far away from the village, presumably because stocks in the immediate vicinity of A'Ukre had already been heavily depleted.

Sustainability of game harvest

To evaluate the degree to which Kayapó hunting practices could be defined as sustainable, observed annualized harvest rates (per km^2) for frequently harvested target species were compared with estimates of maximum production ($P_{\max}$) and MSH within the core hunting catchment of 117 km^2. Of the 16 species listed in Table 3, 9 were harvested well below their MSH, 3 were harvested at levels approaching their MSH, and harvests of 4 clearly exceeded their MSH. Only tapirs were harvested at levels far greater than the MSH calculated for this species (11.2 times), whereas both tortoise species, brown capuchin monkeys and piping guans were overhunted at levels 18–31% above their respective MSH. Harvest rates could be interpreted as sustainable for most species for which it was possible to estimate the MSH, but due to limitations of the harvest model we applied these results must be interpreted with caution (see below).

Comparisons between the observed and sustainable harvest rates were poor predictors of the marked differences in independent estimates of game population densities at A'Ukre and Pinkaití, which clearly suggest that most stocks of key target species had been moderately to severely depleted in the village catchment. For example, the OH/MSH ratio, which describes the proportion of a sustainable offtake that was actually removed, explained only 14% of the variation across target species in the population density ratios between A'Ukre and Pinkaití ($F_{1,22} = 3.57$, $p = 0.072$, $N = 24$). Moreover, although there was a wide variation in population density differentials for species that could not be defined as overharvested, 14 of the 19 species harvested at levels below their MSH were still far less abundant in the hunted site.

Discussion

Game vertebrates are the most valuable non-timber products in Amazonian forests (Peres 2000a), raising serious concerns over the long-term subsistence needs of tribal and non-tribal communities as game stocks become depleted due to longer village persistence times, greater consumer pressure and greater access to more efficient hunting and transportation technology (Jerozolimski and Peres 2003). The Kayapó of A'Ukre are in a state of economic flux, with wage labor and an increasingly diverse portfolio of household income gradually replacing traditional subsistence activities. The mean aggregate annual household income in 2000 was highly variable but relatively high for an Amazonian Indian group (US$ 3253 ± 2560; Morsello 2002), compared to the average annual per capita income in Brazil of US$2850. This can be seen as either good or bad news depending on the long-term wisdom and resource management stewardship of the Kayapó as they maintain sovereignty rights and control access over a large territory. But despite an increasing degree of market integration and reliance on external commodities, all but one of the 15 Kayapó Indian villages of southeastern Amazonia can still rely heavily on forest wildlife to meet their daily protein requirements. For the time being, this is clearly tied to the low density of village catchments and resource users ($\sim$0.035 km^{-2}) across the entire the Kayapó Reserve.

Table 3. Estimates of annual production (P_{max}), observed harvest (OH) and maximum sustainable harvest (MSH) for the 16 most important prey taxa consumed by the Kayapó of A'Ukre.

Species	BM (kg)	Density (ind. km^{-2})	λ_{max}[a]	P_{max}	Numeric harvest (ind. km^{-2})		Biomass harvest (kg km^{-2})		% removed[b]
					OH	MSH	OH	MSH	
Mammals									
Cebus apella	2.7	29.2	1.15	2.63	0.65	0.53	1.75	1.42	122.7
Chiropotes satanas utahicki	2.4	16.5	1.19	1.83	0.27	0.37	0.65	0.88	73.6
Tapirus terrestris	139.6	0.6	1.22	0.08	0.18	0.02	25.55	2.29	1117.7
Tayassu pecari	31.4	5.9	2.32	4.67	0.29	0.93	9.07	29.35	30.9
Pecari tajacu	16.2	8.5	3.49	12.67	0.15	2.53	2.50	41.14	6.1
Mazama americana	36.0	3.0	1.49	0.89	0.05	0.35	1.73	12.74	13.6
Mazama gouazoupira	14.5	1.5	1.63	0.57	0.01	0.23	0.15	3.31	4.4
Dasypus kappleri	10.9	8.0	1.86	4.12	0.24	1.65	2.63	17.98	14.6
Dasypus novemcinctus	3.1	21.8	1.99	13.03	0.07	5.21	0.21	16.36	1.3
Nasua nasua	3.0	5.7	1.26	0.89	0.15	0.18	0.47	0.54	86.6
Dasyprocta agouti	2.9	43.3	3.00	52.01	0.06	20.80	0.17	59.81	0.3
Agouti paca	6.8	4.5	1.95	2.56	0.50	0.51	3.42	3.50	97.7
Gamebirds									
Crax/Mitu[c]	2.6	9.0	1.46	2.48	0.21	0.50	0.56	1.31	42.7
Penelope spp.[d]	1.1	22.3	1.49	6.54	0.38	1.31	0.41	1.44	28.7
Pipile cujubi	1.2	2.8	1.54	0.90	0.21	0.18	0.26	0.22	118.1
Testudine reptiles									
Geochelone spp.	4.4	7.5	1.73	3.30	0.86	0.66	3.78	2.89	130.9

[a] Values taken from Robinson and Redford (1991) and Begazo and Bodmer (1998).

[b] Percentage of the MSH rate that was consumed at A'ukre; values > 100% indicate overhunting.

[c] Includes Bare-faced curassow (*Crax fascicolata)*and Razor-billed curassow (*Mitu tuberosa*).

[d] Includes both sympatric congeners, Rusty-margined guan (*Penelope superciliaris*) and White-crested guan *Penelope pileata*.

Terrestrial vertebrates were undoubtedly the most important subsistence resources extracted from the forest by the Kayapó of A'Ukre, although the transaction value of broadleaf mahogany roundlogs and cold-pressed Brazil nut oil was more significant (Zimmerman et al. 2001; Morsello 2002). During this study, the Kayapó of A'Ukre harvested some 9.6 tons of game meat per year from a minimum of 42 forest vertebrate species, although the eight most important species – belonging to five vertebrate genera (*Tapirus*, *Tayassu*, *Dasypus*, *Cebus* and *Geochelone)* – accounted for 84.8% of the total biomass offtake. Kayapó hunters were able to specialize on large-bodied prey items, with ungulates alone comprising 60% of the overall game biomass harvested (Figure 2). This was possible despite a small amount of time spent hunting; hunters allocated only 4% of their overall time budget to hunting activities, corresponding to about a third of the 11% of time invested in all subsistence activities (Morsello 2002). The highly skewed kill profile towards large mammals, *Geochelone* tortoises, and large gamebirds at A'Ukre corroborates previous studies showing that neotropical hunters prefer large-bodied species wherever these are still available (e.g. Peres 1990; Bodmer 1995; Mena et al. 2000), but switch to smaller-bodied prey of higher reproductive productivity, once preferred game species have been depleted (Jerozolimski and Peres 2003). This considerable degree of prey size selectivity is all the more remarkable considering that the overall size structure and relative abundance of Amazonian large vertebrate communities are heavily skewed towards small-bodied game species (Fa and Peres 2001).

The sheer importance of large ungulates, large armadillos and forest tortoises for the Kayapó can be partly explained by the relatively high biomass density of large terrestrial vertebrates in the A'Ukre territory compared to central-western Amazonian forests censused to date using the same methods (Peres 1996, 2000a, b). This is probably a reflection of the highly seasonal rainfall and highly heterogeneous landscape mosaic consisting of different vegetation types, and high levels of discontinuity in canopy structure even in high terra firme forests, all of which can favor large terrestrial browsers and/or frugivores. Large terrestrial frugivore/granivores at Pinkaití and A'Ukre will also benefit from relatively high levels of soil nutrient availability and a high abundance of large arborescent palms (Baider 2000), which provide clumped but super-abundant fruit resources during several months of the year. For example, 63 of the 72 white-lipped peccary kills were recorded from November to April (Figure 2), a period coinciding with, or immediately following, the extended fruiting season of inajá palms, *Attalea maripa* (Salm 2002). Undoubtedly, the spatial distribution of large concentrations on the ground of mature *Attalea* fruits affected both the landscape-wide movements of the large, highly mobile herds of this species, and the probability of hunters encountering them (Peres 1996).

Meat consumption was highly seasonal throughout the year, peaking during the wet season. However, there was a strong compensatory effect of aquatic sources of animal protein, such as key species of fish (e.g. tucunaré, *Cichla* *ocellaris*) and aquatic turtles (*Podocnemis* spp.), which were consumed by villagers all year-round but became particularly important during the dry season when the low river water level facilitated catches (Figure 2). For example, the mean water level (a good predictor of fishing efficiency) was positively correlated with the number of terrestrial prey items harvested at A'Ukre ($r = 0.428$, $p = 0.06$, $N = 20$) on a monthly basis, indicating that availability of aquatic prey effectively relieved local demand for forest wildlife. The overall game offtake resulted in a mean per capita rate of daily protein intake from forest wildlife of 27.6–34.5 g, assuming that (i) the wild game meat harvested was shared equally among all villagers older than 3 years, and (ii) a range of 20–25% of protein content in fresh wild meat (Leung and Flores 1961). This clearly underestimates the total amount of animal protein consumed because it fails to consider offtakes of aquatic fauna which was beyond the scope of this study. Moreover, a socio-economic survey showed that most of the 23 A'Ukre households made monthly purchases of frozen chicken (80%), bovine meat (60%) or tinned fish (20%) from traders in Redenção (Morsello 2002), which undoubtedly also alleviated protein demand and hunting pressure on wild game. In any case, game meat consumption comfortably exceeded the minimum daily per capita intake of 20 g of protein from high-quality sources as recommended by the World Health Organization (WHO 1973).

Brown capuchin monkeys accounted for the greatest numeric contribution from a single species to the A'Ukre wildlife harvest, although tapirs and white-lipped peccaries, followed by armadillos and tortoises, yielded the largest amount of meat consumed. The heavy reliance on large ungulates and primates is consistent with other studies on patterns of subsistence hunting in Amazonian forest, which show that large mammals often account for over 60% of the kills and over 90% of the meat biomass consumed by different indigenous groups (Vickers 1984; Redford and Robinson 1987; Jerozolimski and Peres 2003).

Successful prey acquisition for this group of central-place foragers, rather than taking place in conveniently accessible sites near the village, appears to be heavily skewed to distant areas near the catchment boundaries between frequently hunted zones visited during day-hunts, and infrequently hunted zones visited during multi-day hunting treks. This is entirely consistent with other Amazonian hunting studies that have considered the spatial structure of the harvest (e.g. Hames and Vickers 1982; Alvard 1994; Souza-Mazurek et al. 2000). However, game yields as a function of radial distance from the village was significantly affected by prey body mass, with smaller, higher-fecundity species more likely to be harvested nearer the settlement.

Yet the heavy reliance on some harvest-sensitive species is at odds with predictions from the sustainable harvest model applied to closed populations and the relatively long settlement history at A'Ukre. Having persisted at their current location and exploited roughly the same catchment area for over 23 years, A'Ukre villagers continue to frequently harvest primates and the two largest ungulate species. These are often severely depleted by hunting at other

Amazonian forests (Peres 1996, 2000a, b) due to their low reproductive rates, low densities, relatively long life span, and ease of capture (Peres 1990; Bodmer 1994; Bodmer et al. 1997). For example, the tapir harvest around A'Ukre (19.54 kg km^{-2} year^{-l}) has been sustained at levels 14 times greater than the MSH predicted for this species (1.40 kg km^{-2} year^{-1}). Under the same conditions, A'Ukre hunters would require a catchment area of 1630 km^2 to maintain a sustainable offtake. However, tapirs continue to be harvested at very high levels although they have become extremely rare in the vicinities of A'Ukre. This suggests that most of the tapirs killed in the core catchment were immigrants drawn from surrounding underharvested (or unhunted) areas as predicted by healthy patterns of landscape scale dispersal across a range of exploitation levels (Novaro et al. 2000; Salas and Kim 2002). This is only possible because of the vast area of uninhabited primary forest surrounding the village catchment, which serves as a year-round source of immigrants. However, this source-sink dynamic would be expected to break-down in other landscape contexts under conditions of considerably larger villages and higher village densities should neighboring village catchments ever coalesce to the point of eliminating interstitial source areas (Peres 2001).

In addition to tapir, 3 of the 24 game species evaluated using the Robinson and Redford (1999) model were unsustainably harvested: brown capuchins, bearded saki monkeys and piping guan. These were frequently killed by Kayapó hunters and their populations were also heavily reduced in the persistently hunted area. Platyrrhine primates typically have low annual birth rates, long periods of infant development, long inter-birth intervals and long, socially mediated delays of first reproduction (Robinson and Redford 1986), which combined with their easily detectable groups, makes them particularly prone to overhunting (Peres 1990). Both the harvest model and field censuses thus indicate that these species had been overhunted.

Nevertheless, the proportion of the sustainable harvest estimates known to be removed by hunters (OH/MSH) was a generally poor predictor of the density differentials between the hunted and unhunted sites surveyed. There are several reasons why model predictions from village kill profiles could be at odds with such density estimates. First, any two forest sites are bound to support slightly different baseline vertebrate abundances even if they are comparable in terms of structure and floristic composition and only 12–16 km apart. Second, the low observed harvest rates of some species simply reflected low local availability – resulting from small residual populations that had already been depleted prior to this study – rather than hunter preference. This appears to be the case of at least giant armadillos and both species of curassow. Finally, the number of fatally wounded individuals that could not be retrieved by hunters (and therefore missing from village samples) was not taken into account in this study and this can range from 10% (Townsend 2000) to over 40% of all retrieved kills (C. Peres, unpubl. data).

The collection of *Geochelone* tortoises, which is a crucial part of ceremonial feasts at A'Ukre, is an additional issue of concern. Because of their low metabolic rates and ease of capture once they are detected, these heterotherms can be conveniently brought into the village and kept alive for up to several months until they were roasted in large numbers in an open bonfire marking the 'tortoise feast'. Such ritual events are an integral part of Kayapó village culture and provide the motivation for long hunting treks into rarely exploited parts of the village territory, Yet *Geochelone* populations appear to be declining even in distant hunting grounds accessed from seasonal camps used during hunting treks. For example, Jerozolimski (2004, unpubl. Thesis) monitored the rate of tortoise captures per unit effort (CPUE) during hunting expeditions by A'Ukre hunters in four consecutive years and estimated a decline in successful captures from 3.37 to 2.20 tortoises per 100 h of hunter search time between 1999 and 2002. Assuming a negative linear slope for the annual CPUE rate over this period ($\beta = -0.384$, $r^2 = 96.8\%$, $N = 4$), we conclude that an additional search time of 38 h and 24 min is required each year in order to capture every additional tortoise.

Tortoises collected near A'Ukre were also considerably smaller (mean = 2.8 kg) than those collected during hunting treks into more remote areas (mean = 5.0 kg; Nascimento 1999), suggesting directional change of body size in a heavily harvested population resulting from greater adult mortality in the severely depleted inner catchment. This illustrates the rather severe local depletion rates for game species in the peripheral A'Ukre catchment even for wide ranging species such as forest tortoises which exhibit high dispersal rates and little site-fidelity in terms of their year-round home range (A. Jerozolimski, pers. comm.).

Although several studies have concluded that large neotropical forest gamebirds such as cracids are easily overhunted because of their slow rate of population recovery (Silva and Strahl, 1991; Begazo and Bodmer 1998), cracids accounted for 68.7% of the total avian biomass harvested and only one of the five genera occurring in the Kayapó Reserve appeared to be overexploited (although chachalacas, *Ortalis motmot*, were never taken). The offtake rate of red-throated piping guans (*Aburria pipile*) was slightly higher than the maximum sustainable harvest estimated for this species on the basis of observed densities, but those of both sympatric common guans (*Penelope superciliaris* and *P. pileata*) and both curassow species (*Mitu tuberosa* and *Crax fasciolata*) were considerably lower. The model indication that curassows had not been harvested unsustainably should, however, be interpreted with caution. These large cracids can serve as good indicators of hunting pressure (Silva and Strahl 1991; Strahl and Grajal 1991), and the small number of kills recorded can also mean that curassows had already been severely depleted. This is consistent with the fact that hunters rarely bypassed an opportunity to kill a curassow, whereas this was often the case with smaller cracids and other gamebirds.

The Robinson and Redford model showed some limitations in evaluating hunting sustainability but successfully pinpointed those species that had been overharvested. In any case, widely extrapolated density and $r_{\max}$ estimates based on populations in optimal habitat conditions or captive animals can result in severe overestimates of potential game production. Even when local density estimates of game species can be incorporated into the model, it is difficult to evaluate the impact of hunting on those species that were not diagnosed as unsustainably harvested (Slade et al. 1998). The short-term nature of this study accounts for further limitations in that residual game stocks may be a legacy of the history of hunting in the recent past when the number of villagers at A'Ukre was 250 strong, or almost twice the village size during the study. In fact, although the proximate cause of the village sub-division in 1995 was an acrimonious dispute between two influential, kinship-based groups of households, it could be argued that this fission – which resulted in the resettlement of approximately half of the village – was instigated by local game scarcity resulting from excessive numbers of consumers (B. Zimmerman, pers. comm.). The harvest rate is also not a static constant and is expected to fluctuate over time as a result of changes in prey availability and consumer population size (Vickers 1988; Winterhalder et al. 1988; Robinson and Redford 1994). Harvest models should thus be refined with considerations of such spatial and temporal dimensions.

Conclusions

The contiguous area 13 million ha of the Kayapó reserve of southeastern Pará, and the upper Xingú Indian reserves of northern Mato Grosso (Figure 1) is larger than that of any strictly protected area in the humid tropics, and has become the main deterrent to frontier expansion in the southeastern Amazon (Peres and Zimmerman 2001). The aspirations of different Kayapó villages have been strengthened through collaborative projects with conservation organizations seeking to safeguard the long-term integrity of their natural resources (Zimmerman et al. 2001). However, it remains unclear to what extent extractive practices such as game hunting will be sustainable in the long run if the village size and village density increases, and the cost-benefit ratio of resettling a village increases and villages become increasingly sedentary due to investments in local infrastructure, and access to schools and medical services.

Subsistence hunting by the Kayapó of A'Ukre has already depressed local game stocks, although observed landscape-scale patterns of game acquisition can be considered to be sustainable for the time being provided that village catchment areas do not overlap and can be expanded (cf. Hill et al. 1997; Emídio-Silva 1998). The severe local depletion of tapirs and white-lipped peccaries is perhaps the most serious subsistence problem currently faced by A'Ukre villagers, but for now this is compensated by the vast extent of pristine forest ecosystems around the village catchment, most of which remains unhunted and faunally intact. A possible solution to dilute local hunting pressure at A'Ukre would be to increase the village catchment area by increasing the length and utilization of hunting trails on the western bank of the river, a forest area that was rarely hunted. Another solution would be to increase the harvest of locally undesirable species (if their poor acceptance can be overcome) such as brocket deer (*Mazama* spp.), collared peccaries and agoutis, which were harvested at levels well below those predicted to be sustainable. The importance of a source-sink population structure for key target species can be illustrated by the high yields sustained under conditions of low village density, which may be the best available option in the absence of enforceable game management policy.

Measuring the regional scale sustainability of subsistence hunting is critical to wildlife conservation in Amazonian forests. Indian reserves represent over one fifth of the Brazilian Amazon or 52% of the total area under any form of non-private protection, and comprise large and often strategically placed wildlands containing relatively undisturbed forests (Peres 1994). Natural resources management can only link biodiversity conservation to the needs of local people if crucial resources are not overexploited to the point of collapse. The perceived value of the forest to indigenous people can therefore become considerably reduced as game populations are overexploited if not eventually driven to local extinction. This will also strengthen the joint cause of conservationists and aborigine-rights advocacy groups for maintaining large Indian Lands in Amazonian forests against encroachment by more insidious agricultural interests that often see this alliance as a conspiracy to thwart development. Further studies on the impacts of extractive activities are required to implement appropriate wildlife management programs to ensure the preservation of both biological and cultural diversity in Amazonia.

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References

Alvard M. 1994. Conservation by native people: prey choice in a depleted habitat. Human Nature 5: 127–154.

Baider C. 2000. Demografia e ecologia de dispersão de frutos de *Bertholletia excelsa* Humb, and Bonpl. (Lecythidaceae) em Castanhais Silvestres da Amazônia Oriental. PhD thesis, Universidade de São Paulo.

Begazo A.J. and Bodmer R.E. 1998. Use and conservation of cracidae (Aves: Galliformes) in the Peruvian Amazon. Oryx 32: 301–309.

Bodmer R.E. 1994. Managing wildlife with local communities: the case of the Reserva Comunal Tamshiyacu-Tahuayo. In: Western D., Wright M. and Strum S. (eds), Natural Connections. Island Press, Washington DC, pp. 113–134.

Bodmer R.E. 1995. Managing Amazonian wildlife: biological correlates of game choice by detribalized hunters. Ecological Applications 5: 872–877.

Bodmer R.E., Eisenberg J.F. and Redford K.H. 1997. Hunting and the likelihood of extinction of Amazonian mammals. Conservation Biology 11: 460–466.

Brasil D.N.P.M. 1974. Projeto RADAM. Folha SB 22 Araguaia e parte da folha SC 22 Tocantins. IBGE. RJ. Vol 4.

Buckland S.T., Anderson D.R., Burnham K.P. and Laake J.L. 1993. Distance Sampling: Estimating Abundance of Biological Populations. Chapman and Hall, London.

Emídio-Silva C. 1998. A caça de subsistência praticada pelos Índios Parakanã (Sudeste do Pará): características e sustentabilidade. MSc thesis, Universidade Federal do Pará, Belémf.

Fa J.E. and Peres C.A. 2001. Game vertebrate extraction in African and Neotropical forests: an intercontinental comparison. In: Reynolds J., Mace G., Robinson J.G. and Redford K. (eds), Conservation of Exploited Species. Cambridge University Press, Cambridge.

Hames R.B. and Vickers W.T. 1982. Optimal diet breadth theory as a model to explain variability in Amazonian hunting. American Ethnologist 9: 358–378.

Hill K., Padwe J., Bejyvagi C., Bepurangi A., Jakugi F., Tykuarangi R. and Tykuarangi T. 1997. Impact of hunting on large vertebrates in the Mbaracayu reserve, Paraguay. Conservation Biology 11: 1339–1353.

ISA. 2004. Amazônia Brasileira 2004. Map and database produced by the Instituto Socioambiental. www.socioambiental.org. Accessed on 30 August 2004.

Jerozolimski A. and Peres CA. 2003. Bringing home the biggest bacon: a cross-site analysis of the structure of hunter-kill profiles in Neotropical forests. Biological Conservation 111: 415–425.

Laake J.L., Buckland S., Anderson D. and Burnham K. 1994. Distance User's Guide V2.1. Colorado Cooperative Fish and Wildlife Research Unit. Colorado State University, Fort Collins.

Leung W. and Flores M. 1961. Food Composition Table for Use in Latin America. INCAP-ICNND, Bethesda, MD.

Mena V.P., Stallings J.R., Regalado B.J. and Cueva L.R. 2000. The sustainability of current hunting practices by the Huaorani. In: Robinson J.G. and Bennett E.L. (eds), Hunting for Subsistence in Tropical Forests. Columbia University Press, New York, pp. 57–78.

Milner-Gulland E.J., Bennett E.L., Abernethy K., Bakarr M., Bodmer R., Brashares J., Cowlishaw G., Elkan P., Eves H., Fa J., Peres C.A., Roberts C., Robinson J., Rowcliffe M. and Wilkie D. 2003. Wild meat – the bigger picture. Trends in Ecology and Evolution 18: 351–357.

Morsello C. 2002. Market integration and sustainability in Amazonian indigenous livelihoods: the case of the Kayapó. PhD Thesis, University of East Anglia, Norwich.

Nascimento H.S. 1999. Hunting sustainability by the Kayapó Indians of A'Ukre, eastern Brazilian Amazonia. MSc Thesis, University of East Anglia, Norwich.

Novaro A.J., Redford K.H. and Bodmer R.E. 2000. Effect of hunting in source-sink systems in the neotropics. Conservation Biology 14: 713–721.

Peres C.A. 1990. Effects of hunting on western Amazonian primate communities. Biological Conservation 54: 47–59.

Peres C.A. 1994. Indigenous reserves and nature conservation in Amazonian forests. Conservation Biology 8: 586–588.

Peres C.A. 1996. Population status of white-lipped and collared peccaries in hunted and unhunted Amazonian forests. Biological Conservation 77: 115–123.

Peres C.A. 1999. General guidelines for standardizing line-transect surveys of tropical forest primates. Neotropical Primates 7: 11–16.

Peres C.A. 2000a. Effects of subsistence hunting on vertebrate community structure in Amazonian forests. Conservation Biology 14: 240–253.

Peres C.A. 2000b. Evaluating the sustainability of subsistence hunting at multiple Amazonian forest sites. In: Robinson J.G. and Bennett E.L. (eds), Hunting for Sustainability in Tropical Forests. Columbia University Press, New York, pp. 31–56.

Peres C.A. 2001. Synergistic effects of subsistence hunting and habitat fragmentation on Amazonian forest vertebrates. Conservation Biology 15: 1490–1505.

Peres C.A. and Lake I.R. 2003. Extent of nontimber resource extraction in tropical forests: accessibility to game vertebrates by hunters in the Amazon basin. Conservation Biology 17: 521–535.

Peres C.A. and Zimmerman B. 2001. Perils in Parks or Parks in Peril? Reconciling conservation in Amazonian reserves with and without use Conservation Biology 15: 793–797.

Redford K.H. and Robinson J.G. 1987. The game of choice: patterns of Indian and colonist hunting in the Neotropics. American Anthropologist 89: 650–667.

Robinson J.G. and Redford K.H. 1986. Intrinsic rate of natural increase in neotropical forest mammals: relationship to phylogeny and diet. Oecologia 68: 516–520.

Robinson J.G. and Redford K.H. 1991. Sustainable harvest of neotropical forest mammals. In: Robinson J.G. and Redford K.H. (eds), Neotropical Wildlife Use and Conservation. University of Chicago Press, Chicago, pp. 415–429.

Robinson J.G. and Redford K.H. 1994. Measuring the sustainability of hunting in tropical forests. Oryx 28: 249–256.

Salas L.A. and Kim J.B. 2002. Spatial factors and stochasticity in the evaluation of sustainable hunting of tapirs. Conservation Biology 16: 86–96.

Salm R. 2002. The ecology of large arborescent palms, *Attalea maripa* and *Astrocaryum aculeatum* in a seasonally dry Amazonian forest. MSc Thesis, University of East Anglia, Norwich.

Schwartzman S., Moreira A. and Nepstad D. 2000. Rethinking tropical forest conservation: perils in parks. Conservation Biology 14: 1351–1357.

Silva J. and Strahl S. 1991. Human impact on populations of chachalacas, guans and curassows (Galliformes: Cracidae) in Venezuela. In: Robinson J.G. and Redford K.H. (eds), Neotropical Wildlife Use and Conservation. University of Chicago Press, Chicago, pp. 37–52.

Slade N.A., Gomulkiewicz R. and Alexander H.M. 1998. Alternatives to Robinson and Redford's method of assessing overharvest from incomplete demographic data. Conservation Biology 12: 148–155.

Souza-Mazurek R.R., Pedrinho T., Feliciano X., Hilario W., Geroncio S. and Marcelo E. 2000. Subsistence hunting among the Waimiri Atroari Indians in central Amazonia. Brazil Biodiversity and Conservation 9: 579–596.

Strahl S.D. and Grajal A. 1991. Conservation of large avian frugivores and the management of neotropical protected areas. Oryx 25: 50–55.

Terborgh J. 1999. Requiem for Nature. Island Press, Washington, D.C.

Terborgh J. 2000. The fate of tropical forests: a matter of stewardship. Conservation Biology 14: 1358–1361.

Townsend W.R. 2000. The sustainability of subsistence hunting by the Siriono Indians of Bolivia. In: Robinson J.G. and Bennett E.L. (eds), Hunting for Sustainability in Tropical Forests. Columbia University Press.

Vickers W.T. 1984. The faunal components of lowland South America hunting kill. Interciencia 9: 366–376.

Vickers W.T. 1988. Game depletion hypothesis of Amazonian adaptation: data from a native community. Science 239: 1521–1522.

Vidal L.B. 1977. Morte e vida de uma sociedade indígena brasileira: os Kayapó-Xikrin do Rio Cateté. São Paulo, HucitecEditora da Universidade de São Paulo.

Whitesides G.H., Oates J.F., Green S.M. and Kluberdanz R.P. 1988. Estimating primate densities from transect in a west African rain forest: a comparison of techniques. Journal of Animal Ecology 57: 345–367.

WHO (United Nations Food and Agricultural Organization and World Health Organization) 1973. Energy and protein requirements: report of a joint FAO/WHO Ad Hoc Expert Committee. WHO Technical Report, Series No. 522, WHO, Geneva.

Winterhalder B., Baillargeon W., Cappelletto F., Daniel I. and Prescott C. 1988. The population ecology of hunter-gatheres and their prey. Journal of Anthropological Archaeology 7: 289–328.
Zimmerman B., Peres C.A., Malcolm J. and Turner T. 2001. Conservation and development alliances with the Kayapó of south-eastern Amazonia, a tropical forest indigenous peoples. Environmental Conservation 28: 10–22.

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Genetic diversity in traditional Ethiopian highland maize accessions assessed by AFLP markers and morphological traits

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Abstract. In the highland regions of Ethiopia the heterogeneity of the land, the climate, and soil favors the presence of a large number of landraces. We analyzed a representative sample of 62 traditional Ethiopian highland maize accessions, using amplified fragment length polymorphism (AFLP®) markers and morphological traits with the aim to group the accessions based on the their genetic profiles and morphological traits, to study agroecological variation and to assess the level of correlation between phenotypic and genetic distances. Eight *Eco*RI/*Mse*I primer combinations and 15 morphological traits were used. The accessions varied significantly for all of the measured morphological traits. Of a total of 650 AFLP markers that were scored, 89.5% were polymorphic. Pair-wise genetic distance estimates based on AFLP data revealed dissimilarity coefficients ranging from 0.32 to 0.69 (mean of 0.57). Cluster analysis of the AFLP data grouped most accessions collected from the Northern highlands into one major cluster. It, however, failed to separate the Western and Southern accessions into different clusters. Regardless of the large variation in environmental conditions between agroecologies, only 9% of the total genetic variation was found between agroecologies, whereas 91% was found within agroecologies in Ethiopia. This finding may be explained by long distance seed exchange, continuous seed introduction and gene flow between agroecologies. The relationship between morphological and AFLP-based distances was significant and positive. Based on this study, three groups of highland accessions, with distinctive genetic profiles and morphological traits were identified. This information will be useful for further collections and conservation of the unique diversity included in the highland maize landraces of Ethiopia.

Introduction

Maize was first introduced in Ethiopia in the 16th or 17th century (Hafnagel 1961). Since its introduction, it has gained importance as a food and feed crop. Currently, it is the second most important crop, exceeded only by teff [*Eragrostis tef* (Zucc) Trotter] in terms of production area. However, it exceeds all other cereals in terms of annual production and yield per ha (EARO 2000). Maize is one of the cereals that provide most of the calorie requirements in the traditional Ethiopian diet. It is prepared and used as unleavened bread, roasted and boiled green ears, parched mature grain porridge and in local drinks like 'tella', 'borde' and 'areke' (Mulatu et al. 1992). Apart from these uses, maize leaves are fed to animals, while dry stalks are used as fuel and for the construction of fences and huts.

Ethiopia is a diverse country in terms of altitude, temperature, rainfall and soil types. Such diversity is apparent within even a short distance in a given locality. Diverse environments result in the presence of diverse vegetation, crop species and varieties in farmers' fields in most parts of the country (Vavilov 1951). Maize varieties that are used in the highland regions of Ethiopia are well adapted, but low-yielding open-pollinating varieties developed by local farmers. Many of these varieties resulted from centuries of planting, harvesting and selection. The highland maize varieties may be grouped into a number of completely or partially isolated populations, which may each be adapted to different highland conditions. Unfortunately, formal breeding programs have had little success in developing improved varieties for the diverse agroecological conditions in the highlands of Ethiopia. In the past decade, only two improved open-pollinating maize varieties were developed for the highland zone (Twumasi-Afriyie et al. 2001).

Effective plant breeding and crop improvement programs depend on the availability of genetic diversity. Landraces are usually the major source of variation for new breeding programs. To assess the genetic diversity present in Ethiopian highland maize accessions, seed samples were collected from 287 highland locations of Ethiopia (Twumasi-Afriyie et al. 2001). A recent field study revealed that these accessions are highly variable for morphological and agronomic characteristics (unpublished results). However, morphological variation does not always reflect real genetic variation because of genotype x environment interaction and the largely unknown genetic control of polygenic morphological and agronomic traits (Smith and Smith 1992).

Molecular markers can be used to study the genetic diversity and genetic relationships among maize accessions directly at the DNA level. Amplified fragment length polymorphism (AFLP®) markers (Vos et al. 1995) have gained importance in crop genetic analyses, mainly due to the high multiplex ratio of this marker system. AFLP markers have been extensively used to study genetic diversity in maize inbred lines (Lubberstedt et al. 2000; Vuylsteke et al. 2000). Although the technique is relatively simple and rapid, the large number of individual plants that need to be processed may limit AFLP analysis of cross-pollinating species like maize. One approach to overcome this limitation is to analyze one, or several, bulked samples per accession, rather than individual plants. Kolliker et al. (2001) demonstrated that bulking equal amounts of leaf material before DNA extraction is an effective approach to produce representative AFLP marker profiles in white clover.

We report here on the results of a genetic diversity analysis of Ethiopian highland maize accessions based on morphological traits and AFLP markers. Our objectives were (i) to assess the amount of genetic diversity and relationships among the highland maize accessions, (ii) to understand the distribution of genetic variation within and among agroecologies and (iii) to assess the correlation between distance estimates based on morphological traits and molecular markers.

Materials and methods

Field evaluation and data recording

A total of 62 maize accessions collected from the Northern, Southern and Western highlands of Ethiopia were used in this study (Table 1). The accessions were grown at Alemaya University in Ethiopia during the 2002 main cropping season in a randomized complete block design with three replications. Each accession was grown in two row plots. Each row had 25 plants, which constitute 44,444 plants per hectare recommended for the testing site. From each accession, 20 plants were selected at random to record 15 morphological traits (Table 2).

DNA extraction

Remnant seeds of the 62 maize accessions were grown in the greenhouse in 2003. For each of the 62 accessions, genomic DNA was extracted from leaf discs, harvested from 15 three-week old plants (one 10-mm leaf disc per plant). For two accessions, individual DNA samples were also isolated from the 15 plants used for bulked sampling. DNA was extracted using the QIAGEN DNeasy plant Mini Kit, (QIAGEN, GmbH, Hilden) with minor modifications to allow homogenization using the FP-120 FastPrep instrument (QBiogene, Carlsbad, CA, USA; Myburg et al. 2001). DNA quantity and quality was determined by agarose gel electrophoresis using lambda DNA as concentration standard.

AFLP analysis

AFLP template preparation was performed using AFLP template preparation kits from LI-COR Biosciences (LI-COR, Lincoln, NE, USA) according to the manufacturers' instructions, except that 10 μl diluted R/L mix, 2.0 mM $MgCl_2$ and 1.0 U Taq polymerase were used in the preamplification step. Polymerase chain reactions (PCRs) were performed using a BIO-RAD iCycler (Version 3.021, BIO-RAD Laboratories, inc). The preselective amplification cycle profile was as follows: incubation for 10 s at 72 °C, followed by 30 cycles of denaturation for 10 s at 94 °C, annealing for 30 s at 56 °C, and extension for 1 min at 72 °C with a 1 s per cycle increasing extension time. Selective amplification was performed on 1:20 diluted (in SABAX water) preselective

Table 1. Traditional Ethiopian highland maize accessions used in the study.

No.	Accession	Collection site	Major agroecology	Altitude[a]
1	Ad-1-01	Gonder	North	2360
2	Ad-1-03	Armachew	North	2771
3	Ad-1-9-6	Adi Arkay	North	1837
4	Ad-1-9-8	Adi Arkay	North	1741
5	Ad-1-1-16	Armachew	North	2527
6	Ad-1-1-17	Armachew	North	1850
7	Ad-1-2-20	Armachew	North	1765
8	Ad-1-3-21	Armachew	North	2354
9	Ad-1-4-26	Dembia	North	2133
10	Ad-1-3-32	Dembia	North	2100
11	Ad-1-3-35	Chilga	North	1900
12	Ad-3-6-40	Gondar	North	2105
13	Ad-3-6-42	Fogera	North	1930
14	Ad-3-7-45	Farta	North	2400
15	Ad-3-7-46	Farta	North	2674
16	Ad-3-7-50	Este	North	2728
17	Ad-4-11–55	Sera	North	2544
18	Ad-5-13–59	Yilmana	North	2266
19	Ad-5-13–60	Yilmana	North	2300
20	Ad-5-13–61	Yilmana	North	2432
21	Ad-5-14–64	HuletEynes	North	1980
22	Ad-5-16–67	HuletEynes	North	2512
23	Ad-5-17–69	GoneraSiso	North	2654
24	Ad-5-17-68	GoneraSiso	North	2651
25	Ad-5-17-70	GoneraSiso	North	2668
26	Ad-5-18-71	Debrework	North	2598
27	Ad-5-18-72	Enemay	North	2474
28	Ad-5-19-76	Awabel	North	2554
29	Ad-5-21-79	Gozamin	North	2529
30	Ad-4-24-81	Gozamin	North	2383
31	Ad-6-28-89	Quarit	North	2000
32	Ad-6-28-92	Sekela	North	2500
33	Ad-6-28-94	Awi	North	1580
34	Ad-6-26-96	Awi	North	1714
35	Ad-1-31-101	Banja Awi	North	2200
36	Aw-03	Merka	South	1950
37	Aw-10	Agere Mariam	South	2180
38	Aw-13	Kofele	South	2500
39	Aw-17	Hitosa	South	2230
40	Aw-18	Boloso	South	1950
41	Aw-21	Arero	South	2160
42	Aw-25	Agere Mariam	South	2290
43	Aw-29	Agere Mariam	South	2200
44	Aw-33	Tiyo	South	2300
45	Aw-35	Tiyo	South	2515
46	Aw-41	Agere Mariam	South	2200
47	Aw-44	Ejere	South	2300
48	Aw-54	Merka	South	2145
49	Baw-01	Wolemra	West	2260

Table 1. Continued.

No.	Accession	Collection site	Major agroecology	Altitude[a]
50	Baw-10	Wolemra	West	1800
51	Baw-11	Dendi	West	2290
52	Baw-12	Ambo	West	2270
53	Baw-13	Weliso	West	2300
54	Baw-14	Jeldu	West	2010
55	Baw-15	Becho	West	2225
56	Baw-17	Sululta	West	2350
57	Baw-18	Sululta	West	2350
58	Baw-20	Ambo	West	2280
59	Baw-22	Dega	West	2250
60	Baw-28	Bedele	West	1880
61	Baw-30	Ambo	West	2305
62	Baw-33	Limu	West	2080

[a] Meter above sea levels.

Table 2. Summary statistics of the agro-morphological characters measured in 62 traditional Ethiopian highland maize accessions.

Characters	Mean	St. Dev.	Minimum	Maximum
Days to tasseling	65.1	3.2	51.5	76.0
Days to silking	71.5	3.0	58.0	80.5
Plant height (cm)	217.8	14.4	161.0	288.0
Ear height (cm)	125.9	26.3	74.0	227.5
Leaf length (cm)	71.3	9.1	51.8	100.8
Leaf width (cm)	9.1	1.0	6.4	12.7
Number of leaves	6.1	0.3	5.2	6.6
Foliage rating	6.2	0.9	4	7.0
Days to maturity	143.8	7.8	108	167.5
Ear diameter (cm)	3.9	0.2	3.3	4.6
Ear length (cm)	18.1	2.2	14.5	22.7
Rows per ear (no)	10.7	1.5	7	13.9
Kernels per row	27.42	3.6	18	36.9
1000 seed weight	295.8	41.3	229	410.0
Yield (kg ha$^{-1)}$	2645.4	195.4	1305.2	4282.3

amplification products with the following cycling profile: 13 cycles of 2 min at 94 °C, 30 s at 65 °C (reduced by 0.7 °C per cycle), and 1 min at 72 °C; followed by 20 cycles of 10 s at 94 °C, 30 s at 56 °C, and 1 min (extended 1 s per cycle) at 72 °C. The selective amplification primer pairs all had three-nucleotide extensions at the 3′ end. In all reactions only the *Eco*RI primers were 5′ labelled with infrared dyes (IRDye 700 or IRDye 800, LI-COR). Initially, eight accessions were chosen to test the amplification successes of different primer combinations. The polymorphism rates and the total number of scorable figments were evaluated in these eight accessions with 32 primer combinations. Eight primer combinations with the highest polymorphism rates and large numbers of clearly scorable fragments were selected to analyze the full set of 62 accessions.

Gel electrophoresis and scoring

An equal volume of loading solution (LI-COR) was added to each selective amplification reaction. Samples were denatured at 95 °C for 3 min and placed on ice for 10 min before loading. A volume of 0.8 μl was loaded with an 8-channel syringe (Hamilton, Reno, Nevada) onto 25-cm 8% Long Ranger gels (BMA, Rockland, ME, USA). Electrophoresis and detection of AFLP fragments were performed on LI-COR IR^2 (model 4200S) automated DNA analyzers. The electrophoresis parameters were set to 1500 V, 40 mA, 40 W, 50 °C, and a scan speed of three. The run-time was set to 4 h and gel images were saved as TIF files for further analysis. The gel images were scored using a binary scoring system that recorded the presence and absence of bands as 1 and 0, respectively. Semi-automated scoring was performed with SAGA$^{\mathrm{MX}}$ (Version 3.2, LI-COR) and followed by manual editing to make adjustments to the automated score where necessary. A locus was scored as polymorphic when the frequency of the most common allele (band present or absent) was less than 0.97 (absent or present in at least two individuals). Bands with the same mobility were considered as identical products (Waugh et al. 1997), receiving equal values regardless of their fluorescence intensity.

Data analysis

Morphological variation

Analysis of variance was performed for all measured traits in order to test the significance of variation among accessions. The standardized mean values (mean of each trait was subtracted from the data values and the result divided by the standard deviation) were used to perform principal component and cluster analyses using NCSS 2000 software (Jerry 2000). To group the accessions based on morphological similarities, cluster analysis was conducted on the Euclidean distance matrix with the unweighted pair group method based on arithmetic averages (UPGMA).

AFLP analysis

The binary data were exported into Microsoft Excel and formatted for use in the NCSS statistical software package. The average Polymorphic Information Content (PIC) for dominant markers was calculated according to Riek et al. (2001) by the following formula:

$$PIC = 1 - \left\lfloor f^2 + \left(1 - f^2\right)^2 \right\rfloor$$

where f is the frequency of the marker in the data set.

Cluster analysis and partitioning of variation

Genetic similarity between accessions was calculated according to Nei and Li (1979) using the formula $\mathbf{S}_{ij} = \frac{2a}{(2a+b+c)}$, where $\mathbf{S}_{ij}$ is the similarity between two accessions i and j, a is the number of bands present in both i and j, b is the number of bands present in i and absent in j and c is the number of bands present in j and absent i. This formula excludes bands absent in both individuals, which cannot be necessarily being attributed to a common cause (Kolliker et al. 2001). Genetic dissimilarity was calculated as $1-\mathbf{S}_{ij}$. Cluster analysis was performed on the Nei and Li (1979) genetic dissimilarity matrix using Ward's minimum variance method (Ward 1963). The Ward method was found to be more suitable for genetic diversity analysis of open-pollinating maize varieties (Warburton et al. 2002). Genetic dissimilarity between accessions was also calculated based on Euclidean distances (Sneath and Sokal 1973), which allowed us to estimate genetic variance within and among agroecologies using the formula described by van Eeuwijk and Baril (2001).

Correlation between dissimilarity matrices

The correlation between the Euclidean distance matrix based on morphology and the Ward distance matrix obtained with AFLP data was tested for significance using a Mantel test (Mantel 1967) and 1000 permuted data sets.

Results

Morphological variation

The analysis of variance revealed highly significant differences ($p = 0.01$; results not shown) among accessions for all of the traits suggesting that there was a high degree of phenotypic diversity among the accessions (Table 2). Grain yield, plant and ear height and days to maturity showed wide variation, while number of leaves, leaf width and ear diameter showed a narrow range of phenotypic variation (Table 2). The first four principal components (PCs), which had eigenvalue higher than one, explained a total of 71.8% of the phenotypic variation (Table 3). In the first PC (42.1%), the most important traits were plant and ear height, leaf length and days to tesseling and silking. Number of rows per ear also appears to be important in the first PC. In the second PC, which explained 12.6% of the total variation, predominant traits were ear traits (yield, ear length, ear diameter and kernels/row) and foliage rating. The third principal component, which accounted for 10.5% of the total variation, was dominated by characters such as number of leaves, ear diameter, yield and ear length, while days to maturity, leaf width and number of leaves were important delineating characters associated with the fourth principal component, which accounted for 6.7% of the total variation.

Genetic dissimilarity and cluster analysis based on morphological data

The average dissimilarity coefficients among accessions based on morphology ranged from 0.1 for two closely related accessions (accession no. 1 and accession no. 20) to 0.68 for distantly related accessions (accession no. 1 and accession no. 4) all collected from the Northern agroecology (Table 1) with an average dissimilarity of 0.3 (data not shown). The dendrogram that resulted from the standardized morphological data shows four clusters (Figure 1). The first cluster contained 36 accessions, most collected from the Northern agroecology. Short plants and early maturity characterized accessions in this group. The second cluster contained 12 accessions, of which 11 were collected from the Western and one from the Southern agroecology. Accessions in this group had tall plants and ear heights. This group also had the maximum yield per ha. The third cluster contained only two accessions with dissimilarity values of 0.4. The fourth cluster contained 12 accessions collected from all three agroecologies.

Detection limit of bulked AFLP and marker polymorphism

We tested the detection threshold of AFLP bands in two 15-plant bulks by analyzing individuals and their bulked leaf samples separately. A total of 120 polymorphic markers were scored in the two bulked samples and 15 individual

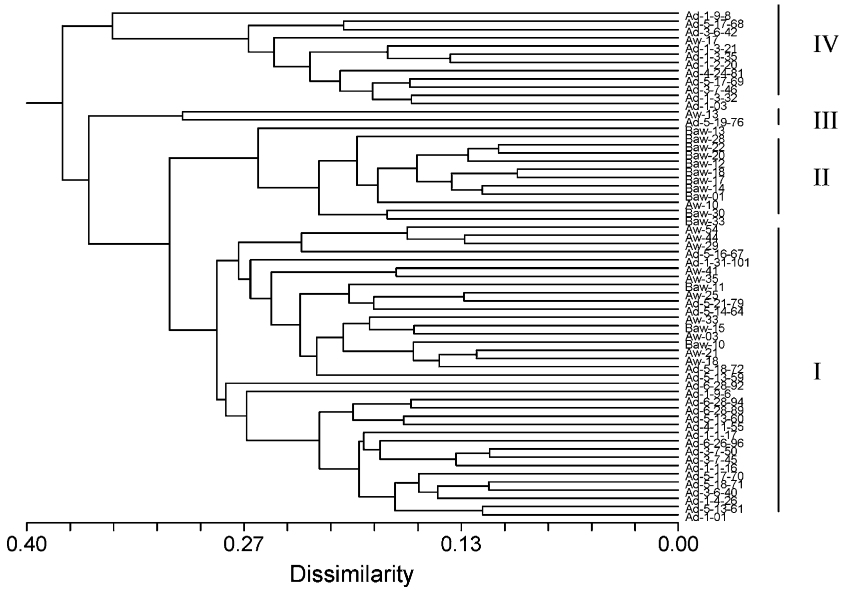

Figure 1. Dendrogram of traditional Ethiopian highland maize accessions derived by UPGMA from the dissimilarity matrix of the morphological data.

Table 3. Eigenvectors, eigenvalues, individual and cumulative percentage of variation explained by the first four principal components (PC) after assessing morphological traits in 62 traditional Ethiopian highland maize accessions.

Characters	PC1	PC2	PC3	PC4
Days to tasseling	*−0.32*	−0.20	0.03	−0.23
Days to silking	*−0.32*	−0.19	0.00	−0.21
Plant height (cm)	*−0.37*	−0.09	−0.06	0.08
Ear height (cm)	*−0.36*	−0.09	−0.08	0.12
Leaf length (cm)	*−0.34*	−0.06	−0.01	−0.13
Leaf width (cm)	−0.24	0.10	−0.13	*−0.40*
Number of leaves	−0.06	0.03	*0.59*	*−0.31*
Foliage rating	−0.15	*0.49*	0.17	−0.22
Days to maturity	−0.15	0.02	0.29	*0.67*
Ear diameter	−0.21	*0.39*	*−0.37*	0.11
Ear length (cm)	−0.22	*0.39*	*−0.34*	0.07
Rows per ear	*−0.33*	−0.10	0.14	0.14
Kernels per row	−0.14	*0.35*	0.21	0.23
1000 seed weight	−0.28	−0.14	0.27	0.13
Yield (kg ha−1)	0.09	*0.44*	*0.36*	−0.12
Eigenvalue	6.31	1.88	1.55	1.00
Individual percent	42.05	12.57	10.51	6.67
Accumulated variation %	42.05	54.61	65.12	71.79

Table 4. Relationships between AFLP band frequencies in individual plants and representation in two bulks of 15 individuals based on the average of three primer pair combinations.

Band frequency in individual plants	% Bands represented in bulks of accessions		Average of the two accessions
	'Baw-01'	'Ad-1-03'	
Up to7%	0.58	0.46	0.52
7–20%	0.82	0.83	0.83
21–50%	0.85	0.92	0.89
50–75%	100	100	100
75–100%	100	100	100
Over all mean (%)	90	89	89.5

samples (15 individual per accession) using three selective primer combinations (Table 4). As shown in Table 4, bands, which are only present in single plant (7%), are present in bulks of accession 'Baw-01' (58%), and 'Ad-1-03' (46%). High proportion (83%) of bands which are only present in less than 20% (3 out of 15) of the individual plants were present in bulks across the two accessions. However, all bands that are shared by more than 50% of the individual plants were represented in bulked samples in both accessions across the three primer pair combinations (Table 4). As an example, Figure 2 shows the AFLP profiles generated from bulked leaf samples demonstrated that most of the bands present in individual plants were present in AFLP profiles from bulked leaf samples.

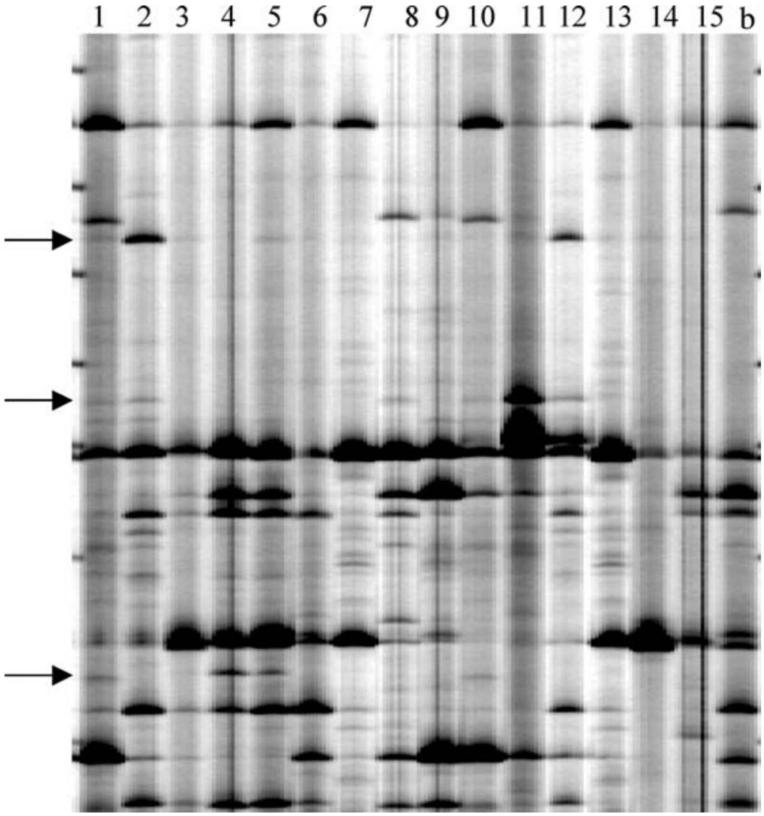

Figure 2. An example of the LI-COR AFLP image generated using E-AAC/M-CGG primer combinations showing banding patterns of 15 individuals (1 – 15) and their bulked leaf samples (b). A molecular marker is indicated at the beginning and at the end of the gel. Arrows shows examples of bands present in individuals and absent in bulked samples.

To assess the genetic diversity of the 62 highland maize accessions, a total of 650 AFLP bands with fragment sizes ranging from 52 to 720 bp were generated using eight selective AFLP primer pair combinations. Of these, 89.5% were polymorphic among the 62 accessions (Table 5). The number of polymorphic bands per primer combination ranged from 56 to 98 with an average number of 72.8 (Table 5). PIC values for primer enzyme combinations ranged from 0.279 to 0.370, with an overall mean of 0.325.

Genetic dissimilarity and cluster analysis based on AFLP data

In order to evaluate the molecular diversity of the 62 accessions, the pairwise genetic dissimilarity was calculated for the 1891 pairs of Ethiopian highland maize accessions using AFLP data (data not shown). Pairwise dissimilarity ranged from 0.32 (accession no. 1 and accessions no. 13) to 0.69 (accession no.

Table 5. Degree of polymorphism and average polymorphism information content for the eight AFLP primer combinations used to analyze the 62 Ethiopian maize accessions.

No.	Primer combination[a]	Total number of bands	Number of polymorphic bands	% of Polymorphic bands	PIC
1	E-AGG/ M-CAG	73	64	87.7	0.370
2	E-ACG/ M-CCG	72	66	91.6	0.320
3	E-ACA/ M-CGA	109	98	89.9	0.279
4	E-ACA/ M-CCC	86	76	88.0	0.321
5	E-AAC/ M-CAC	72	68	94.5	0.359
6	E-ACG/ M-CGG	74	68	91.8	0.321
7	E-AAC/ M-CCG	69	56	81	0.327
8	E-AAC/ M-CGG	95	86	90.5	0.300
	Total	650	582	NA	NA
	Mean	81.25	72.8	89.5	0.325

[a] E, *Eco*RI & M, *Mse*I.

1 and accession no. 40) with an overall mean of 0.57. More than 71% of the pairwise comparisons exhibited genetic dissimilarity higher than 0.5.

To visualize the genetic relationships among the accessions, a dendrogram was generated based on the dissimilarity matrix of the AFLP data using Ward minimum variance as clustering method (Figure 3). The dendrogram showed three major clusters. Cluster I consisted of 20 accessions, all collected from the Northern agroecology. Accessions in this cluster had short plant height

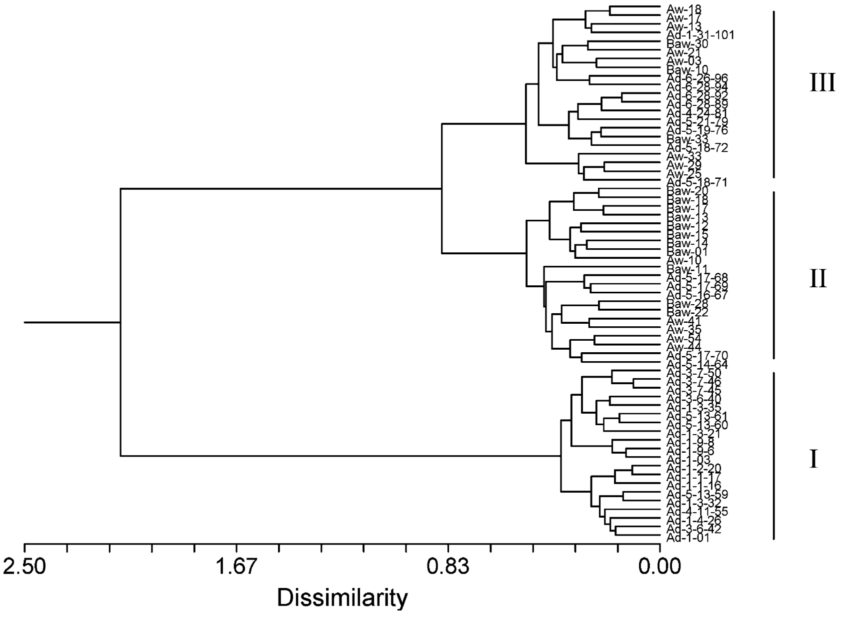

Figure 3. Dendrogram of traditional Ethiopian highland maize accessions derived by Ward' minimum variance method from the dissimilarity matrix of AFLP data.

(average 178.5 cm) and matured earlier (average 123 days) than any of the clusters. Cluster II consisted of 21 accessions collected from three agroecologies. Accessions in this cluster were tall plants (on average 220 cm) and they needed more than 150 days to reach maturity. The group also had the highest mean values for ear traits (18.2 cm in ear length, 30 kernels per row, 11 rows per ear and 3884 kg/ha in grain yield). Cluster III contained 21 accessions, characterized by tall and late maturing plants that had broad and long leaves. This cluster also had the lowest mean values for all of the ear traits.

Partitioning of genetic variation

Partitioning the total genetic variability using the analysis of distance method (van Eeuwijk and Baril 2001) revealed that 91% of the total variation was found within and the remaining 9% among agroecologies (Table 6) suggesting limited genetic differentiation among the agroecologies. Furthermore, partitioning of the within agroecology variation into different agroecologies, indicated that accessions collected from the Northern agroecology contributed 54.3% of the total variation. The Southern and the Western agroecologies contributed only 21.7 and 24% to the total variability, respectively (Table 6).

Correlation between dissimilarity matrices

In order to assess the relationships between distances derived from morphology and AFLP markers, a distance matrix was constructed for each assay and compared using the Mantel matrix correspondence test. This test demonstrated that there was a significant and positive correlation between the two distances matrices ($r = 0.39$; $p < 0.001$).

Discussion

Knowledge about genetic diversity and relationships among diverse germplasm is useful for plant breeders. It supports their decisions on the selection of

Table 6. Partitioning of the total genetic variation of traditional Ethiopian highland maize accessions into within and between agroecology variation.

Sources of variation	Number of accession	Variance component	Percentage of variation	Mean genetic distance
Total	62	10.0		0.57
Within	–	9.1	91.0	
Northern	35	4.9	54.3	0.57
Southern	13	1.0	21.7	0.43
Western	14	2.2	24.0	0.45
Among	–	0.9	9.0	

parents for crossing and is helpful to widen the genetic basis of breeding programs. A genetic improvement program has been initiated at Ambo, Ethiopia in collaboration with CIMMYT with the goal of producing improved maize cultivars for the highlands of Eastern African countries. To initiate the improvement effort, a basic understanding of the genetic diversity and relationships among the highland maize accessions was considered essential. We report here on the results of a genetic diversity analysis of 62 traditional Ethiopian highland maize accessions from different highlands of Ethiopia using molecular markers and morphological traits. This study allowed us to distinguish three groups of maize accessions with distinctive genetic profiles and morphological traits, which will be useful for breeding, collection and conservation strategies in the highlands of Ethiopia.

The 62 accessions represent genetic diversity in a much larger set of 287 accessions collected from different highland regions of Ethiopia. The broad range in the means of accessions for the various traits implies great potential for the development of improved open-pollinating varieties, inbred lines and hybrids for these regions. The wide range in days to maturity (108 – 186.5) for example, suggests flexibility for the development of cultivars for the various highlands of Ethiopia with different rainfall and length of growing season. The existence of broad morphological and agronomical diversity among the highland maize accessions is further substantiated by principal component analysis (Table 3), which indicated that the total variation was fairly distributed across all of the morphological and agronomical traits.

To determine the detection limits and suitability of bulked AFLP analysis for the measurement of genetic diversity in maize accessions, we compared the results of AFLP gel profiles from 15 individual plants and their bulked leaf samples. The AFLP patterns obtained from bulked leaf samples were highly representative of the AFLP patterns obtained from individual plants of the same accessions (Figure 2). Across the two accessions, 12 out of 120 bands (10%) present in at least one individual plant were absent in the bulked samples of the respective accession (Table 4). The detection limit found in this study varied somewhat among primer combinations. Some bands that appeared to be of low frequency (less than 3 out of 15) were detectable in bulked samples, while other present in higher frequency (up to 6 out of 15) were not detected in bulked samples. This observation was in agreement with the work of Kolliker et al. (2001), who reported that some bands that were present in individual white clover plants (a cross-pollinated crop) at a higher frequency (20 – 50%) were absent in bulked samples, whereas some bands present in individual plants at low frequency (less than 5%) were represented in bulked samples. The authors speculated that complex competition processes during PCR amplification in AFLP technique could be the reason for this.

Kolliker et al. (2001) who worked in white clover found 99% genetic similarity among three independently replicated bulked samples of the same white clover cultivar. In addition, Dubreuil et al. (1999) showed that bulking DNA from 15 plants was an effective approach for the study of genetic diversity in outbred maize populations. These authors showed that allele frequencies estimated within the populations through individual genotyping were highly correlated (up to 0.99) to those estimated through bulk genotyping. These results show that bulk sampling is highly reproducible and suggest that this approach can be used as a cost effective method for characterizing cross-pollinated crops.

As shown in Table 4, out of 120 polymorphic bands scored, only 12 fragments were absent from bulked samples across the two accessions. Eight of these bands (5 in accession 'Baw-01' and 3 in accession 'Ad-1-03', data not shown) were present below the threshold detection level (3/15). The failure to amplify such low frequency bands in bulked samples will slightly over estimate the genetic distance between accessions. However, the occurrence of these events was very low in our study (8/120) and would not have changed the distance estimate much. On average the marker profiles of bulked samples should be an accurate reflection of the allelic composition of the accession. Thus pooling leaf samples before DNA extraction is an effective means of producing representative profiles of individual plants. This allowed higher sample throughput during DNA extraction and minimized reagent cost for genetic diversity estimation among Ethiopian highland maize accessions.

The proportion of polymorphic bands (89.5%, Table 5) obtained in the present study is high compared to the work of Lubberstedt et al. (2000) who reported an average polymorphism rate of 84% in early European maize inbred lines selected from different heterotic groups. The average PIC value (0.325, Table 5) in our study was also close to the high end of the range (0.29–0.33) previously reported for maize (Lubberstedt et al. 2000; Vuylsteke et al. 2000). The high PIC values may be due to the fact that we prescreened AFLP primer combinations and selected the eight primer combinations (Table 5) with the highest polymorphism rates and largest numbers of clearly scorable fragments.

The range and average dissimilarity based on AFLP data (range: 0.32–0.69; mean: 0.57) observed in the present study were similar to that reported by Rebourg et al. (2001; range: 0.106–0.793; average of 0.55) for European maize populations. The average genetic diversity among Ethiopian highland maize accessions is therefore as diverse as observed among maize populations collected from the whole of Europe. This might be due to the nature of the materials used in the study. The highland accessions are open-pollinating varieties developed by local farmers over centuries and there has been a continuous introduction of seed into these regions. Another factor might be our sampling strategy, which maximized the geographical and morphological range among the 62 selected highland maize accessions.

The dendrogram obtained from cluster analysis of AFLP data revealed that the Northern accessions are more differentiated compared to the Western and Southern accessions (Figure 3). The separation of the Northern accessions from the rest of the accessions might be (a) due to strong selection by local farmers for adaptation to the drier growing conditions in the Northern agroecology, (b) due to the little introduction of high yielding and uniform varieties into this agroecology, and (c) due to the general restriction of seed movement into the Northern region from other agroecologies as mountains and rivers separate them. There was, however, no clear separation between accessions collected from the Western and Southern agroecologies. The close relationship between the Western and Southern agroecologies might be the result of several factors: Firstly, in these agroecologies, maize is the stable food (mainly as porridge) and hence local farmers have selected similar accessions suitable for food properties. Secondly, these two agroecologies are physically in close proximity and there might be gene flow between farmers' varieties. Finally, there have been continuous introductions of high yielding and uniform varieties released in the surrounding intermediate regions by government and Sasakawa-Global 2000 extension programs (Sasakawa-Global 2000 2002). The average yield of introduced varieties (5.6 ton/ha) was three times higher than that obtained from traditional maize varieties (1.6 ton/ha). All these activities together with the tradition of local framers to acquire seeds from distant places might be the reasons for the low genetic differentiation between the Southern and the Western agroecologies.

The relationship between molecular and phenotypic diversity was studied through the comparison of distance matrices obtained from AFLP markers and morphological traits. Unlike the present study, Gerdes and Tracy (1994) found a low correlation between distance matrices based on phenotypic and RFLP markers ($r = 0.167$) assayed in 45 sweet corn inbreds. In comparison with sweet corn inbreds, traditional Ethiopian highland maize accessions appear to be environmentally more stable, as suggested by the relatively higher agreement between phenotypic and molecular analysis ($r = 0.39$; $p = 0.001$) and indicates that the observed phenotypic variation was at least partly caused by genetic factors and/or genome regions contributing to genetic diversity at AFLP or phenotypic level might be different.

This study allowed us to distinguish three groups of maize accessions, with distinctive genetic profiles and morphological traits. The first group constitutes the early maturing, short-statured accessions (Figure 3, cluster I), which were collected from the Northern agroecology from which they probably acquired earliness. The second group includes the tall, high yielding varieties (Figure 3, cluster II), which are currently the most important landraces grown in the Southern and Western parts of Ethiopia. The third group includes tall, late maturing and low yielding accessions (Figure 3, cluster III), which are being cultivated in some parts of the Northern, Western and Southern highlands of Ethiopia. Therefore, accessions from the Northern agroecology may be used as base materials for the development of improved varieties for the drier parts in the highlands of Ethiopia, while accessions from the Western and Southern agroecologies can be used for the development of high yielding varieties suitable for high potential maize growing regions of Ethiopia.

In conclusion, the high genetic diversity observed among the traditional Ethiopian highland maize accessions suggests ample opportunity for the development of improved varieties for different highland parts of Ethiopia. From a conservation perspective, more accessions should be collected from the Northern agroecology in order to broaden the genetic basis of breeding materials for the development of drought tolerant varieties. Absence of differentiation between the accessions collected from the Western and Southern agroecolgies strongly suggests that most of the traditional accessions in these agroecologies being replaced by recently introduced maize varieties. Therefore, additional collection missions in these regions should focus at higher altitudes where the current extension programs have not launched yet.

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References

Dubreuil P., Rebourg M., Merlino and Charcosset A. 1999. The DNA – pooled sampling strategy for estimating the RFLP diversity of maize populations. Plant Molecular Biology Report 17: 123–138.

EARO 2000. Ethiopian Agricultural Research Organization, Research Strategy Plan for Maize. Addis Ababa, Ethiopia.

Gerdes J.T. and Tracy W.F. 1994. Diversity of historically important sweet corn inbreds as estimated by RFLPs, morphology, isozymes and pedigree. Crop Science 34: 26–33.

Hafnagel H.P. 1961. Agriculture in Ethiopia. Food and Agricultural Organization of the United Nations, Rome, Italy.

Jerry H. 2000. Number Cruncher Statistical Systems (NCSS). Statistical software, Utah.

Kolliker R., Jones E.S., Jahufer M.Z.Z. and Forster J.W. 2001. Bulked AFLP analysis for the assessment of genetic diversity in white colver (*Trifolium repens* L.). Euphytica 121: 305–315.

Lubberstedt T., Melchinger A.E., Dußle C., Vuylsteke M. and Kuiper M. 2000. Relationships among early European maize inbreds: IV. Genetic diversity revealed with AFLP markers and comparison with RFLP, RAPD, and pedigree data. Crop Science 40: 783–791.

Mantel N. 1967. The detection of disease clustering and a generalized regression approach. Cancer Research 27: 209–220.

Mulatu K., Bogale G., Tolessa B., Dessalegn Y. and Afeta A. 1992. Maize production trends and research in Ethiopia. In: Tolessa B. and Ransom J.R. (eds.), Proceedings of the First National Maize Workshop in Ethiopa. Addis Ababa, Ethiopia, pp. 26–34.

Myburg A.A., Remington D.L., O'Malley D.M., Sederoff R.R. and Whetten R.W. 2001. High-throughput AFLP analysis using infrared dye-labeled primers and an automated DNA sequencer. BioTechniques 30: 348–357.

Nie M. and Li W.H. 1979. Mathematical model for studying genetic variation in terms of restriction endonucleases. Proceedings of the Natural Academic Science USA 76: 5269–5273.

Rebourg C., Gouesnard B. and Charcosset A. 2001. Large scale molecular analysis of traditional European maize populations. Relationships with morphological variation. Heredity 86: 574–587.

Riek J.De., Calsyn E., Everaet I., van Bockstaele E. and De Loose M. 2001. AFLP based alternative for the assessment of distinctness, uniformity and stability in sugar beet varieties. Theoritical Applied Genetics 103: 1254–1265.

Sasakawa-Global 2000 2002. Agricultural Project in Ethiopia: Activities and Output. An assessment report, Sasakawa-Global 2000, Addis Ababa, Ethiopia.

Smith J.S.C. and Smith O.S. 1992. Fingerprinting crop varieties. Advances in Agronomy 47: 85–140.

Sneath P.H.A. and Sokal R.R. 1973. Numerical Taxonomy. WH Freeman, San Francisco.

Twumasi-Afriyie S., Habatmu Z., Kassa Z., Bayisa Y. and Sewagegn T. 2001. Development and Improvement of Highland Maize in Ethiopia. 2nd National maize workshop of Ethiopia, Addis Ababa, Ethiopia.

van Eeuwijk F.A. and Baril C.P. 2001. Conceptual and statistical issues related to the use of molecular markers for distinctness and essential derivation. Acta Horticulture 546: 35–53.

Vavilov N.I. 1951. Phytogeographic basis of plant breeding. In: The origin, variation, immunity and breeding of cultivated plants. Chronica Botanica 13: 13–54.

Vos P., Hogers R., Bleeker M., Reijans M., De Lee T., Hornes M., Frijters A., Pot J., Poleman J., Kuiper M. and Zabeau M. 1995. AFLP®: a new technique for DNA fingerprinting. Nucleic Acids Research 23: 4407–4414.

Vuylsteke M., Mank R., Brugmans B., Stam P. and Kuiper M. 2000. Further characterization of AFLP data as a tool in genetic diversity assessments among maize (*zea mays* L.) inbred lines. Molecular Breeding 6: 265–276.

Warburton M.L., Zianchun X., Crossa J., Franco J., Melchinger A.E., Frisch M., Bohn M. and Hoisington D. 2002. Genetic characterization of CIMMYT inbred maize lines and open pollinated populations using large scale fingerprinting methods. Crop Science 42: 1832–1840.

Ward J.H. 1963. Hierarchical grouping to optimize an objective function. Journal of the American Statisticl Association 56: 236–244.

Waugh R., Bonar N., Baird E., Thomas B., Graner A. and Hayes P. 1997. Homology of AFLP products in three mapping populations of barely. Molecular & General Genetics 255: 311–321.

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Towards a definition of a crop wild relative

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Abstract. Crop wild relatives are an important socio-economic resource that is currently being eroded or even extinguished through careless human activities. If the Conference of the Parties (COP) to the CBD 2010 Biodiversity Target of achieving a significant reduction in the current rate of loss is to be achieved, we must first define what crop wild relatives are and how their conservation might be prioritised. A definition of a crop wild relative is proposed and illustrated in the light of previous Gene Pool concept theory. Where crossing and genetic diversity information is unavailable, the Taxon Group concept is introduced to assist recognition of the degree of crop wild relative relatedness by using the existing taxonomic hierarchy.

Abbreviations: CBD – Convention on Biological Diversity; COP – Conference of the Parties to the CBD; CWR – Crop wild relative; FAO – Food and Agriculture Organisation of the United Nations; GM – Genetic modification; GP – Gene pool; PGR – Plant genetic resources; TG – Taxon group

Introduction

The Convention on Biological Diversity (CBD 1992) and the subsequent International Treaty on Plant Genetic Resources for Food and Agriculture (FAO 2001) have proved a watershed in plant genetic resources (PGR) conservation in many ways, particularly by re-focusing conservation activities onto *in situ* conservation. *In situ* conservation, using the definition provided in the text of the CBD (Convention on Biological Diversity 1992), incorporates two distinct approaches: conservation of wild species in nature and on-farm conservation of domesticated varieties or breeds. Within the context of socio-economic plant diversity conservation, the change of emphasis away from further collecting of cultivated material for *ex situ* conservation in gene banks towards the *in situ* conservation of locally adapted land races and the wild relatives of crops within or outside existing protected areas, has necessitated the research and development of new conservation methods (Hawkes 1991; Maxted et al. 1997a).

The focus of crop wild relative (CWR) maintenance is conservation in genetic reserves, primarily due to the large numbers of species included and the difficulty of collecting and conserving *ex situ* their entire genetic diversity. CWRs are those species related to a crop, but what constitutes a CWR and how closely related to a crop does a taxon have to be to be considered a CWR? In the light of contemporary biotechnological advances in GM technology, most if not all species are potential gene donors to a crop. However, within the utilitarian sense of conservation for food and agriculture it remains important to be able to accurately define the relationship between a crop and its close wild relatives, so that conservationists competing for limited conservation resources may objectively prioritise taxa for study (Kell and Maxted 2003; Meilleur and Hodgkin 2004). This is a particularly pressing need given the current threats to genetic diversity from genetic erosion and extinction, as recognised by the Conference of the Parties (COP) to the CBD 2010 Biodiversity Target (www.biodiv.org/2010-target), as well as a number of other strategies and treaties, such as the Global Strategy for Plant Conservation, the International Treaty on Plant Genetic Resources for Food and Agriculture and the European Plant Conservation Strategy.

To meet many of the 2010 biodiversity targets[1] and the targets and requirements of other relevant strategies and legislation, we need to be able to assess biodiversity change; therefore, a clear baseline against which to assess change is essential. For Europe, for example, the European Community funded project, European Crop Wild Relative Diversity Assessment and Conservation Forum (PGR Forum – www.pgrforum.org) is making a significant contribution by providing the baseline information and the tools required to monitor this change. However, to continue working collectively and globally towards achieving the objectives of the 2010 Biodiversity Target, there is first a need to agree on what constitutes a crop wild relative, as there is currently no generally accepted definition.

Although lists of crop wild relatives exist, notably those proposed for Europe by Zeven and Zhukovsky (1975) and Heywood and Zohary (1995), and for individual countries by Schlosser et al. (1991) for the former German Democratic Republic and by Mitteau and Soupizet (2000) for France, no precise definition of what constitutes a crop wild relative is provided and the taxa have been selected subjectively on the basis of expert knowledge. Here we discuss previous CWR and Gene Pool concepts, and propose a working definition of a crop wild relative and how this definition can be applied.

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[1] Particularly targets 2.1, ‘Restore, maintain or reduce the decline of populations of species of selected taxonomic groups’; 3.1, ‘Genetic diversity of crops, livestock, and harvested species of trees, fish and wildlife and other valuable species conserved ....’; and 8.2, ‘Maintain biological resources that support sustainable livelihoods, local food security and health care, especially of

Crop gene pool concepts

From his observations of crops and their wild relative diversity Vavilov (Vavilov 1920, 1922) noted that similar patterns of variation were found between crops and their wild relatives in unrelated crop complexes. Comparative genomics have more recently revealed that both gene content and gene order are conserved widely across related species and genera, and this has been most thoroughly demonstrated in the grasses (Devos and Gale 1997). However, Vavilov's Law of Homologous Series, which preceded modern molecular genetics, was proposed to systematize such examples of parallelism (Vavilov 1920, 1922) and he illustrated his concept using patterns of variation among vetches, lentils and peas. These reproductively isolated genera each show similar patterns of variation, which are likely to have arisen as a response to similar natural and artificial selection pressures. The continuing importance of Vavilov's law is that it has predictive value, in that it can be used to try to identify desirable traits such as disease resistance or drought tolerance in related species. Thus Vavilov was one of the first to recognise the importance of conserving the breadth of a crop's genetic diversity, both within the crop itself, but also importantly within the wild species related to the crop, among which there could be natural or artificial introgression.

These views were formalised by Harlan and de Wet (1971) as the Gene Pool concept. Within each crop there was a potential pool of genetic diversity available for utilisation and a gradation of that diversity dependent on the relative crossing ability between the crop itself and the primarily non-domesticated species in the primary, secondary or tertiary Gene Pool of the crop. They distinguish three Gene Pools as follows:

- Primary Gene Pool (GP-1) within which GP-1A are the cultivated forms and GP-1B are the wild or weedy forms of the crop;
- Secondary Gene Pool (GP-2) which includes the coenospecies (less closely related species) from which gene transfer to the crop is possible but difficult using conventional breeding techniques;
- Tertiary Gene Pool (GP-3) which includes the species from which gene transfer to the crop is impossible, or if possible requires sophisticated techniques, such as embryo rescue, somatic fusion or genetic engineering.

Using the crop, cowpea (*Vigna unguiculata* (L.) Walp. subsp. *unguiculata)* as an example from a recent ecogeographic monograph of African *Vigna* (Maxted et al. 2004), then the Gene Pool concept may be applied as indicated in Table 1.

However, the division of the broader Gene Pool into its primary, secondary and tertiary units is only possible when extensive information is available on patterns of genetic diversity and relative crossing ability for the species in question.

Although applied widely to identify practical conservation and use targets, the Harlan and de Wet (1971) concept does have limitations (Maxted et al. 1997b): for instance, it necessarily requires an approximation of the relative ease

Table 1. Gene pool concept applied to cowpea (*Vigna unguiculata* (L.) Walp. subsp. *unguiculata*.).

Crop taxon	1° Gene Pool	2° Gene Pool	3° Gene Pool
V. unguiculata	A. *V. unguiculata* subsp. *unguiculata: Unguiculata* Group, *Biflora* Group, *Sesquipedalis* Group, *Melanophthalmus* Group B. All wild and weedy infra-specific *V. unguiculata* taxa	*V. nervosa*	Other *Vigna* species

Table 2. Numbers of plant species in the Euro-Mediterranean region and CWR and percentages of species in each CWR group (Kell et al. in prep.).

Floristic grouping	Number of species	Percentages of species
Euro-Mediterranean Species	30,729	100
All CWR species	23,818	77.5
Agricultural and Horticultural CWR	19,091	62.1
Forestry CWR	2798	9.1
Ornamental CWR	7388	24.0
Medicinal and Aromatic CWR	19,574	63.7

of hybridisation between the crop and the wild relative and it can only be used for designating conservation priority within a specific crop Gene Pool rather than both within and across different crop Gene Pools. Applications of this genetically based concept have been limited because more often than not, crossing ability and patterns of genetic diversity between crops and their wild related taxa are absent for all but the major crop complexes. If European and Mediterranean CWR are taken as an example; there are 23,818 crops and CWR species present in the region (out of a total flora of 30,729 species), see Table 2, and Kell et al. (in prep.). It is estimated that the Gene Pool concept could only be applied to approximately 226 out of the 1,025 genera, 22% of the total. The sheer number of crop species worldwide (7,000 species; FAO 1998) along with the potential total number of higher plant species (270,000 species, Groombridge and Jenkins 2002), each of which must to a degree be a crop wild relative, makes the possibility of obtaining the necessary genetic diversity information for all CWR taxa a distant reality, even with falling costs and ease of molecular genetic analysis. Also, when attempting to establish priorities for national PGR programmes, decision makers often need to set conservation priorities across the breadth of the entire flora covering numerous crop Gene Pools, not just in relation to a single crop, as proposed by Harlan and de Wet (1971).

What constitutes a crop wild relative?

A simple definition of a CWR would be a taxon found within the primary or more remotely the secondary Gene Pool of a crop, and between which gene exchange is relatively simple. Hybridisation occurs easily within this group, resulting in fertile hybrids with normal chromosome pairing and gene segregation. This simple application of the Harlan and de Wet (1971) concept remains functional for the crop complexes where hybridisation experiments have been performed and the pattern of genetic diversity within the Gene Pool is well understood. However, for the majority of crop complexes, particularly those in the tropics, the wild species related to crops have been described and classified using a combination of morphological characteristics, and the degree of genetic differentiation among species remains unknown. Where the data are available to objectively apply the Harlan and de Wet concept, it will remain the best assessment of what constitutes a crop wild relative. However, where the necessary crossing and genetic diversity data are unavailable there remains a need to find an alternative means of estimating the degree of relatedness of crops and their wild relatives.

Proposed application of taxon groups

PGR Forum has pragmatically circumvented the lack of crossing and genetic diversity data for the majority of European crops and related taxa by using the existing taxonomic hierarchy. This can be applied to define a crop wild relative's rank as follows:

Taxon Group 1a – crop
Taxon Group 1b – same species as crop
Taxon Group 2 – same series or section as crop
Taxon Group 3 – same subgenus as crop
Taxon Group 4 – same genus
Taxon Group 5 – same tribe but different genus to crop

For CWR taxa for which we have little or no genetic diversity data, the Taxon Group concept can be used to assist in setting conservation priorities. For example, if this concept were applied to the less well studied *Vigna* crop, zombi bean (*V. vexillata* (L.) A.Rich. var. *vexillata*), then the Taxon Group concept may be applied as indicated in Table 3.

When attempting to apply the Taxon Group concept it should be acknowledged that taxonomists do not always provide a detailed infra-generic ranking for genera when they publish a classification. Thus where certain levels of the taxonomic hierarchy are absent, the next higher Taxon Group should be applied. For example, if a crop is located in a genus where sections have not been defined but subgenera have, then the crop would be placed in TG1a, and other taxa within the same species (i.e. varieties or subspecies) as the crop would be placed in TG1b. It would not be possible to use TG2, but species found in the same subgenus would be members of TG3 and those in other subgenera in TG4. If no sections or subgenera had been defined, all species in

Table 3. Taxon group concept applied to zombi bean and its CWRs (*V. vexillata* (L.) A.Rich. var. *vexillata*).

Taxon group 1a (= crop)	Taxon group 1b (= same species)	Taxon group 2 (= same section)	Taxon group 3 (= same subgenus)	Taxon group 4 (= same genus)	Taxon group 5 (= more remote genera)
V. vexillata var. *vexillata*	*V. vexillata* *var. angustifolia* var. *davyi* var. *dolichonema* var. *lobatifolia* var. *macrosperma* var. *ovata*	Section *Plectotropis* *V. kirkii*	Subgenus *Plectotropis* Section *Pseudoliebrechtsia* *V. nuda* *V. longissima*	Subgenus *Vigna* Subgenus *Haydonia* Subgenus *Ceratotropis* Subgenus *Lasiospron* Subgenus *Sigmoidotropis* Subgenus *Macrorhyncha*	*Phaseolus* *Dysolobium* *Lablab* *Macroptilium* *Oxyrhynchus* *Physostigma*

the same genus as the crop would be placed in TG4 and those in other related genera in TG5.

Knowledge of differences in crop and wild species ploidy levels also has an impact on the application of the Taxon Group concept. Even if a taxonomist considered two species closely related, placing them in the same section on the basis of morphological similarity, differences in ploidy level may cause difficulties in the survival of hybrids and therefore in utilisation. However, as indicated above, wherever the Gene Pool relationships are well understood, for instance, in cases where cytogenetics and ploidy levels have been studied, the Gene Pool concept would have priority and the Taxon Group concept would not be applied.

Application of the Taxon Group concept assumes that taxonomic distance is positively related to genetic distance. Flint (1991), Heywood (1994) and Johnson (1995) all point out that this relationship may not hold because of inconsistencies amongst taxonomists when describing species; species are not all separated by the same, standard genetic distance. Nevertheless, it is believed that the taxonomic hierarchy is likely to be an approximation of actual genetic distance and therefore, for practical purposes, classical taxonomy remains an extremely useful means of estimating genetic relationships.

Specifically in relation to the PGR Forum project, it was initially intended to apply the Taxon Group concept to the Euro + Med Plantbase database for the European and Mediterranean flora by automatically tagging each taxon record as to which crop the taxon was related and to which Taxon Group the individual taxon belonged. However, the Taxon Group tagging of all Euro + Med Plantbase taxa was ultimately not possible because the series, section and subgeneric hierarchy of the genera included were not linked to individual species in the database structure. However, a sample of the genera were linked manually to demonstrate how the Taxon Group concept could be applied, see Kell et al. (in prep.) for further discussion. Application of the Taxon Group concept in this form to taxonomic databases is seen as essential to enable the comparatively large number of CWR taxa to be prioritised for conservation action, however, the application of the concept to individual CWR genera can be easily achieved using the accepted classification. It should also be noted that the Taxon Group concept can be utilised to prioritise 100% of crop and CWR taxa for conservation action, as long as the existing classification of the genus contains infra-generic structure, as opposed to the approximate 22% of crop and CWR taxa that can be prioritised using the Gene Pool concept.

Proposed definition of a crop wild relative

If it is accepted that the Gene Pool concept together with the Taxon Group concept proposed above provide the best pragmatic means available to determine whether a species is a CWR, a working definition of a crop wild relative is possible:

A crop wild relative is a wild plant taxon that has an indirect use derived from its relatively close genetic relationship to a crop; this relationship is defined in terms of the CWR belonging to Gene Pools 1 or 2, or taxon groups 1 to 4 of the crop.

While the CWR definition may most commonly be applied to species used in food and agriculture, the concept is equally applicable to ornamentals, medicinal plants, and forestry species. A broad definition of a CWR would be any taxon belonging to the same genus as a crop. Applying the proposed Taxon Group concept, it would be a member of TG1 to TG4. Harlan and de Wet (1971) apply a similar breadth to their Gene Pool concept for ease of usefulness of related species, commenting that the secondary Gene Pool is equivalent to generic limits of the crop. However, the use of this broad application of the Taxon Group concept would result in the inclusion of a very large percentage of known taxa. If the European and Mediterranean floras are taken as an example, 77.5% of species in the Euro + Med region (Euro + Med Plantbase, www.euromed.org.uk) would be regarded as CWR. Therefore it is important to underline that being a crop wild relative is itself a relative concept and that there is a need to estimate the degree of CWR relatedness, if for no other reason than to assist in establishing conservation priorities. Therefore, taxa which belong to GP1B or TG1b and TG2 may be considered close CWRs of higher priority, and those in GP2 or TG3 and TG4 more remote CWRs afforded lower priority. Those in GP3 and TG5 would be excluded from being considered CWRs of that particular crop. Therefore it can be argued that application of the Gene Pool and Taxon Group concepts to determine whether a species is or is not a CWR is pragmatic, and that the two concepts used together can be applied to establish the degree of crop wild relative relatedness and thus assist in establishing conservation priorities. This strategy has been applied within the European CWR project, PGR Forum (www.prgforum.org).

The concepts combined could also be of value in assessing ‘risk’ of genetic pollution of CWRs by genetically modified and conventional modern crop varieties. Risk can be assessed using combined estimations of hazard and exposure (Wilkinson et al. 2003). Exposure is a quantifiable estimate of the probability of the hazard occurring. Combining the Gene Pool and Taxon Group concepts can provide a basis for estimating the likelihood of gene flow occurring, even in poorly studied taxa where genetic information is minimal or absent.

The Gene Pool and Taxon Group concepts applied to a crop and its wild relatives would ideally be expected to be congruent, but as discussed above and acknowledged by Harlan (1992), inconsistencies among taxonomists when describing species mean that where both taxonomic and genetic information is available the two concepts may not match perfectly. This can be illustrated by applying the Gene Pool and Taxon Group concepts for two European crops and their wild relatives as is shown in Table 4. It is interesting to note the close correlation between the application of the Gene Pool and Taxon Group

Table 4. Application of gene pool and taxon group concepts for the crops *Vicia narbonensis* and *Beta vulgaris* and their wild relatives.

Crop	Gene pool concept					
	GP1A[a]	GP1B	GP2	GP3		
Narbon bean	*Vicia narbonensis* L.	*V. narbonensis* L.	*V. kalakhensis* Khattab, Maxted & Bisby	All other *Vicia* species		
	var. *narbonensis*	var. *salmonea* (Mout.) H. Schäfer var. *jordanica* H. Schäfer var. *affinis* Kornhuber ex Asch. & Schweinf. var. *aegyptiaca* Kornhuber ex Asch. & Schweinf.	*V. johannis* Tamamschjan in Karyagin *V. galilaea* Plitm. & Zoh. in Plitm. *V. serratifolia* Jacq. *V. hyaeniscyamus* Mout.			
	Taxon group concept					
	TG1A[b]	TG1B	TG2	TG3	TG4	TG5
Narbon bean	*V. narbonensis* L.	*V. narbonensis* L.	Sect. *Narbonensis* (Radzhi) Maxted	All non-section *Narbonensis* (Radzhi) Maxted	All *Vicia* subgenus *Vicilla* Schur species	*Lens* Miller, *Lathyrus* L., *Pisum* L. and *Vavilovia* A. Fed. Species
	var. *narbonensis*	var. *salmonea* (Mout.) H. Schäfer var. *jordanica* H. Schäfer var. *affinis* Kornhuber ex Asch. & Schweinf.	*V. kalakhensis* Khattab, Maxted & Bisby *V. johannis* Tamamschjan in Karyagin *V. galilaea* Plitm. & Zoh. in Plitm.	*Vicia* L. subgenus *Vicia* species		

Table 4. Continued.

Crop	Gene pool concept					
		var. *aegyptiaca* Kornhuber ex Asch. & Schweinf.	*V. serratifolia* Jacq.			
			V. hyaeniscyamus Mout. *V. eristalioides* Maxted			
Crop	Gene pool concept					
	GP1A	GP1B	GP2	GP3		
Beet	*Beta vulgaris* L. subsp. *vulgaris*	*B. vulgaris* L.	Section *Procumbentes:*	Section *Corollinae*:		
	Cultivar groups: leaf beet, garden beet, fodder beet, sugar beet	subsp. *maritima* z(L.) Arcang.	*B. procumbens* Sm.	*B. lomatogona* Fisch. et May.		
		subsp. *Adanensis* (Pamuk.) Ford-Lloyd & Williams	*B. webbiana* Moq.	*B. macrorhiza* Stev.		
		B. macrocarpa Guss. *B. patula* Ait.	*B. patellaris* Moq.	*B. corolliflora* Zos. ex Buttler *B. intermedia* Bunge *B. trigyna* Waldst. et Kit. Section *Nanae*: *B. nana* Boiss. et Heldr.		
	Taxon group concept					
	TG1A[c]	TG1B	TG2	TG3	TG4	TG5
Beet	*Beta vulgaris* L. subsp. *vulgaris*	*B. vulgaris* L.	Section *Beta*		Section *Procumbentes*	

Cultivar groups: leaf beet, garden beet, fodder beet, sugar beet	subsp. *maritima* (L.) Arcang.	*B. macrocarpa* Guss.	*B. procumbens* Sm.
	subsp. *adanensis* (Pamuk.) Ford-Lloyd & Williams	*B. patula* Ait.	*B. webbiana* Moq.
			B. patellaris Moq. Section *Corollinae* *B. lomatogona* Fisch. et May. *B. macrorhiza* Stev. *B. corolliflora* Zos. ex Buttler *B. intermedia* Bunge *B. trigyna* Waldst. et Kit. Section *Nanae* *B. nana* Boiss. et Heldr.

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[a] Gene pool concept for *Vicia narbonensis* is taken from Enneking and Maxted (1995).

[b] Taxon group concept for *Vicia narbonensis* is derived from the classification provided in Maxted (1993).

[c] Taxon group concept for *Beta* is derived from the classification provided in Ford-Lloyd (2005).

concepts for the crops and their wild relatives, particularly for *Vicia narbonensis*, but also for *Beta vulgaris* and its wild relatives. Although the accepted classification of *Vicia* utilises the full taxonomic hierarchy (i.e. series, sections and subgenera are designated), for *Beta*, the taxonomic rank subgenus has not been used, therefore, no taxa can be included in Taxon Group 3 (= same subgenus) and all remaining *Beta* taxa not present in section *Beta*, which contains the crop, are grouped in Taxon Group 4 (= same genus but excluding the section containing the crop). The correlation between the application of the Gene Pool and Taxon Group concepts and the flexibility of applying the Taxon Group concept even where the full taxonomic hierarchy has not been applied underlines its usefulness. However, it should be stressed that where both genetic and taxonomic information are available, genetic information should be given weight when defining crop wild relative relatedness. Application of the Taxon Group concept is pragmatic and will prove very helpful in defining the degree of relatedness of a wild species to a crop for the bulk of plant species where genetic diversity data is absent but the Taxon Group concept is a more subjective assessment than direct comparison of genetic diversity.

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References

Convention on Biological Diversity 1992. Convention on Biological Diversity: Text and Annexes. Secretariat of the Convention on Biological Diversity, Montreal, pp. 1–34.

Devos K. and Gale M. 1997. Comparative genetics in the grasses. Plant Molecular Biology 35: 3–15.

Enneking D. and Maxted N. 1995. Narbon bean: *Vicia narbonensis* L. (Leguminosae). In: Smartt J. and Simmonds N.W. (eds), Evolution of crop plants, 2nd edn. Longman Group, Harlow Essex, pp. 316–321.

FAO 1998. The State of the World = s Plant Genetic Resources for Food and Agriculture. FAO, Rome.

FAO 2001. International Treaty on Plant Genetic Resources for Food and Agriculture. FAO, Rome.

Flint M. 1991. Biological Diversity and Developing Countries: Issues and Options. Overseas Development Administration, London.

Ford-Lloyd B.V. 2005. Sources of genetic variation, the genus *Beta*. In: Biancardi E., de Biaggi M., Campbell L.G. and Skaracis G.N. (eds), Genetics and Breeding of Sugar Beet. Science Publishers Inc, Enfield, USA.

Groombridge B. and Jenkins M. 2002. World atlas of biodiversity. Prepared by the UNEP World Conservation Monitoring Centre. University of California Press, Berkeley, USA.

Harlan J. and de Wet J. 1971. Towards a rational classification of cultivated plants. Taxon 20: 509–517.

Harlan J. 1992. Crops and Man. American Society of Agronomy, Madison.

Hawkes J. 1991. International workshop on dynamic *in situ* conservation of wild relatives of major cultivated plants: summary of final discussion and recommendations. Israel Journal of Botany 40: 529–536.

Heywood V. 1994. The measurement of biodiversity and the politics of implementation. In: Forey P., Humphries C. and Vane-Wright R. (eds), Systematics and Conservation Evaluation. Systematic Association Special Volume 50. Oxford University Press, Oxford pp.15–22.

Heywood V. and Zohary D. 1995. A catalogue of the wild relatives of cultivated plants native to Europe. Flora Mediterranea 5: 375–415.

Johnson N. 1995. Biodiversity in the balance: approaches to setting geographic conservation priorities. Biodiversity Support Program, Washington, D.C.

Kell S. and Maxted N. 2003. (compilers). Report of Workshop 1. European Crop Wild Relative Diversity Assessment and Conservation Forum – PGR Forum. www.prgforum.org.

Maxted N. 1993. A phenetic investigation of *Vicia* L. subgenus *Vicia* (Leguminosae, Vicieae). Botanical Journal of the Linnean Society 111: 155–182.

Maxted N., Ford-Lloyd B. and Hawkes J. 1997a. Plant Genetic Conservation: the *In situ* Approach. Chapman & Hall, London, pp. 1–451.

Maxted N., Hawkes J., Guarino L. and Sawkins M. 1997b. The selection of taxa for plant genetic conservation. Genetic Resources and Crop Evolution 44: 337–348.

Maxted N., Mabuza-Dlamini P., Moss H., Padulosi S., Jarvis A. and Guarino L. 2004. African *Vigna*: an Ecogeographic Study. International Plant Genetic Resources Institute, Rome, Italy.

Meilleur B. and Hodgkin T. 2004. *In situ* conservation of crop wild relatives status and trends. Biodiversity and Conservation 13: 663–684.

Mitteau M. and Soupizet F. 2000. Preparation of a preliminary list of priority target species for *in situ* conservation in Europe. In: Laliberté B., Maggioni L., Maxted N. and Negri V. (eds), (compilers). ECP/GR *In situ* and On-farm Conservation Network Report of a Task Force on Wild Species Conservation in Genetic Reserves and a Task Force on On-farm Conservation and Management Joint meeting, 18–20 May 2000. Isola Polvese, Italy.

Schlosser S., Reichhoff L. and Hanelt P. 1991. Wildpflanzen Mitteleuropas. Nutzung und Schutz, Deutscher Landwirtschaftsverlag Berlin GmbH.

Vavilov N. 1920. The law of homologous series in variation. Proceedings of the III All-Russian plant breeding conference, Saratov, p. 16.

Vavilov N. 1922. The law of homologous series in variation. Journal of Genetics 12: 47–89.

Wilkinson M., Sweet J. and Poppy G. 2003. Risk assessment of GM plants: avoiding the gridlock. Trends in Plant Science 8: 208–212.

Zeven A. and Zhukovsky P. 1975. Dictionary of Cultivated Plants and Their Centres of Diversity. Excluding ornamentals, forest trees and lower plants. PUDOC, Wageningen.

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Household differentiation and on-farm conservation of biodiversity by indigenous households in Xishuangbanna, China

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Abstract. With diversification of field type among households in same eco-environment and social situation, even in the same ecosystem, merging household socio-economics with biodiversity initiative values to determine incentives and optimum strategy of on-farm conservation of biodiversity. Botany survey of agroecosystems at landscape level in Daka and Baka, Xishuangbanna, Yunnan, China, as well as household differentiation of biodiversity in agroecosystem and on-farm conservation strategy merging household socio-economic characters were studied. There were 73 families 179 species distributed in 0.1 ha of different agroecosystems in Daka, and 70 families 166 species distributed in 0.08 ha different agroecosystems of Baka respectively. The cosmopolitan families, such as Gramineae and Compositae decreased the percentage of tropical families and subtropical families. Botany survey among 12 random selected households from Daka in 46 sampling plots of different agroecosystems showed significant differentiation of the species richness indices of natural biodiversity and agrobiodiversity as there were differences of cognition and utilization of plant species besides management practices among households. Dengrogram using the Ward method of hierarchical cluster analysis based on annual questionnaire interview of 60% household from 1998 to 2001 in Daka showed disparity among different households' socio-economics which underpins management diversity. There were significant correlation coefficients between household socio-economics and species richness indices of different agroecosystems. Fallow size had significant positive correlation coefficients with species richness index of rubber plantation. By contraries, production input had negative correlation coefficients with species richness index of upland rice field. Meanwhile, cereal crop income had significant positive correlation coefficient with agro-species richness index of rubber plantation. By contraries, other income such as off-farm income had negative correlation coefficients with agro-species richness index of rubber plantation. Innovations of the expert farmer on agrobiodiversity on farm conservation were admiration.

Introduction

Agrobiodiversity has been widely accepted as a scientific term only in recent years. It has been defined as "management and direct use of biological species, including all crops, semi-domesticates and wild species" (Huijun et al. 1996). Farmers maintain a level of agrobiodiversity through their farm-specific production system, employing individual decision-making at the farm level. Conservation and sustainable use of agrobiodiversity on farm level is a new challenge and there are many lessons to be learned from the field (Brookfield and Padoch 1994; Wood and Lenné 1997; Rerkasem et al. 2002). Meanwhile, the role of agrobiodiversity in farm-household livelihood and food security, as well as relationship between agrobiodiversity and society has also become a focus of interest (Hardon-Baars 2000). Biodiversity and agrobiodiversity has been given more and more recognition in China, including gene, species and ecosystem diversity (Chunlin et al. 2003; Yuming et al. 2004). Agrobiodiversity plays an important role in all agroecosystems. In sum, policies and actions to support agrobiodiversity at many levels are needed, and will lead to multidimensional economic and ecological gains in both the short term and the long term. The strategy for on-farm agrobiodiversity conservation will only succeed if the needs and problems of indigenous communities are solved (Pinedo-Vasquez et al. 2002).

Contrasts among provinces, counties, and villages are common because natural resources, eco-environment, social and ethnic identities are different. There are also differences among households in the same eco-environment and social situation, even in the same ecosystem (Huijun et al. 2002). What are the impacts of such diffferences? How should we assess the differences of natural biodiversity and agrobiodiversity among households? Can we assume that an increase of agroecosystem field type diversity will improve the future food and economic security, as well as sustainable development? The authors choose Daka and Baka, Xishuangbanna Yunnan China, two of the demonstration sites of the Global Environmental Facility and United Nations University project on People, Land management and Environmental Change as a case study where we spend 7 years studying biodiversity of agroecosystems and socio-economic development.

Materials and methods

Study area

Xishuangbanna Dai Autonomous Prefecture is located in southern part of Yunnan province. SW China, within the north latitude 21°10′–23°40′ and east longitude 99°55′–101°51′, and with the area of 19200 km^2 (Figure 1). This prefecture is the only area in China where stands of virgin tropical rainforest can be found. Xishuangbanna land area is only 0.2% of China, but it has 5282 higher plant species that takes 1.8% of plant species in the world, 14.9% of China and 34.8% of Yunnan Province's. Xishuangbanna is a multi-cultural nationality area. Dai, Hali, Yao, Jinuo and Bulang people have a long history living in Xishuangbanna. Thirteen ethnic groups are recognized by the State Council of China in this area. This prefecture is characterized by both cultural

Figure 1. The study area, Daka and Baka, in southernmost Yunnan Province, China.

and biological diversity. The agroecosystems of the region strongly reflect this dual richness.

Daka is a Hani/Ahka village located in Menglun town, Mengla county in Xishuangbanna Prefecture. Area of Daka is 727 ha, consist of community forest, rubber and fallow in turn. Its most recent census recorded 304 people in 53 families in the village. Daka is located about eight kilometers from Menglun town and 10 km from the Menglun State Nature Reserve at approximately 21°41′ N, 101°25′ E. The average annual temperature in Daka is 21.5 °C, rainfall averages 1563 mm per year. The prevailing soils are leached red earths. The original vegetation in the Daka area is tropical seasonal rainforest, now long managed by human populations.

Baka is a village of Jinuo township, Jinhong City, Xishuangbanna Prefecture, with an elevation of 720 m. Area of Baka is 173 ha, consist of fallow and cash crop plantation. Its most recent census recorded 269 people in 68 families in the village. The village is close to Menglun State Nature Reserve at approximately 21°59′ N, 101°9′ E and 6 km away from Xishuangbanna Tropical Botanic Garden. The average air temperature is 21.5 °C, annual rainfall 1556.3 mm per year, and annual mean relative humidity is 82%. The original vegetation is tropical seasonal rainforest.

Field methods

Landscape level: 11 quadrats of different agroecosystems in Daka and 9 in Baka were established and studied. Botanical survey is based on guidelines on assessment of plant species in agricultural landscapes (Zarin et al. 2002). The habitat of different agroecosystems was recorded. Trees and shrubs with more than 6 cm girth at breast height were identified and their girth measured at

1.3 m from ground level, and the height measured together. Young trees and shrubs with less than 6 cm girth at breast height were identified and individual tree number recorded. Four 1×1 m grass quadrats were established in the corner of the quadrat to investigate the individual number of seedlings and grasses. On-plot investigation of utilized plants of different agroecosystems was finished at the same time.

Household level: The determination of sampling households and sampling plots is based on the Household-level Agrobiodiversity Assessment (HH-ABA) (Huijun et al. 2002). In Daka, 20% households were determined randomly for plot survey in base of the residence booklet with the assistance of suggestion by local households. The land distribution and land shape determines sampling plots of HH-ABA, the shape and area of sampling plots is based on the land owned by the household. We have chosen homegarden, fallow field, upland rice field, rubber plantation and *Cassia siamea* plantation as the research targets according to the actual situation of Daka. Forty six quadrates of 12 households were established and studied. Management diversity including land preparation manner, land construction manner, water and soil erosion control, pest and weed control, fertilizer keep etc., were investigated on farm. Population densities and distribution patterns, cultivation pattern, seed origin, harvest quantities of some key agrobiodiversity were determined at the same time. In addition, we conducted annual questionnaire interviews of socioeconomic characters of 60% of the population of the whole village. Questionnaire interview including demographic and cultural aspects, land and crop yield, gender aspects, produce and life input, income resource, limitation factors. All fieldwork has been undertaken from 1998 to 2001.

Data analysis

(1) *Species richness and utility*: using the methods of Gleason' species richness index ($D_{\mathrm{Gl}} = S/\mathrm{Ln}\ A$, S: number of species, A: quadrat size), and the agro-species richness index determined by Huijun and Zhenyu (1998), which means the utilized species of a certain quadrate to analyze the species richness of different household and of different agroecosystems (Keping 1994; Huijun and Zhenyu 1998; Coffey 2002). Agro-species richness index can be modified from Gleason' species richness index ($D'_{\mathrm{Gl}} = S'/\mathrm{Ln}\ A$, S': number of utilized species, A: quadrat size). At the same time, the number and percentage of utility species were analyzed.

(2) The comparative analysis and similarity analysis among different sampling plots: using the methods of Whittaker index ($\beta_{\mathrm{ws}} = S/\mathrm{ma} - 1$, S: the total number of species in the quadrat, ma: the average number of species in each sub-quadrat) and Jaccard' coefficient index ($C_{\mathrm{J}} = j/(a + b - j)$. j: number of species in both quadrat; a and b: number of species respectively in quadrat A and B) for comparative analysis and similarity analysis among different sampling plots (Huijun and Zhenyu 1998; Coffey 2002).

(3) Principal component analysis and cluster analysis of household's socio-economic characters with analysis software of SPSS 11.0 (Zhigang 1999) as principal component analysis and cluster analysis are both statistical tools for condensing data sets (Coffey 2002). Correlation coefficient analysis and statistics test including *F*-test and *t*-test between socio-economic characters and species richness indices of different agroecosystems with Microsoft Excel.

Results and discussions

Landscape level assessment and conservation

There were 73 families, 139 genera and 179 species distributed in 0.1 ha of different agroecosystems in Daka, and 70 families 146 genera and 166 species distributed in 0.08 ha different agroecosystems of Baka respectively. The cosmopolitan families, such as Gramineae, Compositae and Papiloinaceae take about 20% in Daka and 30% in Baka that means land management decreased the percentage of tropical families and subtropical families. Compared with tropical rainforest in Xishuangbanna, the percentage of tropical families and subtropical families in different agroecosystems are decreased greatly.

According to our botanical survey, there are 10 important kinds of species in agroecosystems of Daka and Baka, such as *Pometia tomentosa*, *Mitrephora wangii* and *Horsfieldia tetratepala* belongs to the third level category of vulnerable and endangered species under national conservation. *Pterospermum menglunense* and *Tetrastigma lenticelatum* are endemic to Xishuangbanna. These species have been destroyed in the agroecosystems of Daka and Baka. Floristic element analysis of agrobiodiversity assessment provided scientific basis of priority conservation of natural biodiversity and agrobiodiversity.

The species richness index is a simple and useful measurement of diversity. Biodiversity and agrobiodiversity of different agroecosystems of Daka and Baka was measured and studied respectively. There were great variations in diversity indices of different agroecosystems. In Daka, the species richness index varied from 2.0 in wet rice fields to 10.0 in holly hill forest, while the agro-species richness index varied from 1.1 in wet rice field to 5.2 in holly hill forest (Table 1). At the same time, the species richness index varied from 1.5 in orchard to 11.1 in Chinese cardamom cultivated under natural forest while the agro-species richness index varied from 1.3 in orchard to 4.3 in Chinese cardamom cultivated under natural forest in Baka.

The Whittaker indices varied from 0.58 to 1 in Daka. This means there were differences of species composition among agroecosystems. Correspondingly, there were great variations of Jaccard' coefficient index among different agroecosystems. The similarity index varied from 0 to 0.26 in Daka. For instance, the biggest similarity index between monoculture rubber plantation and *Cassia siamea* plantation as monoculture perennial crops is only 0.26. At the same time, there are great discrepancies of plant community among different

Table 1. Species richness indices of different agroecosystems in Daka and Baka.

Quadrat and agroecosystems	Size (M^2)	Number of species	Number of utilized species	Percentage of utilized species	D_{GI}	D'_{GI}
Daka						
1. Community forest	100	41	18	43.9	8.9	3.9
2. 3-year fallow field	100	43	22	51.2	9.3	4.8
3. Passion fruit plantation	100	27	14	51.9	5.9	3.0
4. Monoculture rubber plantation	100	19	14	73.7	4.1	3.0
5. Holly hill forest	100	46	24	52.2	10.0	5.2
6. *Cassia siamea* plantation	100	24	21	87.5	5.2	4.6
7. Homegarden	100	18	15	83.3	3.9	3.3
8. Paddy field	100	9	5	55.6	2.0	1.1
9. Water reservior	100	17	16	94.1	3.7	3.5
10. Chinese cardamom under forest	100	20	14	70.0	4.3	3.0
11. Tea cultivated under forest	100	28	24	85.7	6.1	5.2
Baka						
1. Upland rice field	100	14	8	57.1	3.0	1.7
2. Rubber + passion fruit	100	20	11	55.0	4.3	2.4
3. Holly hill forest	100	42	15	35.7	9.1	3.3
4. Orchard	100	7	6	85.7	1.5	1.3
5. Chinese cardamom under forest	100	51	20	39.2	11.1	4.3
6. 2-year fallow field	100	26	13	50.0	5.6	2.8
7. *Cassia siamea* plantation	100	36	16	44.4	7.8	3.5
8. Homegarden	100	18	15	83.3	3.9	3.3
9. Paddy field	100	18	7	38.9	3.9	1.5

agroecosystems as the Whittaker indices varied from 0.63 to 1 in Baka, and the similarity indices are low (below 0.23). For example, the biggest similarity index between upland rice field and wet rice field in Baka is only 0.23. The mean of β_{W} among all agroecosystems in Daka and Baka is 0.9 and 0.9 while mean of C_{J} is only 0.06 and 0.05 in Daka and Baka correspondingly. Great variation of the diversity indices means that different agroecosystems contain different species composition, and lead to different succession processes during land conversion (Zapfac et al. 2002). Meanwhile, land conversion from community forest to rubber plantation lead to biodiversity loss while species richness index decline from 8.9 to 4.1 in Daka, similar to biodiversity loss from forest to crop land in an Amazon forest zone (Fujisaka et al. 1997). Most of all, holly hill forest maintains high plant species richness in both Daka and Baka as indigenous knowledge, especially traditional belief helps to conserve biodiversity.

Household level assessment and conservation

Households manage rich biodiversity in agroecosytesms. For example, there are 156 species in 4400 m^2 sample plots of 3-year fallow field and in which 67 species are utilized by local households. The peasant household is the basic unit of agrobiodiversity conservation and rural sustainable development in China since 1978–1982 under the Household Responsibility System. Different households have different strategies and developed different technologies for agroecosystem management, agrobiodiversity conservation and economic development. The results showed that there were great discrepancies of plant species richness among different households (Table 2). For example, the average of species richness indices of 3-year fallow fields among the 11 sampled households is 6.0, while the maximum of the index is 55% more than average and the minimum is 63% less than the average. At the same time, the average of the agro-species richness indices of 3-year fallow fields among the 11 sampled households is 2.7, while the maximum is 37% more than the average and the minimum is 44% less than the average.

Homegarden is one of the important agroecosystems of local people in Xishuangbanna. As local people introduce some wild species into homegarden that are collected usually in the wild, some biodiversity and agrobiodiversity have been preserved in homegarden. Sampled households differ significantly in terms of the Gleason's species richness index and the modified agro-species richness index (Table 2). Some smallholders in Daka, for instance, did not plant wild vegetables in their gardens, instead they relied on collection of these species from fallow forests. Others chose to plant these "wild" vegetables to assure that the family found their supply easily. Meanwhile, others prefer to cultivate exotic vegetable varieties. For example, β_{w} and C_{J} of homegarden between household 4 and household 7 is 0.98 and 0.01 indicate otherguess species component. Furthermore, β_{w} and C_{J} of homegarden indicated that plant community similarity among different households were low. Similarly, the choice of plant species, their arrangement and management varies between and within tropical homegardens in the same community in Nicaragua (Mendez et al. 2001). The mean of β_{w} among all households is 0.82, 0.68, 0.68, 0.69, 0.57 and 0.66 of homegarden, 3-year fallow fields, rubber plantation, upland rice fields and *Cassia siamea* plantation while mean of C_{J} is only 0.1, 0.19, 0.19, 0.28 and 0.21 correspondingly.

In addition, household disparity within agroecosystem has resulted from management diversity among different households. For instance, some households seldom dig tree roots when preparing fallow cultivation for better natural regeneration. Some households plant alley crops such as taro in upland rice fields to conserve water and soil besides food harvest, etc (Figure 2). Some households weed by hand while some households use weedicide. Some households cover rubber roots with herb stems to conserve water and soil. Some household practice monoculture of rubber plantation while others practice agroforestry system of rubber alley cropping with tea as monoculture is one of factors leading to agrobiodiversity loss (Uppeti and Uppeti 2002).

Relating the diversity index above with socio-economic data of those households, the authors find that economic value of the biological resource in homegarden varied substantially among different households (Figure 3).

Table 2. Species richness indices of different agroecosystems among different households in Daka.

Agroecosystems	Household	Size (M^2)	Number of species	Number of utilized species	Percentage of utilized species	D_{Gl}	D'_{Gl}
Homegarden	1	240	51	38	74.5	9.3	6.9
	2	144	41	20	48.8	8.2	4.0
	3	340	35	27	77.1	6.0	4.6
	4	423	65	61	93.8	10.7	10.1
	5	151	45	39	86.7	9.0	7.8
	6	105	44	35	79.5	9.5	7.5
	7	240	32	24	75.0	5.8	4.4
	8	84	29	20	69.0	6.5	4.5
	9	65	32	28	87.5	7.7	6.7
	Mean	199	42	32	76.2	8.1	6.3
3-year fallow field	1	400	25	13	52.0	4.2	2.2
	2	400	31	10	32.3	5.2	1.7
	3	400	13	9	69.2	2.2	1.5
	4	400	26	15	57.7	4.3	2.5
	5	400	33	15	45.5	5.5	2.5
	6	400	56	22	39.3	9.3	3.7
	7	400	43	18	41.9	7.2	3.0
	8	400	41	18	43.9	6.8	3.0
	9	400	27	15	55.6	4.5	2.5
	10	400	56	20	35.7	9.3	3.3
	11	400	46	22	47.8	7.7	3.7
	Mean	400	36	16	44.4	6.0	2.7
Rubber plantation	1	400	19	9	47.4	3.2	1.5
	2	400	31	18	58.1	5.2	3.0
	3	400	18	10	55.6	3.0	1.7
	4	400	23	13	56.5	3.8	2.2
	5	400	28	17	60.7	4.7	2.8
	6	400	22	15	68.2	3.7	2.5
	7	400	22	13	59.1	3.7	2.2
	8	400	19	9	47.4	3.2	1.5
	9	400	21	12	57.1	3.5	2.0
	Mean	400	23	13	56.5	3.8	2.2
Upland rice field	1	400	43	30	69.8	7.2	5.0
	2	400	45	16	35.6	7.5	2.7
	3	400	30	18	60.0	5.0	3.0
	4	400	38	19	50.0	6.3	3.2
	5	400	54	28	51.9	9.0	4.7
	6	400	36	15	41.7	6.0	2.5
	7	400	49	30	61.2	8.2	5.0
	8	400	42	23	54.8	7.0	3.8
	9	400	41	18	43.9	6.8	3.0
	Mean	400	42	22	52.4	7.0	3.7

Table 1. Continued.

Agroecosystems	Household	Size (M^2)	Number of species	Number of utilized species	Percentage of utilized species	D_{GI}	D'_{GI}
Cassia siamea plantation	1	416	57	21	36.8	9.5	3.5
	2	400	74	30	40.5	12.4	5.0
	3	400	41	19	46.3	6.8	3.2
	4	400	34	12	35.3	5.7	2.0
	5	412	73	34	46.6	12.1	5.6
	6	400	50	19	38.0	8.3	3.2
	7	400	41	19	46.3	6.8	3.2
	8	396	40	16	40.0	6.7	2.7
	Mean	403	51	21	41.2	8.5	3.5

This provides some basic ideas for household-level agrobiodiversity on-farm conservation. For example, some households have kept rich biodiversity and developed rich agrobiodiversity and realized high economic value in home-gardens to be regarded as expert farmers. We can summarize their experience and technology and demonstrate their methods to other households who have kept and developed poor biodiversity and agrobiodiversity with low and

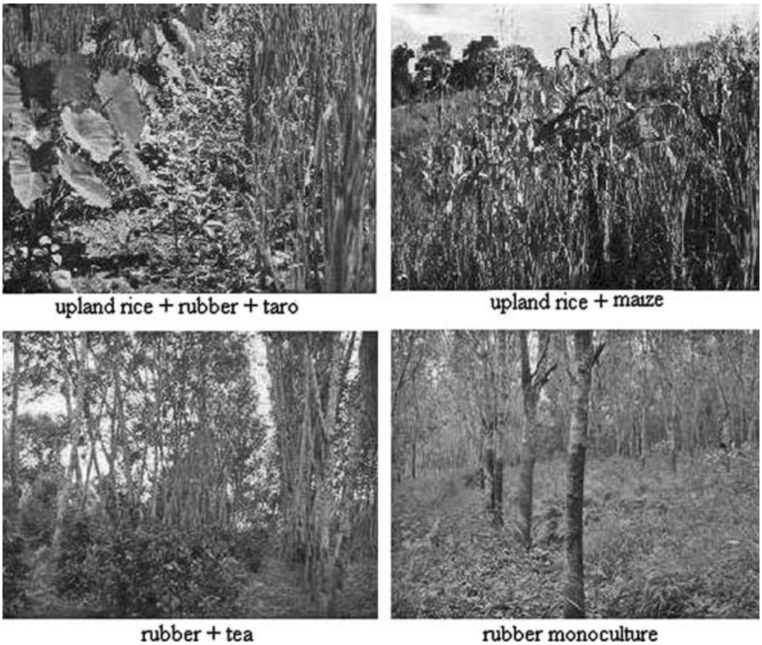

Figure 2. Household disparity of upland rice field and rubber plantation in Daka. Photo by Fu Yongneng.

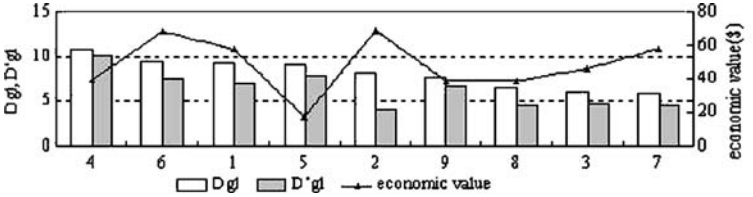

Figure 3. Economic value and species richness indice of homegarden among different households.

unstable economic value. It is important to adapt agricultural practices and land use to local agroecological and socio-economic conditions adjusted to local diverse needs and aspirations, and building upon local successful experiences as recognition of farmers' innovation in agrobiodiversity management has increased over the past decade (Montecinos and Salazar 2000; Backes 2001).

In addition, agrobiodiversity assessment at landscape level is the base for assessment at household level. Household level comprehensive result corresponds to landscape level assessment. The correlation coefficient of agrobiodiversity assessment between household level and landscape level is 0.933 and 0.945 of natural biodiversity and agrobiodiversity show consistency in results at different level. In addition, correlation coefficients between household level and landscape level both are notable at 0.01 level of *t*-test (Table 3). Biodiversity is the base of agrobiodiversity of different agroecosystems. The correlation coefficient between biodiversity and agrobiodiversity are 0.697 and 0.601 of household level and landscape level. On the other hand, rich biodiversity does not necessarily correspond with rich agrobiodiversity with different agricultural technology. In addition, the correlation coefficients between natural biodiversity and agrobiodiversity both at household level and landscape level do not achieve significance even at 0.05 level of *t*-test.

Table 3. Correlation coefficient of agrobiodiversity assessment between household and landscape level of 5 different agroecosystems in Daka.

	Household D_{Gl}		Landscape D_{Gl}		Household D'_{Gl}		Landscape D'_{Gl}	
	r	*t*	*r*	*t*	*r*	*t*	*r*	*t*
Household D_{Gl}	1							
Landscape D_{Gl}	0.933	12.48	1					
Household D'_{Gl}	0.697	2.35	0.536	1.30	1			
Landscape D'_{Gl}	0.65	1.95	0.601	1.63	0.945	15.30	1	
$t_{0.05,\ \mathrm{df}\ =\ 3}$								3.18
$t_{0.01,\ \mathrm{df}\ =\ 3}$								5.84

Household disparity of socio-economic characters

It was necessary to test the hypotheses linking on-farm agrobiodiversity with household socio-economics. According to repeated annual questionnaire interviews from 1998 to 2001, the socio-economic characters of sampled households vary greatly (Table 4). This mainly resulted from land distribution policy among households. The present status of farmland tenure is still based on the past population of 1983. Since 1983 the farmland tenure of different households has not changed. Some households have more land since the land belongs to the old people does not return to the village after the old people pass away. However, some households have less land now because of the later marriage and adding children. Households with enough wet rice and fallow land can transfer most of fallow to rubber plantation to get cash income besides food consumption while households with less wet rice or fallow can only transfer part of fallow to rubber plantation for food consumption mainly.

Classification of farm households into homogeneous groups is helpful to investigate questions such as why certain categories of households are wealthier; why some categories of households more successful at growing certain crops or rearing animals and what constraints each household category faces in terms of agricultural production. Understanding these questions allows solutions to be identified, which could help the poorer and/or the less technically able households. Principal components analysis of socio-economic characters shows that other income, cash crop income, gross person income, production input, as well as cereal crop income and population are principal factors. Meanwhile, a dengrogram using the Ward Method of hierarchical cluster analysis with SPSS 11.0 software (Zhigang 1999) of socio-economic characters among sampled households shows low combinative level among households that indicates household socio-economics' variability too. In addition, 12 households can be divided into 3 clusters according to 6 principal factors (Figure 4), especially according to other income and gross person income at 0.01 level of *F*-test, as well as cash crop income at 0.05 level of *F*-test (Table 5). For example, household 1 was divided into one independent cluster as who had great amount of other income of off-farm income.

Correlation coefficient of agrobiodiversity and socio-economics of sampled households

The study of traditional agroecosystems includes both biophysical and socio-economic variables, essential for understanding these complex systems was considered appropriate (Mendez et al. 2001). Socio-economic diversity forces farmers to try different crops and varieties for their livelihood. It is through this attempt of trying to overcome the prevailing production constraints that the agroecosystems diversity is introduced. For example, rich households prefer to select varieties with good quality in spite of low yield. On the other hand, poor

Table 4. Disparity of average socio-economic characters during 1998 to 2001 of 12 sampled households (Size: ha; income/input: $, the same below).

	1	2	3	4	5	6	7	8	9	10	11	12	Mean
Male	3.0	3.3	3.0	2.5	4.0	2.0	2.0	2.8	1.8	3.0	4.0	2.0	2.8
Female	1	2	2	3	3	3	1	3	3	2	4	2	2.4
Population	4	5	5	5	5	5	3	5	5	5	8	4	4.9
Under 16 age	1.0	1.0	0.5	1.3	2.0	2.0	0.3	1.8	2.3	0.3	2.3	2.0	1.4
16–40 age	2.5	3.3	2.8	2.0	3.0	2.0	1.5	2.0	2.3	1.8	2.8	2.0	2.3
40–60 age	0	0	2	1	2	0.75	1	1.25	0.25	2	0	1.5	1.0
Above 60 age	0.5	1	0	1	1	0	0	0.25	0	0	0	1	0.4
Labor	3	3	5	3	3	3	3	3	3	3	4	4	3.3
Paddy size	0.21	0.51	0.21	0.59	0.59	0.21	0.15	0.67	0.11	0.11	0.39	0.22	0.33
Fallow size	0.32	3.03	1.37	1.23	1.23	0.62	0.29	1.15	0.66	0.33	1.69	2.31	1.19
Cash crop size	0.32	3.03	1.37	1.23	1.23	0.62	0.29	1.15	0.66	0.33	1.69	2.31	1.19
Production input	88	84	124	53	53	54	29	67	27	205	69	75	77
Rubber income	341	560	431	393	393	195	389	406	196	310	341	330	357
Chinese cardamom income	45	163	156	243	243	223	33	62	114	156	108	84	136
Tea/passion fruit income	47	82	126	109	109	104	32	55	25	73	65	35	72
Cereal crop income	3	91	4	37	37	26	2	0	3	42	36	5	24
Other income	1090	51	212	0	0	0	0	218	0	0	73	0	329
Gross person income	300	176	150	150	150	110	153	109	74	126	87	128	143

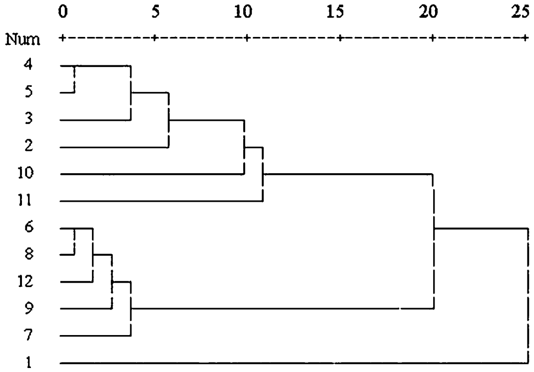

Figure 4. Dendrogram using Ward method of sampled households in Daka.

households prefer to select varieties with high yield in spite of bad quality for home consumption. Culture and traditions also influence what to grow in addition to labor and gender issues as pertaining to resource management. Socio-economic disparity underpins and helps to explain management diversity and agrobiodiversity among households as management diversity is helpful for biodiversity conservation (Muller 2002).

The exact nature of the relationship between household socio-economics on the one hand and species richness indices of biodiversity and agrobiodiversity, on the other, is very difficult to establish. Do households with higher income levels manage more or less biodiversity and agrobiodiversity? For example, it is reported that poorer households are currently facing more restricted access to community forests than 'less poor' or relatively better off households for some key forest products in Nepal (Adhikari et al. 2004). For example, some researchers have suggested that agricultural intensification is likely to lead to crop specialization and a loss of diversity while some researchers have argued that intensification maintains or even increases agro-diversity with highly population density (Conelly and Chaiken 2000). In addition, labor inputs were high considering the small size of the homegardens, although no clear relationships between labor investment and plant number were observed. (Mendez et al. 2001). Using principal component analysis, we focus to the correlation coefficient of household population, cash crop size and income, cereal crop income and production input in detail.

Fallow size, cash crop size, and cash crop income has significant positive correlation coefficients with species richness index of rubber plantation at 0.05 level of *t*-test, as well as cereal crop income has significant positive correlation coefficient with rubber plantation at 0.01 level of *t*-test (Table 6). With more cereal crop income from wet rice field, households prefer to transfer fallow fields into rubber plantation with extensive management to keep natural biodiversity. On the other hand, production input has negative correlation coefficients with species richness index of upland rice field and 3y fallow field at

Table 5. *F*-test of hierarchical cluster analysis of sampled households in Daka.

	Cluster 1		Cluster 2		Cluster 3		Cluster MS	df	Error MS	df	F	$F_{0.05}$	$F_{0.01}$
Households	1		2, 3, 4, 5, 10, 11		6, 7, 8, 9, 12								
Item	Average	S^2	Average	S^2	Average	S^2							
Population	4	–	5.5	1.5	4.4	0.8	3.3	2	1.2	9	1.77		
Cash crop income	433	–	677	14508.2	457	5884.3	132280.1	2	10675.3	9	7.08		
Cereal crop income	3	–	41	785.4	7	113.7	3146.5	2	486.8	9	3.72		
Other income	1090	–	56	6811.6	44	9504.8	419.3	2	8008.6	9	61.88		
Gross person income	300	–	140	920.2	115	838.7	1709.1	2	884.0	9	16.23		
Production input	88	–	98	3442.4	50	474.8	6179.3	2	2123.5	9	1.48	4.26	8.02

Table 6. Correlation coefficient of species richness indices and main socio-economics component of sampled households.

	Homegarden		Rubber plantation		Upland field		3y fallow field		*Cassia siamea*	
	D_{Gl}	t	D_{Gl}	t	D_{Gl}	t	D_{Gl}	t	D_{Gl}	t
Male	0.10	0.28	0.46	1.54	0.39	1.23	−0.50	−1.79	0.71	3.72
Female	0.38	1.20	0.18	0.50	−0.15	−0.40	0.25	0.69	−0.04	−0.10
Population	0.37	1.12	0.21	0.58	−0.38	−1.19	−0.16	−0.44	0.19	0.52
Paddy size	0.26	0.75	0.41	1.29	0.28	0.80	−0.05	−0.14	0.18	0.49
Fallow size	0.02	0.06	0.67	3.27	−0.01	−0.02	−0.29	−0.82	0.50	1.74
Cash crop size	0.02	0.06	0.67	3.27	−0.01	−0.02	−0.29	−0.82	0.50	1.74
Cash crop income	0.23	0.64	0.62	2.62	−0.05	−0.14	−0.46	−1.55	0.36	1.08
Cereal crop income	0.41	1.29	0.90	12.60	0.21	0.58	−0.01	−0.02	0.66	3.04
Other income	0.10	0.27	−0.45	−1.49	−0.07	−0.18	−0.35	−1.05	0.07	0.19
Gross person income	0.24	0.67	−0.08	−0.22	0.16	0.43	−0.45	−1.49	0.30	0.87
Production input	−0.20	−0.54	−0.27	−0.76	−0.59	−2.40	−0.72	−3.94	0.09	0.23
$t_{0.05,\ n\ =\ 7}$										2.37
$t_{0.01,\ n\ =\ 7}$										3.50

Table 7. Correlation coefficient of Agro-species richness indices and main socio-economics component of sampled households.

	Homegarden		Rubber plantation		Upland rice field		3y fallow field		*Cassia siamea*	
	D'_{Gl}	t	D'_{Gl}	t	D'_{Gl}	t	D'_{Gl}	t	D'_{Gl}	t
Male	−0.05	−0.13	0.26	0.74	0.27	0.78	−0.52	−1.89	0.80	5.77
Female	0.45	1.52	0.22	0.62	−0.54	−2.03	0.31	0.92	−0.24	−0.67
Population	0.27	0.77	0.19	0.51	−0.71	−3.81	−0.17	−0.47	−0.05	−0.13
Paddy size	0.16	0.45	0.23	0.66	−0.01	−0.02	−0.05	−0.12	0.40	1.24
Fallow size	−0.29	−0.84	0.54	2.02	−0.48	−1.68	−0.56	−2.18	0.44	1.46
Cash crop size	−0.29	−0.84	0.54	2.02	−0.48	−1.68	−0.56	−2.18	0.44	1.46
Cash crop income	0.08	0.21	0.53	1.98	−0.26	−0.74	−0.47	−1.61	0.63	2.76
Cereal crop income	0.03	0.08	0.83	6.95	−0.39	−1.21	−0.29	−0.85	0.54	2.00
Other income	−0.03	−0.08	−0.59	−2.42	0.46	1.54	−0.25	−0.72	0.08	0.22
Gross person income	0.02	0.05	−0.19	−0.51	0.53	1.97	−0.39	−1.20	0.43	1.41
Production input	−0.31	−0.92	−0.26	−0.75	−0.18	−0.48	−0.67	−3.21	0.37	1.13
$t_{0.05,\ n\ =\ 7}$										2.37
$t_{0.01,\ n\ =\ 7}$										3.50

0.05 level and 0.01 level of *t*-test respectively. Production input includes weedicide, and this has destroyed natural vegetation greatly.

Meanwhile, cereal crop income has significant positive correlation coefficient with agro-species richness index of rubber plantation at 0.01 level of *t*-test (Table 7). Households with more income from wet rice fields prefer to interplant more kinds of cash crops with rubber leading to more and stable cash income in spite of market changes. This finding is similar to the diversity of the agricultural production was found to be important in ensuring food security and reducing the risk of temporary food shortages in a Philippine upland region (Frei and Becker 2004). On the other hand, other income such as off-farm income has negative correlation coefficients with agro-species richness index of rubber plantation at 0.05 level of *t*-test. For example, agroforestry systems of rubber plantation with tea and with pineapple need more labor to manage. Household with more off-farm income prefer to monoculture rubber with limitation of labor. Population has negative correlation coefficients with agro-species richness index of upland rice field at 0.01 level of *t*-test for household food demand mainly.

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References

Adhikari B., Di Falc S. and Lovett J.C. 2004. Household characteristics and forest dependency: evidence from common property forest management in Nepal. Ecological Economics 48(2): 245–257.

Backes M.M. 2001. The role of indigenous trees for the conservation of biocultural diversity in traditional agroforestry land use systems: the Bungoma case study: in-situ conservation of indigenous tree species. Agroforestry Systems 52(2): 119–132.

Brookfield H. and Padoch C. 1994. Appreciating agrodiversity: a look at the dynamics and diversity of indigenous farming systems. Environment 36(5): 6–11. 36–45.

Chunlin L., Heng L., Zhiqin O., Xiangyun Y., Qin L. and Bruce T. 2003. Strategies for agrobiodiversity and promotion: a case study from Yunnan, China. Biodiversity and conservation 12(6): 1145–1156.

Coffey K. 2002. Quantitative methods for the analysis of agrodiversity. In: Brookfield H. and Padoch C. (eds), Cultivating Biodiversity – Understanding, Analysing and Using Agricultural diversity. ITDG Publishing, London pp.78–95.

Conelly W.T. and Chaiken M.S. 2000. Intensive farming, agro-diversity, and food security under conditions of extreme population pressure in Western Kenya. Human Ecology 28(1): 19–51.

Frei M. and Becker K. 2004. Agro-biodiversity in subsistence-oriented farming systems in a Philippine upland region: nutritional considerations. Biodiversity and Conservation 13(8): 1591–1610.

Fujisaka S., Escobar G. and Jeneklaas E. 1997. Plant community diversity relative to human land uses in an Amazon forest colony. Biodiversity and Conservation 7(1): 41–57.

Hardon-Baars A. 2000. The role of agrobiodiversity in farm-household livelihood and food security: a conceptual analysis. In: Almekinders C. and Boef de W. (eds), Encouraging diversity. Intermediate Technology Publications Ltd, London pp. 31–35.

Huijun G., Zhiling D. and Brookfield H. 1996. Agrobiodiversity on the ground and among the people: methodology from Yunnan. PLEC News and Views 6: 14–22.

Huijun G. and Zhenyu W. 1998. Agrobiodiversity. In: Huijun G. and Chunlin L. (eds), Biodiversity of Yunnan, SW China. Yunnan Science and Technology Press, Kunming pp.112–113.

Huijun G., Padoch C., Yongneng F., Zhiling D. and Coffey K. 2002. Household level agrobiodiversity assessment. In: Brookfield H. and Padoch C. (eds), Cultivating Biodiversity – Understanding, Analysing and Using Agricultural diversity. ITDG Publishing, London pp.70–77.

Keping M. 1994. The measurement of community diversity. In: Biodiversity Committee of Chinese Academy of Sciences. (eds), Principles and Methodologies of Biodiversity Studies. Chinese Science and Technology Press, Beijing pp.141–165.

V.E. Mendez, R. Lok and E. Somarriba 2001. Interdisciplinary analysis of homegardens in Nicaragua: micro- zonation, plant use and socioeconomic importance. Agroforestry Systems 51(2): 85–96.

Montecinos C. and Salazar R. 2000. The CBDC programme: an experiment in strengthening community management of agrobiodiversity. Encouraging diversity 128(133): 128–133.

Muller S. 2002. Diversity of management practices required to ensure conservation of rare and locally threatened plant species in grassland: a case study at a regional Sale (Lorraine France). Biodiversity and Conservation 11(7): 1173–1184.

Pinedo-Vasquez M., Pasqualle J.B., Torres D.D.C and Coffey K. 2002. A tradition of change: the dynamic relationship between biodiversity and society in sector Muyuy, Peru. Environmental Science & Policy 5(1): 43–53.

Rerkasem K., Yimyam N., Korsamphan C., Thong-ngam C. and Rerkasem B. 2002. Agrodiversity lessons in mountain land management. Mountain Research and Development 22(1): 4–9.

Uppeti B.R. and Uppeti Y.G. 2002. Factors leading to agro-biodiversity loss in developing countries: the case of Nepal. Biodiversity and conservation 11(9): 1607–1621.

Wood D. and Lenné J.M. 1997. The conservation of agrobiodiversity on-farm: questioning the emerging paradigm. Biodiversity and Conservation 6(1): 109–129.

Yuming Y., Kun T. and Hao Jiming 2004. Biodiversity and biodiversity conservation in Yunnan, China. Biodiversity and Conservation 13(4): 813–826.

Zapfack L., Engwald S. and Sonke B. 2002. The impact of land conversion on plant biodiversity in the forest zone of Cameroon. Biodiversity and Conservation 11(11): 2047–2061.

Zarin D.J., Huijun G. and Enu-Kwesi L. 2002. Guidelines on the assessment of plant species in agricultural landscapes. In: Brookfield H. and Padoch C. (eds), Cultivating Biodiversity—Understanding, Analysing and Using Agricultural diversity. ITDG Publishing, London pp.57–69.

Zhigang G. (eds) 1999. Analysis Methods on Social Statistics: Apply of SPSS Software. China Renmin University Press, Beijing.

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Conservation and documentation of the medicinal plant resources of India

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Abstract. In India, activities in the field of medicinal plants, including conservation of germplasm, have been enhanced significantly during the past couple of decades and a huge volume of data is being generated out of these works. For maintaining the records in a consolidated form, documentation is required to store and manage all information on the related studies. In accordance with the implementation of various plans and programmes, some pioneer organisations started developing databases on medicinal plants. Based on the knowledge on contemporary works, as collected from published literature and websites, this article presents information on current activities in India in two important aspects of the field, namely, (1) conservation of medicinal plants; and (2) management of data generated from such studies. Another important aspect of the article is the announcement of a plant conservation related software, 'PlantCon'. This digitised database contains data of 40 selected nationally prioritised medicinal plants (list enclosed). The notable difference of 'PlantCon' from other databases lies in its conservation-related information which is up-to-date and covers a wide area of Indian geographical sites. The database provides information in a user-friendly manner.

Introduction

India is one of the world's top 12 megadiversity countries (Singh and Chowdhery 2002) with 10 biogeographic regions (Rodgers and Panwar 1990); in addition it has over 40 sites which are known for their high endemism and genetic diversity (Nayar 1996). Myers et al. (2000), in their updated list of world's biodiversity hotspots, included two from India. The climatic and altitudinal variations, coupled with varied ecological habitats of this country, have contributed to the development of an immensely rich vegetation with a unique diversity in medicinal plants which provides an important source of medicinal raw materials for traditional medicine systems as well as for pharmaceutical industries in the country and abroad.

As a result of the increasing demand for medicinal plants, most of which is still met by wild collection, a constant pressure is created on existing resources, leading to continuous depletion of some of the species in the forests, and at the same time forest land is losing its natural flora at an alarming rate – 1.5 m.ha. every year – and what is left at present is only 8% against a mandatory 33% of the geographical area (Shivarajan and Balachandran 1999). Survey reports also show that supplies of some of the medicinal raw materials are running short in the pharmaceutical industries in India (Report of the Task Force: Tewari 2000). To control the situation, various measures like commercial cultivation, habitat conservation, setting up of natural reserves, implementation of laws for restricting the export of plants (Rao et al. 2003), etc., have been taken up. Resource development by cultivation and conservation of useful medicinal plants is, therefore, a matter of serious concern. Initiatives have been taken in this respect at various Government and non-Government sectors, and documentation of these works has become a necessary part of the programme. With rapid advancement in information technology, storage and retrieval of data using electronic devices are felt to be more useful than publishing in journals or books, because this helps in speeding up the searching process for relevant material.

In the present communication, an attempt has been made to present an overview of the activities on medicinal plants and their conservation that has been undertaken by major institutions/organisations in the country, and to discuss briefly about documentation and management of data generated in the field. With this objective in mind, a digital database has been developed incorporating data related to medicinal plants and their conservation in India. This database could also serve the purpose of establishing a nation-wide network among the people involved in similar work.

Medicinal plant conservation – Indian scenario

India has more than one fourth (8000) of the world's known medicinal plant species (30,000), of which 90% are found in forest habitats (Krishna Kumar and Katakam 2002). Along with the awareness of the need for biodiversity conservation, conservation of medicinal plants in particular is one of the most burning issues faced today in India. Through conservation, plant species are preserved and protected from various environmental hazards, including those caused by human interference. This process also allows a plant's natural regeneration in its own habitat. Conservation at the site where plants occur naturally, i.e., 'habitat conservation' or '*in situ* conservation', is the most common method of conservation. In addition to this, with the help of advanced technologies applied in conservation research, cultivation of germplasms away from their original habitats has become a common practice. This method, known as '*ex situ* conservation', has gained significant importance because it is used for safeguarding species that are at risk of destruction, replacement and genetic distortion. At present, about 10 million hectares, i.e., 4.5% of the geographical area of India, are under the *in situ* conservation programme (Singh and Chowdhery 2002) which includes setting up of biosphere reserves, sanctuaries, national parks, sacred groves and protected areas. The *ex situ* conservation programmes involve collection, preservation, multiplication and dissemination of economically important, endemic, rare and threatened species germplasms.

Medicinal plant conservation centres in India

As in many other countries, various programmes on medicinal plants have been adopted in India and different strategies are employed for their conservation. Activities at the national level are being carried out in a number of organisations, of which important roles are being played by major institutions funded by the Government of India. The Council of Scientific and Industrial Research (CSIR) institutes involved in such programmes are Central Institute of Medicinal and Aromatic Plants (CIMAP), National Botanical Research Institute (NBRI), Central Drug Research Institute (CDRI) and the Regional Research Laboratories (RRLs) at Jammu, Bhubaneswar, Jorhat, Palampur, Bhopal and Thiruvananthapuram. The Indian Council of Agricultural Research (ICAR) implements an All India Coordinated Research Project on Medicinal and Aromatic Plants in association with the National Bureau of Plant Genetic Research (NBPGR), National Research Center for Medicinal and Aromatic Plants (NRCMAP) and Indian Institute of Horticultural Research (IIHR).

The activities of Botanical Survey of India (BSI), supported by the Department of Environment and Forests, Government of India, include establishment of regional circles and experimental gardens at different geographic regions of India, viz., Dehradun (Northern Circle), Allahabad (Central Circle), Shillong (Eastern Circle), Pune (Western Circle), Coimbatore (Southern Circle) and Port Blair (Andaman and Nicobar). Three other stations are at Jodhpur (Arid Zone), Gangtok (Sikkim–Himalaya Circle) and Itanagar (Arunachal Pradesh Field Station). It is known from a very recent report (Sanjappa 2004) that 10 experimental botanical gardens are making efforts to rehabilitate medicinal plants that are under serious threat. The Indian Council of Forest Research (ICFRE) has undertaken a programme for developing '*Vanaspati Van*' (i.e. Reserve Forest) and cultivation of medicinal plants. G.B.Pant Institute of Himalayan Environment and Development, an institute of the Ministry of Environment and Forest, Government of India, conserves the biological diversity of North-Western Himalayan region. Tropical Botanical Garden and Research Institute (TBGRI) in Kerala has undertaken a major programme on the conservation and sustainable use of the medicinal plant wealth of peninsular India. Major activities of TBGRI include development of display garden, field gene bank, *in vitro* gene bank and seed gene bank. This is a part of the G-15 GBMAP (Gene Bank for Medicinal and Aromatic Plants) programme sponsored by the Department of Biotechnology (DBT), Government of India. Three cryo-preservation gene banks for medicinal plants have been established by DBT. The Tropical Forest Research Institute at Jabalpur emphasises cultivation of medicinal plants that can be grown among trees.

Apart from these Government and non-Government Organisations, several industries and private organisations promote commercial cultivation of medicinal plants (Shah and Kalakoti 1996; Bhatt 2002; Nair 2002; Purohit and Vyas 2004) by farmers.

Documentation and digitisation of information on medicinal plants in India

The worldwide increased activity in conservation, cultivation and use of medicinal plants towards the end of the past millennium is reflected in the magnitude of the work in this field, as evidenced by the information documented through published literature. Until the early 1970s, printed publications were the almost exclusive means available for recording and disseminating all scientific information (Bhatt 1995). But, with the developments in information technology and telecommunications, literatures are being presented to the media in the electronic format in addition to hard copies. Now-a-days, a number of major journals have websites. Attempts have also been made subsequently to pool and compile data from various sources and to present them in a comprehensive form. The databases thus developed are available to users through online vendors and CDROMs.

Digitisation of information, i.e. development of electronic databases, is necessary in the study of medicinal plants for thorough understanding of important genetic resources. A large number of information sources is now accessible on the World Wide Web, providing comprehensive information on pharmacology, agriculture, management of natural resources, economic properties of the herbs, traditional herbal drugs, active ingredients, plant parts used, biological activities, therapeutic uses, chemical constituents, etc. (Sharma et al. 2002). While data on medicinal plant activities covering such a vast area have been computerised, information on conservation via the electronic media is limited and is in scattered form. However, information in this sector is necessary to all concerned in dealing with the development of sustainable alternatives to destructive harvesting and over-exploitation of useful medicinal plants. Several groups in India have, therefore, initiated activities in this emerging field. The Bioinformatics Centre of TBGRI has been organising centralised online databases: ‘Plant Info’, provides data on endemic medicinal plants and trees of Kerala, ‘Garden Info’ contains data on plants conserved in TBGRI, and ‘Seed Pack’ is a database on the seed bank of TBGRI. INMEDPLAN (Indian Medicinal Plants National Network of Distributed Databases) is an initiative network of several Indian organisations with expertise in different aspects of medicinal plants to build a multidisciplinary (botanical, horticultural, pharmacological and other) information pool by sharing their resources. The information is provided on request to the network secretariat at FRLHT, Bangalore. FRLHT's online databases are 'Encyclopaedia of Indian Medicinal Plants' containing details of around 7361 plant species and 'Medicinal Plant Conservation Concern', focusing on 880 species of traded medicinal plants of India.

National Institute of Science Communication & Information Resources (NISCAIR) has developed a computerised version of the bimonthly abstracting journal, The Medicinal and Aromatic Plant Abstract (MAPA). The data from 1988 onwards (about 30,000 records) are held in electronic form and distributed in CDROMs. CDRI, Lucknow has developed the Natural Products Database, NAATS, which contains factual information on medicinal plants. Detailed data on botanical characters, collection site details, pharmacological screening results, chemical structures of active constituents, uses in folk medicine and in established traditional medicine are provided. Central Institute of Medicinal and Aromatic Plants CIMAP) has developed databases – REFMAP (References on Medicinal and Aromatic Plants) and MAPI (Major Aromatic Plants of India) – having compiled and collated information on medicinal and aromatic plants.

Recently, BSI has set up a number of computer centres in their regional circles with the objective of developing a computerised National Data Base for systematic storage and retrieval of data related to herbarium collections, live collections, plant genetic resources, plant distribution and nomenclature. The Southern Circle at Coimbatore has a mainframe computer and PCs mainly engaged in databasing of National Flora and Type collections. The computer centre at North Circle, Dehradun, has established a computerised database on medicinal plants. The Environmental Information System (ENVIS) Centre on Floral Diversity of BSI, Kolkata, has developed the databases 'COBOMAN' for input of data on rare and threatened plants of India, 'Medicinal Plants' for providing information on important medicinal plants, and 'CITES Plants' which provides information on plants which are restricted for export.

Table 1 presents a precise description of the existing electronic databases which have already been developed in India and made available to the users.

Electronic database developed at the Bose Institute

Rapid advancements in medicinal plant conservation science, in keeping with the high-technology methods (though most of these are still in the experimental stage) of storage and preservation, make it necessary to create new databases incorporating data of relatively current studies. Sobral (2001), in a recent study on plant conservation, has emphasised the inadequate management system related to plant germplasm information. Consequently, in India, building up of a national medicinal plant conservation database is considered to be the need of the hour (Prajapati et al. 2003).

During a considerably long period of studies on medicinal plant conservation (*in vitro* and field gene bank) at the Bose Institute, a large volume of data

Table 1. Existing electronic database systems on medicinal plants in India.

Sr. no.	Name of database	Expanded form of the abbreviated name of the database	Special features of database	Institutions/organisations creating database
1.	CITES Plants	Convention on International Trade in Endange red Species	Appendices of 3 categories of plants – threatened, vulnerable and that require close vigil with pictorial identification	BSI, ENVIS Howrah 711103, WB www.envisbsi.org/citesplant.htm
2.	COBOMAN	Not available	Scientific name, image, status, distribution, habitat and ecology, conservation on measures taken and proposed, biology and potential value, cultivation, description, reference	BSI, ENVIS ww.envisbsi.org/ FAMILY.htm
3.	Encyclopedia of Indian Medicinal plant		Scientific name, trade details, image, propagation agro-technique, seed storage, distribution, ecomap, pharmacology, pharmacognosy	FRLHT, Bangalore http://encyclopedia frlht.org.in/
4.	Garden Info	Garden Information	Data on plants conserved at TBGRI	TBGRI, Thiruvanthapuram, Kerala 695562
5.	MAPA	Medicinal & Aromatic Plant Abstract	Computerised version of bi-monthly Abstracting journal on medicinal and aromatic plants	NISCAIR, Dr. K.S. Krishna Marg, NewDelhi 110012

6.	MAPI	Major Aromatic Plants of India	Compiled and collated information on aromatic plants of India	CIMAP, Lucknow 226015, UP
7.	Medicinal Plants		Image, synoname, English, vernacular, trade name, traditional and modern use, phytography, distribution, ecology, cultivation, chemical content	BSI, ENVIS www.envisbsi.org/ medi.htm
8.	Medicinal Plants of Coservation Concern		Scientific name, family, habit, threat status, use, distribution, vernacular name, trade name, taxon, data sheet	FRLHT, Bangalore http://envis.frlht.org.in /iucnlist.php
9.	NAATS	Natural Products Database	Botanical features, collection details, pharmacological data, chemical structure of active constituents, uses in folk and traditional medicine, literature detail	CDRI Chattar Manzil Palace Lucknow 226001 UP
10.	Plant Info	Plant Information Series	Scientific name, English, Sanskrit, Malayalam name, uses in medical systems	TBGRI, www.tbgri.org /plantinfo/ plant01042003_Local/index.asp
11.	REFMAP	References on Medicinal and Aromatic Plants	Information on literature references on medicinal and aromatic plants	CIMAP
12.	Seed Pack		Data on seed bank at TBGRI	TBGRI

has been accumulated from in-house research as well as from the works going on in different centres of the country either through personal communication or from published literature. Furthermore, Bose Institute Plant Conservation group has taken up an initiative in developing a computerised database on medicinal plants, which is felt necessary in this context. To do the proposed work, 40 medicinal plants have initially been selected, most of which are prioritised by the National Medicinal Plant Board and a few by State Plant Boards. These plants are found to be used frequently in Ayurvedic formulations and have proved to be important in our socio-economic system. So, current knowledge on this group of plants will help botanical and Ayurvedic researchers, forest officials and traders throughout the country, irrespective of the geographic location of the working station.

The database provides information in a user-friendly manner. Though emphasis has been given on the conservation aspect, the other necessary information it contains are the plants' identities (common names, generic and species names) based on current nomenclature, morphological descriptions of plants (inclusive of vegetative and reproductive features) with images, usage of plant parts against diseases, natural distribution of plants, etc. This database is unique in presenting not only the current measures taken for conserving important medicinal plant germplasms but also in providing the contact addresses of centres where the plants are being conserved in storage (of seeds) or under *in vitro* conditions, or are cultivated in fields.

The database, which is now being made available to users on CDROMs, should be of practical help by presenting a clear idea about what, how and where the plants are conserved. The information will also be helpful in planning future programmes in conservation research.

Screen views of 'PlantCon'

The major divisions of the database are : (1) a plant's identity, that includes its nomenclature; (2) *in situ* conservation; (3) *ex situ* conservation; (4) conservation programmes of different centres; (5) conservation-oriented bills, laws and relevant information; (6) details of conservation centres (*ex situ*); and (7) relevant conservation terminology. A schematic diagram of the database is shown in Figure 1.

Other subdivisions include, morphology (with image), medicinal usage and natural distribution of the plants.

Data collection

Data for the identity, morphology, usage and distribution of 40 nationally prioritised medicinal plants (list of names in Table 2) were collected and compiled mostly from current literature; systematic position of plants and their current threatened status were checked from ENVIS centres of the BSI and

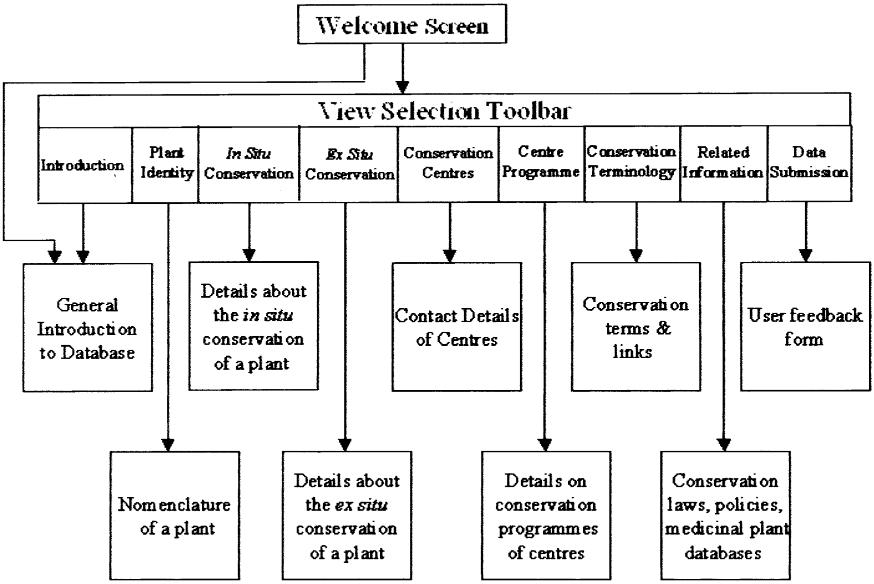


Figure 1. A schematic presentation of the principal views of the database 'PlantCon'.

FRLHT. Images presented in the database are scanned photographs of plants from our own collection (Bose Institute, Department of Botany) as well as from those of others who have been kind enough to give their consent for incorporating photographs from their online documents. Data on *in situ* and *ex situ* conservation were collected, in most cases, through personal correspondence with different Government and non-Government organisations/institutions/centres/gardens, etc., situated in India. Regarding advanced types of conservation measures, information on *in vitro* culture, storage, etc., have been collected from printed reports, the Internet and from our own *in vitro* gene bank.

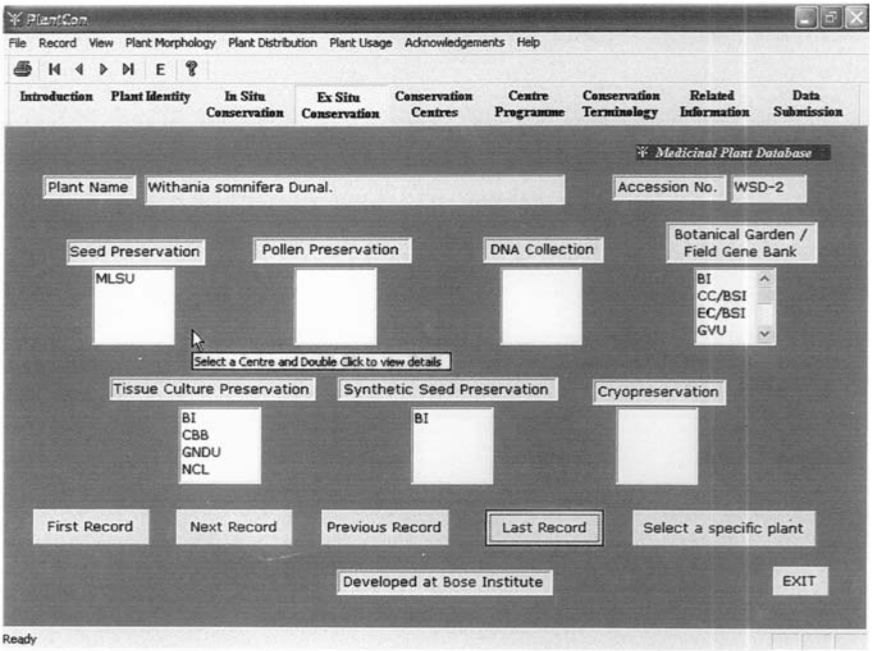
User's benefit from the database

Detailed information related to conservation, such as the names of the plants under conservation, the types of measures followed, places where the practices are carried on, the names of the units (organisations) involved in the various programmes and the addresses of the contact persons for correspondence are all necessary to those working in this field. To researchers in the field, areas still lacking in information, e.g., plant tissue conservation through pollen banks, DNA banks or cryo-preservation, could provide guidelines in pursuing further research in these sectors.

Table 2. List of plants.

Sr. no.	Name of plants
1.	*Abrus precatorius* L.
2.	*Aconitum ferox* Wall. Ex Seringe
3.	*Aconitum heterophyllum* Wall. Ex Royle Se
4.	*Aegle marmalos* (L) Correa EX Schultz
5.	*Ambroma augusta* (L.) L.f.
6.	*Andrographis paniculata* (Burm.F) Wallich
7.	*Asparagus racemosus* Willd.
8.	*Bacopa monnieri* (L.) Pennell
9.	*Berberis aristata* DC.
10.	*Bergenia ciliata* (How.) Stern.
11.	*Cassia senna* Linn.
12.	*Chlorophytum borivilianum* (Roxb.) Baker
13.	*Coleus forskohlii* (Poir.) Briq.
14.	*Commiphora wightii* (A.) Bhandari
15.	*Coptis teeta* Wall.
16.	*Emblica officinalis* Gaertn.
17.	*Garcinia cambogia* (Gaertn.) Desr.
18.	*Gloriosa superba* Linn.
19.	*Glycyrrhiza glabra* Linn.
20.	*Gymnema sylvestris* R.Br.
21.	*Hemidesmus indicus* (L.) Schult.
22.	*Kaempferia galanga* Linn.
23.	*Myristica fragrans* Houtt.
24.	*Nardostachys jatamansi* DC.
25.	*Ocimum sanctum* L.
26.	*Phyllanthus amarus* Schum. & Thonn.
27.	*Picrorhiza kurroa* Royle Ex Benth
28.	*Piper longum* Linn.
29.	*Plantago ovata* Forsk.
30.	*Psoralea corylifolia* Linn.
31.	*Rauvolfia serpentina* (L) Benth Ex Kurz
32.	*Santalum album* Linn.
33.	*Saraca asoca* (Roxb.) De Wilde
34.	*Saussurea costus* (Fale.) Lipsch.
35.	*Solanum nigrum* Linn.
36.	*Swertia chirata* (Roxb. Ex. Flem.) Kar.
37.	*Tectona grandis* L.F.
38.	*Tinospora cordifolia* (Willd.) Hook. F. & Thomas.
39.	*Viola odorata* Linn.
40.	*Withania somnifera* Dunal.

In trade, authenticity of raw material is a major area of concern. This matter is related primarily to a plant's identity, stated by its common name, botanical name and morphology. Due to the lack of knowledge about the collecting material, there may be chances of adulteration of raw materials supplied to the industry. Data of popularly used commercial plants and their detailed morphological description with images could directly help users in the commercial



Plant Name: Withania somnifera Dunal.
Accession No.: WSD-2
Seed Preservation: MLSU
Pollen Preservation:
DNA Collection:
Botanical Garden / Field Gene Bank: BI, CC/BSI, EC/BSI, GVU
Tissue Culture Preservation: BI, CBB, GNDU, NCL
Synthetic Seed Preservation: BI
Cryopreservation:

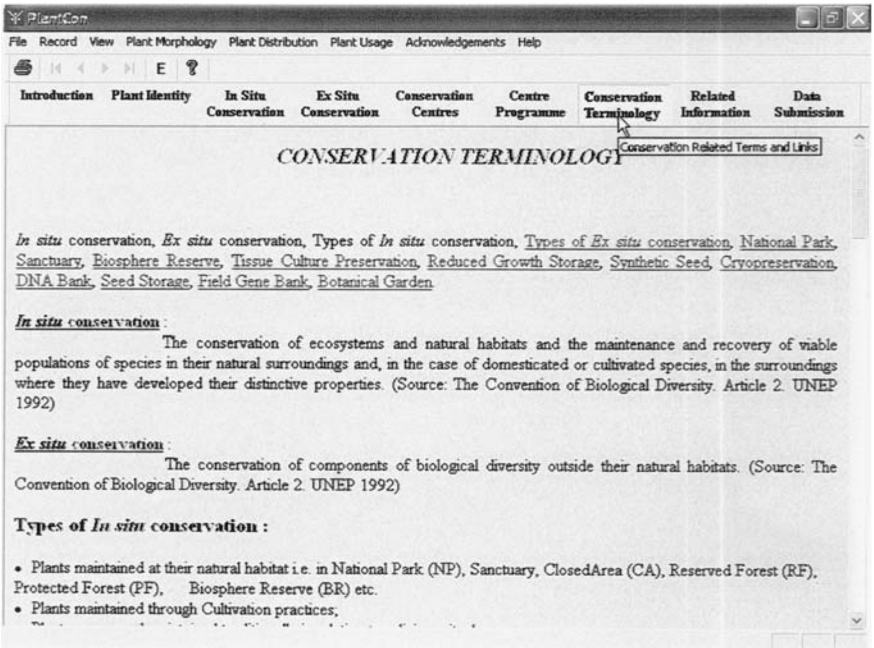
Figure 2. A screenshot of '*Ex situ* Conservation' view of the database 'PlantCon'.

field. The information on conservation measures and possible sources/regions where the plants are being cultivated or conserved could help people to be conscious about sustainable collection.

Implementation of the 'PlantCon' Database

A relational database system (RDBMS) software has been designed and implemented using MS-Access working under the MS Windows 98 Operating System (OS). A total of 13 fully normalised tables have been used to provide information on plant identity, morphology, usage, distribution, *in situ* and *ex situ* conservation status and conservation centres. The data for each plant are identified by a unique accession number (primary key), which facilitates the access of data from different tables as well as the design of queries.

A menu driven user friendly front-end to the database has been created using MS Visual C++ (Enterprise Edition version 6.0). There are a total of seven views for displaying data under different categories. Each of these views enables the user to browse through the database and also to search data related to specific plants or conservation centres. Images of plants can be seen from the view related to plant morphology. Two representative screen shots of the user interface are presented in Figures 2 and 3.



CONSERVATION TERMINOLOGY

In situ conservation, *Ex situ* conservation, Types of *In situ* conservation, Types of *Ex situ* conservation, National Park, Sanctuary, Biosphere Reserve, Tissue Culture Preservation, Reduced Growth Storage, Synthetic Seed, Cryopreservation, DNA Bank, Seed Storage, Field Gene Bank, Botanical Garden

***In situ* conservation** :

The conservation of ecosystems and natural habitats and the maintenance and recovery of viable populations of species in their natural surroundings and, in the case of domesticated or cultivated species, in the surroundings where they have developed their distinctive properties. (Source: The Convention of Biological Diversity. Article 2. UNEP 1992)

***Ex situ* conservation** :

The conservation of components of biological diversity outside their natural habitats. (Source: The Convention of Biological Diversity. Article 2. UNEP 1992)

Types of *In situ* conservation :

- Plants maintained at their natural habitat i.e. in National Park (NP), Sanctuary, ClosedArea (CA), Reserved Forest (RF), Protected Forest (PF), Biosphere Reserve (BR) etc.
- Plants maintained through Cultivation practices;

Figure 3. A screenshot of 'Conservation Terminology' view of the database 'PlantCon'.

In addition to these, other views with details of the programmes undertaken by different centres, terminology related to conservation and other conservation related information with possible hyperlinks have been provided. There is also a provision for on-line submission of new data from users, which could be incorporated in future versions of the database.

The software has been tested to execute different hardware configurations running the Windows 98 Operating System and higher versions (Windows 2000 and Windows XP). The beta-version of the database may be provided to users on request.

Conclusion

Herbal medicines occupy a vital sector of health care system in India and medicinal plants represent a major national resource. It is important to ensure their conservation for sustainable utilization. The present paper highlights this important aspect. Development of a database 'PlantCon' containing structured compilation of hitherto scattered data on conservation of 40 prioritised medicinal plant (Table 2) could help in filling up the lacunae still felt in research, trade and other spheres of medicinal plant sector.

References

Bhatt K.K.S. 1995. Medicinal Plant Information Databases. Non-wood Forest Product FAO – Food and Organisation of the United Nations, Viale dells di Caracalla, 00100 Rome, Italy.

Bhatt R.C. 2002. Farmers are ready to cultivate medicinal, aromatic and other economic species in Uttaranchal. MFP News XII: 13–14.

Krishna Kumar A. and Katakam A. 2002. Credit for conservation. Frontline 19: 9–22.

Myers N., Mittermeier R.A., Mittermeier C.G., daFonseca G.A.B. and Kent J. 2000. Biodiversity hotspots for conservation priorities. Nature 403: 853–858.

Nair G.K. 2002. KAU plans to develop medicinal plants. The Hindu Business Line – Financial Daily from the Hindu Group of Publication May 17, Friday.

Nayar M.P. 1996. Hotspots of Endemic Plants of India, Nepal and Bhutan, Thiruvananthapuram, TBGRI. Vedams eBooks, New Delhi, India.

Prajapati N.D., Purohit S.S., Sharma A.K. and Kumar T. 2003. A Hand Book of Medicinal Plants – A Complete Source Book. Agrobios (India), Jodhpur.

Purohit S.S. and Vyas S.P. 2004. Medicinal Plant Cultivation: A Scientific Approach including Processing and Financial Guidelines. Agrobios (India), Jodhpur.

Rao C.K., Geetha B.L. and Suresh G. 2003. Red list of Threatened Vascular Plant Species in India. Director, Botanical Survey of India, ENVIS Centre for Floral Diversity, Botanical Survey of India, Central National Herbarium, Indian Botanic Garden, Howrah (India).

Rodgers W.A. and Panwar H.S. 1990. A Biogeographical Classification for Conservation Planning. Wildlife Institute of India, Dehradun, India.

Sanjappa M. 2004. Medicinal Plants and their Conservation with Reference to Peninsular India. Seminar Proceedings of National Seminar on Medicinal Plants, Plant Products & Patents, 30th September–3rd October, Kolkata, India.

Shah V. and Kalakoti B.S. 1996. Development of *Coleus forskahlii* as a medicinal crop. Proceedings of the International Conference on Domestication and Commercialisation of Non-timber Forest Products in Agroforestry Systems hosted by ICRAF, Nairobi, Kenya, 19–23 Feb.

Sharma A., Dwivedi N. and Khanuja S.P.S. 2002. Sourcing information on R&D and trade of medicinal and aromatic plants through web data mining: some utility sites. Journal of Medicinal and Aromatic Plant Sciences 24: 82–103.

Shivarajan V.V. and Balachandran I. 1999. Ayurvedic Drugs and Their Plant Sources. Oxford and IBH Publishing Co. Pvt. Ltd., New Delhi, India, pp. 9.

Singh N.P. and Chowdhery H.J. 2002. Biodiversity conservation in India. In: Das A.P. (ed.), Perspective of Plant Biodiversity. Department of Botany, North Bengal University, West Bengal, India, pp. 501–527.9–11 November 2000, Bishen Singh Mahendra Pal Singh, Dehra Dun, India.

Sobral B.W.S. 2001. The role of bioinformatics in germplasm conservation & use. In: Engels J.M.M., Ramanatha Rao V., Brown A.H.D. and Jackson M. (eds), Managing Plant Genetic Diversity. Cabi Publishing, CAB International, Wallingford, Oxon, UK, pp.171–178.

Tewari D.N. 2000. Report of the Task Force on Conservation and Sustainable Use of Medicinal Plants, Government of India Planning Commission.

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Wildlife in the life of local people of the semi-arid Argentine Chaco

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Key words: Argentina, Armadillos, Chaco, Conservation, Hunting, Peccaries, Pediolagus, Tayassu, Wild meat

Abstract. The semi-arid Argentine Chaco is inhabited by mestizo people, who live on an economy of subsistence based on the use of natural resources and livestock ranching. I investigated the dietary and economic importance of wildlife for local people. Through interviews and participant observation, I found that wildlife is used primarily as food, providing about a third of the total meat consumed by local peasants. Local people use at least 26 species of wildlife although they concentrate on few species. Small species, Chacoan cavies and armadillos, are consumed most, representing 48% of the total wild meat consumed. Consumption of wild meat follows seasonal patterns determined by hunting methods, preferences for meat quality and species activity patterns. The consumptive value of wild meat is high in comparison with wages, but lower in comparison with forest exploitation. Illegal commercialization of wildlife is practiced mainly by villagers and by outsiders and it affects endangered species. Patterns of use of wildlife by local people differ from other Latin American groups in terms of the range of species hunted and the role that hunting plays in local people' livelihoods. The first steps towards conservation of this increasingly threatened region should involve decreasing hunting by local people of the more vulnerable species and controlling all illegal commercial hunting.

Introduction

Wildlife is an important resource for many people in Latin America, who use it for various purposes, although food and cash income are the most common uses (Prescott-Allen and Prescott-Allen 1982; Ojasti 1996; Fang et al. 1999; Robinson and Bennet 2000a; Fragoso et al. 2004; Silvius et al. 2004). Many studies have shown that subsistence hunting has a strong impact on wildlife populations, often producing local extirpations (Robinson and Bennet 2000b; Bennet and Robinson 2000; Cullen et al. 2004). Thus, when there is a tight and conflictive relationship between local people and wildlife, the challenge is to find a compromise between local people's needs and wildlife conservation. The role of wildlife in the life of local people, however, is highly variable, reflecting socio-economic, environmental and cultural differences.

Even tough mestizo people (non-indigenous) are the main wildlife users in Latin America (Ojasti 1996; Ortiz von Halle 2002), the importance of wildlife for them is poorly known (Smith 1976; Vickers 1984; Redford and Robinson 1987; Bodmer 1995; Ojasti 1996; Naranjo et al. 2004). Large numbers of mestizo peasants inhabit the poorest regions of Latin America and their hunting impacts wildlife populations (Bodmer et al. 1997; Ortiz von Halle 2002; Naranjo et al. 2004). For this reason, it is imperative to better understand the role of wildlife in their livelihoods.

Most studies on the use of wildlife by local people in Latin America have focused on humid tropical regions, but less attention has been paid to semi-arid ecosystems (Ojasti 1996; Robinson and Bennet 2000a; Silvius et al. 2004). A Latin American semi-arid system of great interest is the Chaco, one of the most endangered eco-regions of the world (Bucher and Huszar 1999; Zak et al. 2004) that harbors high levels of biodiversity and endemism (Mares 1992). The semi-arid Argentine Chaco is the least developed and poorest region of the country, inhabited by mestizo people who live spread throughout the forest in small settlements and in several villages. Peasants and villagers use wildlife for different purposes (Bolkovic 1999; Barabarán and Saravia-Toledo 2000; Barbarán 2001) and are apparently overharvesting some species (Altrichter and Boaglio 2004). As in many forested places in developing countries with growing human populations, the challenge in the Chaco is to implement wildlife conservation strategies that will not negatively affect the livelihoods of the local people. However, the necessary basic information on the economic and dietary importance of subsistence hunting for local people is lacking. I assessed the role of wildlife in the livelihoods of non-indigenous people in a semi-arid ecosystem by addressing the following objectives: (1) to determine the species hunted; (2) to identify the uses of wildlife; (3) to estimate the extent to which rural and village people depend on wild meat as a source of food and cash; (4) to determine temporal patterns of wildlife use; (5) to determine how the consumption of wild meat is related to the consumption of domestic meat.

Study area

The Chaco is a vast plain extending across part of Argentina, Bolivia and Paraguay. Originally the Chaco was parkland or savanna with patches of hardwood intermingled with grasslands (Bucher 1982). In recent decades, human activities have transformed parts of the Chaco into a dense thorny shrubland (Bucher and Huszar 1999). The Chaco is divided in three sub-regions based on an east–west rainfall gradient: humid, transition, and semi-arid Chaco (Morello and Adamoli 1968; Bucher 1982). The study area covers 1.2 million hectares of the semi-arid Chaco locally called '*Impenetrable*' (24°30′–25°30′ SL and 62°50′–61°40′ WL; Figure 1). The semi-arid Chaco is the driest and most markedly seasonal, with rainfall between 450 and 700 mm, most of which (80%) falls between October and April. The vegetation is a medium-tall xerophilous forest with a canopy layer of about 12 m tall

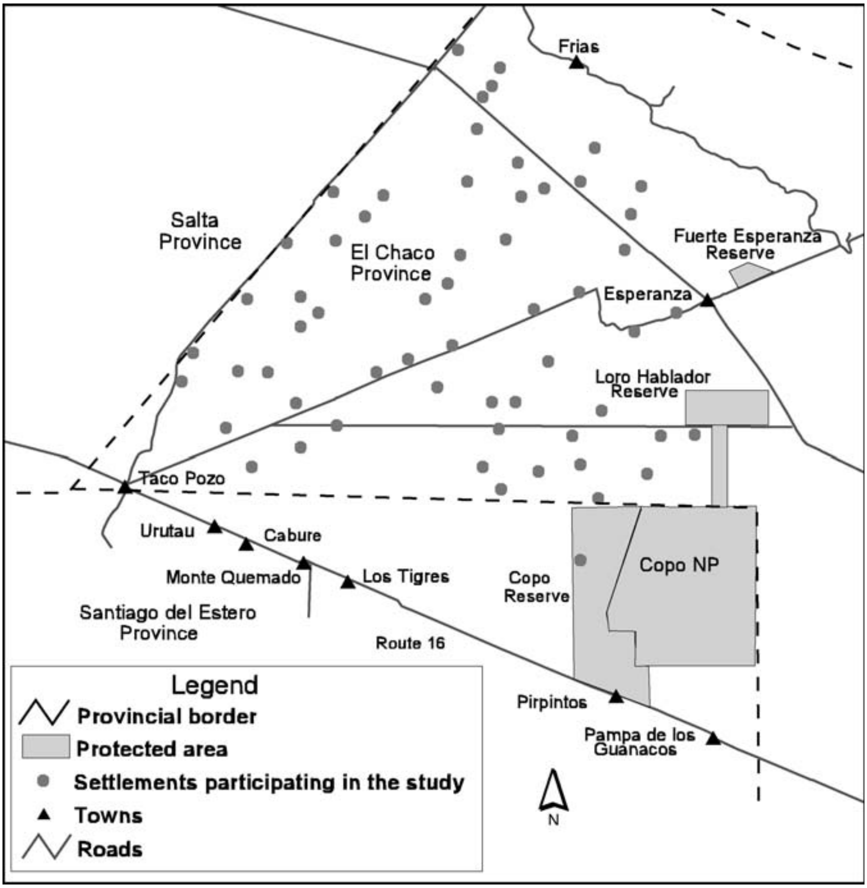

Figure 1. Study area.

surpassed by a few species of taller trees reaching 16–18 m (Bucher 1982). The dominant species of trees are *Schinopsis quebracho-colorado*, *Aspidosperma quebracho-blanco* and *Bulnesia sarmientoi*. The shrub layer is dominated by species of *Acacia*, *Mimosa*, *Prosopis*, and *Celtis*. Cacti *Opuntia* and *Cereus*, grasses and bromeliads are abundant in the understory.

The study area is mostly rural with people living in about 200 small settlements spread throughout the forest, separated from each other by about 5 km. Most of these settlements consist of one household, but some have up to seven. There are also several villages located along a paved inter-provincial road (Figure 1) with 20–1300 households. Rural peasants have a subsistence economy based on small-scale livestock ranching and forest exploitation for charcoal and fence posts. Most villagers are former peasants who moved into town. They have diverse sources of income, and many of them have farms.

Methods

Dietary importance of wildlife

I collected information on meat consumption among both rural peasants and villagers. However, different levels of detail were gathered from both populations. Rural peasants' diet in terms of meat consumption was recorded over a 1 year period. Villagers were interviewed only once and were asked to mention the wild species they had consumed over the past year and to estimate a monthly average frequency of consumption. Scientific names of wildlife are in Table 1.

Rural population: I randomly selected a sample of 58 rural households from different settlements (18% of the total number of settlements and 11% of the total number of households in the study area). I visited the selected families seven times from June 2001 to July 2003, and spend between a few hours and 3 days with them. To estimate the importance of wildlife as a source of food, I relied on interviews and people's records of their consumption of meat. From June 2002 to July 2003, a member of each household recorded every day the type of meat consumed in the house.

I used several means to assess the reliability of the information recorded by the people. My unexpected visits to families helped me to corroborate what they had recorded with what they were eating that day and previous days. My assistant and I talked with different members of the family at the same time, but separately as a further validation of the accuracy of responses. Local teachers assisted the research by collecting information on the wild meat that their students consumed during one month. By knowing the family origin of the students, I was able to compare the children's information with that provided by their families. I was also able to cross check some of the information with neighbors. I eliminated those cases where the information was dubious or inconsistent. At the end of the study, 38 families (from the original sample of 58) had kept consistent records of their consumption of meat during a complete year.

From the information collected by these families I determined the species consumed, frequency of consumption, seasonal patterns of consumption, proportions of wild and domestic meat consumed, and proportion of households that consume each type of wild meat. The variable "consumption of meat" was measured as days per year that each type of meat is consumed per household, and cannot be directly translated into number of animals consumed. I obtained averages of consumption for each type of meat among all households. For example, Chacoan cavy was consumed on average 32.9 days/year/household (Table 1). For seasonal comparisons of wild meat consumption, I considered two seasons as recognized by local people according to temperature, which correspond roughly to wet and dry season: hotter months (September–April) and colder months (May–August).

Table 1. Wild species consumed in the *Impenetrable*, July 2002–June 2003.

English name	Scientific name	Consumption per rural family (Mean days/year and SD)	Proportion by species (%)	Proportion of households that consume wild meat (%)	
				Rural	Village
Mammals					
Chacoan cavy	*Pediolagus salinicola*	32.9 (0.52)	36.5	95	37.4
Three-banded armadillo	*Tolypeutes matacos*	16.5 (1.07)	18.4	100	
Brocket deer	*Mazama gouazoubira*	8.6 (0.32)	9.6	75	68.2
Collared peccary	*Tayassu tajacu*	6.2 (0.33)	6.9	57.5	40
Six-banded armadillo	*Euphractus sexcinctus*	3.0 (0.15)	3.3	57.5	
Chacoan peccary	*Catagonus wagneri*	2.6 (0.17)	2.9	27.5	16.1
White-lipped peccary	*Tayassu pecari*	1.7 (0.1)	1.9	17.5	22.0
Plains vizcacha	*Lagostomus maximus*	1.7 (0.09)	1.9	27.5	22.0
Larger hairy armadillo	*Chaetophractus villosus*	0.6 (0.07)	<1	38.9	
Nine-banded armadillo	*Dasypus novemcinctus*	0.3 (0.03)	<1	8.3	
Naked-tailed armadillo	*Cabassous chacoensis*	0.2 (0.01)	<1	13.9	
Mountain lion	*Puma concolor*	0.4 (0.04)	<1	5	2.5
Geoffroy's cat	*Oncifelis geoffroyi*	0.1 (0.01)	<1	<3	0
Brazilian rabbit	*Sylvilagus brasiliensis*	0.1 (0.02)	<1	<3	0
Small hairy armadillo	*Chaetophractus Vellerosus*	0.06 (0.01)	<1	8.3	
All armadillos *				100	84
TOTAL		**74.8**	**82.4**		
Birds					
Chaco chachalaca	*Ortalis canicollis*	5.6 (0.17)	6.2	62.5	30.7
White-tipped Dove	*Leptotila verreauxi*	3.2 (0.14)	3.6	40	
Brushland Tinamou	*Nothoprocta cinerensis*	1.4 (0.11)	1.6	17.5	
Black-legged seriema	*Chunga burmeisteri*	1.1 (0.05)	1.2	19.4	14.6
Quebracho Crested-Tinamou	*Eudronia Formosa*	0.3 (0.05)	<1	7.5	
Ringed Teal	*Calloneta leucophrys*	0.3 (0.03)	<1	7.5	
Tataupa Tinamou	*Crypturellus tataupa*	0.03 (0.01)	<1	<3	
Rhea Americana	*Rhea Americana*			0	4.4
Small birds*				77.9	5.5
Total		**11.8**	**13.1**		
Reptiles					
Tortoise	*Geochelone*sp.	0.03 (0.01)	<1	<3	0
Tegu lizard	*Tupinambis rufescens*	3.4 (0.39)	3.7	47.5	28.4
Total		**3.4**	**3.8**		
Fish				0	7.6

*Different species of armadillos and of small birds were not distinguished by people in the villages.

To learn about hunting patterns, I participated in hunting events and conducted in-depth interviews with 15 hunters. These hunters were specifically selected, because local people mentioned them as having more knowledge about hunting and wildlife. Four of these hunters participated in the research process by keeping a journal, where they recorded date and site of hunting, distances traveled, and species, sex and reproductive stage of animals killed.

Villages: I randomly selected 157 households from 7 villages (3.2–30% of the total number of households per village). To survey the villages, I used structured interviews covering similar topics assessed in the rural area. A field assistant stayed for several days in each village (in family houses) from May to August 2003 and interviewed one adult member (52% women, 48% men) of each selected household. Data on estimated frequency of consumption of wild meat provided by interviewees were compared with our own observations while staying with families in villages. In addition to the random sample of households, I interviewed 20 key informants from different villages to obtain more detailed information on hunting. Key informants were regular hunters, native or long-term residents of the region.

Economic importance of wildlife

I estimated the economic importance of wildlife as: (a) a source of cash, (b) its consumptive value and (c) its economic value.

Source of cash

I obtained information on legal and illegal commercialization of wildlife, prices, and modalities of trade through non-structured interviews with local people, hunters, government officials and park rangers. I estimated the proportion of households obtaining cash from wildlife commercialization and the relative importance of this income, but it was not possible to estimate the actual income.

Consumptive value

I determined the cost of replacing the amount of wild meat consumed with purchased meat (Bodmer et al. 1994). To estimate the amount of wild meat consumed, I relied on counting skulls and armadillo shells that people collected, on interviews, and on people's own records. I used average adult weights reported in the literature (Mares et al. 1989) for each species and considered 60% of weight as edible (Martin 1985). I extrapolated the average amount of wild meat consumed per family during the year of study to the entire rural region (roughly 360 families).

Economic value

I estimated the economic value that hunting represents for local people by comparing the value of meat acquired through harvesting with alternative ways of obtaining the money necessary to buy the same amount of meat. The options available for rural people to obtain cash are wage labor and logging in their properties for fence posts. For this analysis, I only used hunting of peccaries.

Results

Access to domestic meat

All rural households owned cattle, goats, and chickens. Many households also had pigs, sheep and other farm birds. Local people did not know exactly the number of cows and goats they own, but it was possible to estimate that there was a large variation among households; while some do not have more than 10, others have around 500. Cows are kept for sale while other domestic animals are mainly used for household consumption. None of the interviewed rural households purchased meat; they consumed either their own animals or wild animals. Most villagers acquired domestic meat by purchasing it in local markets and some of them used their own animals. Thirty-four percent of village households owned farms and about 70% had livestock.

Use of wildlife as food

Sixteen species of wild mammals, eight birds, two reptiles, and an unknown number of fish species were consumed by local inhabitants. However, only six species were consumed by more than 50% of households (Table 1). Rural peasants and villagers expressed similar preferences for wild meat: The general consensus was that the three-banded armadillo is the tastiest of all the wild meat. Other species mentioned as favorites were the Chacoan cavy, brocket deer, and collared and white-lipped peccaries.

Rural

Consumption of meat in the rural area was high. On average, households consumed meat 27 days per month (SD = 3.2, $n = 38$), of which 72.5% (SD = 11.7) of days represented domestic and the rest wild meat. Often, meat was the only food served as the meal. Consumption of both types of meat varied throughout the year and the two were negatively associated (Spearman correlation, $\rho = -0.53, p < 0.01$). Consumption of domestic meat was higher during the colder months, while consumption of wild meat followed the opposite pattern. In the colder months, beef was the most consumed, whereas goat was the most consumed in the hotter months (Figure 2).

Almost all interviewees (97%) expressed a preference for including wild meat in their diet, but none of them relied entirely upon wild animals, although in some cases (8%) wildlife constituted about 50% of their meat consumption. Wild meat (adding all species) was consumed on average 7.7 days per month per household (SD = 1.7). In terms of total number of days that meat was consumed, wild species comprised a similar proportion (27.5%) to beef (29.7%) and goat (27.8%), and more than chicken (13.2%) or pork (1.8%). Mammals provided the main source of wild meat in terms of frequency of consumption (83%; Table 1). The most frequently consumed species were the

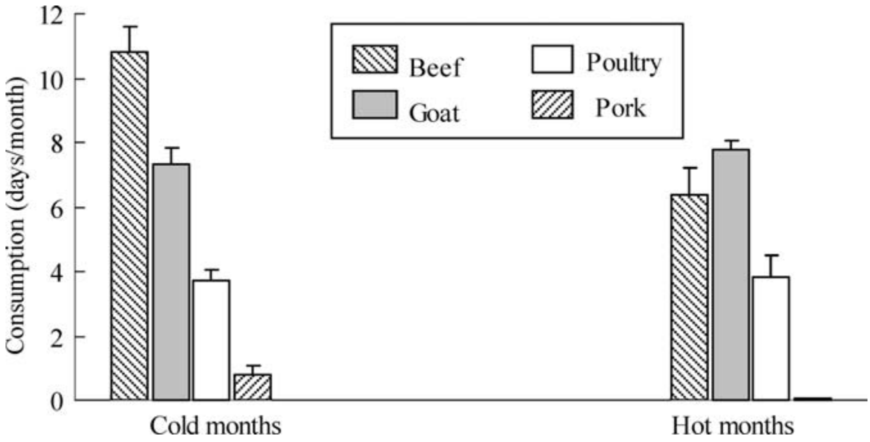

Figure 2. Seasonal consumption of domestic meat (average number of days/month/household ± SE).

Chacoan cavy and the three-banded armadillo (Table 1). In terms of biomass, mammals constituted 92% of the total amount of wild meat consumed. Chacoan cavy provided 35% and peccaries 25% of the amount of wild meat consumed per family per year (Table 2). Ungulates provided similar amount of meat than Chacoan cavies (40%). There was a large variation among households in the amount of meat consumed (Table 2). While some households did not harvest cavies, others killed up to 130 during the year of study, representing about 252 kg of edible meat. The 38 households participating in the study killed about 3250 wild animals during the year of study, obtaining an average of 167 kg of edible meat per household (Table 2).

Table 2. Average, standard deviation and range of the amount of wild meat (total weight*0.6) consumed per household in the rural area and proportion of each species in the total amount of wild meat consumed from July 2002 to June 2003.

Species	Meat consumed per household/year (kg)			Proportion of total (%)
	Average	SD	Range	
Chacoan cavy	59.2	61.1	0–232	35.4
Peccaries	42.6	71.1	0–252	25.5
Brocket deer	25.1	24.5	0–101	15.0
Armadillos	21.6	17.0	2–67	12.9
Birds	6.5	10.9	0–41	3.9
Vizcacha	5.2	10.8	0–48	3.1
Reptiles	4.9	6.7	0–23	2.9
Others	2.1	8.7	0–50	1.3
Total	167.2			100

Consumption of different species varied through the year (Figure 3). Chacoan cavies were consumed more frequently than other species all year except during the coldest months (May–July), when armadillos were consumed more frequently. Armadillos and peccaries were consumed more frequently during the colder months than during the rest of the year (t-test, $t = -2.45$, df $= 10$, $p < 0.001$; $t = -2.92$, df $= 10, p < 0.05$ respectively). The reason expressed by hunters for this seasonal pattern was that they prefer the higher fat content of the meat of these species during the colder months. Tegu lizards were consumed almost exclusively during the summer, when they became active ($t = 2.82$, df $= 10$, $p < 0.05$). Chacoan cavies, brocket deer and birds were consumed with similar frequency during the year ($t = 0.63$, df $= 10, p = 0.5$; $t = 1.5$, df $= 10, p = 0.1$; $t = 1.14$, df $= 10, p = 0.27$, respectively).

Villages

Consumption of meat in villages was also high. Most households consumed meat almost every day, and most of this meat was purchased. Only a few (2%) households obtained their meat mainly from hunting. Most households (94%) had consumed wild meat at least once during 2003. The species consumed were the same as those in the rural area, with the exception of fish and rhea (Table 1). Fish were taken from an artificial canal that crosses the region along the paved road where villages are located. The proportion of households consuming each species was smaller than in the rural area (Table 1). Only brocket deer and armadillos were consumed by more than 50% of households (Table 1). Armadillos, vizcachas, and Chacoan cavies were the most consumed according to interviewees' estimated frequency (between 8 and 12 times per year/household), followed by tegu lizard, chachalaca and brocket deer (between 5 and 7 times per year/household). All species were consumed more

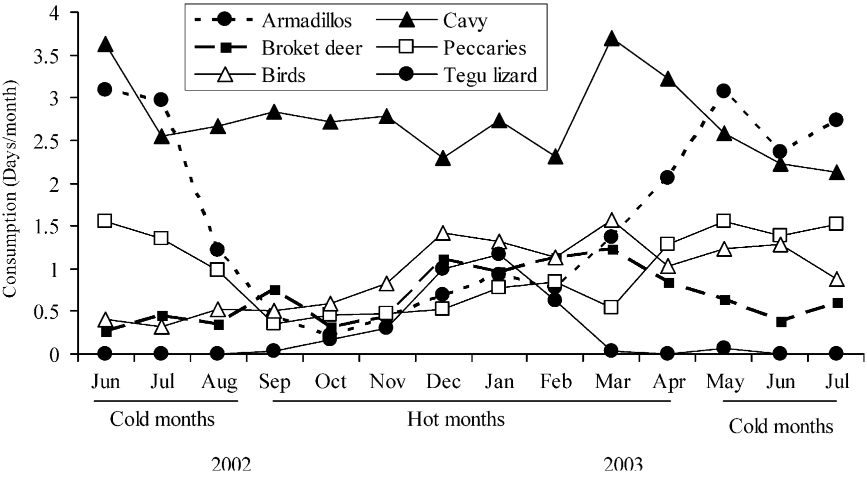

Figure 3. Consumption of wild meat throughout the year (average days/month/household).

frequently in the rural area except vizcachas (10 per year in the villages in comparison with 2 per year in the rural area).

Hunting methods

Most rural peasants (95%) hunted, either actively seeking game or as a secondary activity while working in the forest or in agricultural fields. Hunting was practiced mainly by males. Women and children often hunted Chacoan cavies and armadillos, and children also hunted doves using slingshots. Hunting methods differed between rural and village hunters in some aspects. Rural hunters generally hunted alone or with members of their family, and the harvested meat was consumed by the hunter's household. They went hunting by walking, biking or riding horses, only during the day, and never spent more than 1 day hunting. Hunting range was generally within 5 km from the settlement. The most commonly used technique to hunt employed dogs. Firearms were used for some species, but others such as armadillos, tegu lizards, and collared peccaries were often killed with axes, clubs or machetes. Village hunters, in contrast, commonly hunted in groups, used vehicles for transportation and often spent more than 1 day in the forest. These hunters commonly hunted at night, using spotlights. Distances traveled by village hunters varied between 5 km and 100 km from town. Harvested meat was shared among hunters and among relatives and friends. The techniques used by rural and village hunters were similar with the exception that village hunters used almost exclusively firearms.

Other uses of wildlife

Local people mentioned few uses of wild species for medicinal purposes or handcrafts. The fat of tegu lizard is the most commonly used medicine for multiple purposes such as cuts, snake bites, and colds. The fat of pumas and boas (*Boa constrictor*) was also mentioned as a curative for contusions and muscular pain. Some people mentioned that the fat of the peccaries is used for cough, and their feces or the content of their intestines is used to cure the wounds that the same peccaries inflict on dogs. The hides of hunted animals were generally wasted, with some exceptions when people used them to make shoes, hats, and parts for saddles.

Local people also used some wild species as pets, or for adornment and luck. About 60% of the interviewed households had blue-fronted Amazon parrots (*Amazonia aestiva)* as pets. Other less common pets were peccaries, tamandua anteaters (*Tamandua tetradactyla*), armadillos, and some species of birds. Almost all interviewees had some animal part as an ornament in their houses. Skins of felines and of tamanduas were the most common adornment found hanging on the walls. Shells of large armadillos were also used as adornments.

It was common to find parts of animals such as skulls, feet and shells that people saved under the belief that they bring good luck for future hunting. Fourteen percent of interviewees occasionally used some animal parts such as the skin of anteaters, brocket deer and peccaries to make huts, shoes, belts and saddles.

Economic importance of wildlife

Source of cash

Wildlife does not currently provide an important source of cash. Skins of tegu lizard and live parrot chicks are the only wildlife products that can be legally commercialized as part of a National Office of Fauna project. For the families involved with the project, this represents an important source of income, but it is limited to a month or two per year.

Illegal commercialization of wildlife was common, but not very meaningful for the majority of the population. I identified two types of commercialization of wildlife. One is a small-scale trade of meat, pelts and live animals, providing modest and occasional cash income to some rural households (<10%) who have a vehicle for transportation or live close to towns. Additionally, in some cases, people sell parrots to illegal buyers who visit the rural area or exchange them for merchandise. Some rural people also occasionally sell belts and hats that they make from the skins of giant anteaters (*Myrmecophaga tridactyla*) and peccaries. The other type of commercialization of wildlife I identified provides higher cash income to a small percentage of village households (<5%) who are dedicated to this activity. This is the trade of live animals such as giant armadillos (*Periodontes maximus*), peccaries and jaguars (*Panthera onca*) for illegal hunting farms or zoos. These people are also involved with the illegal sale of hides and occasionally guide foreign sport hunters to hunt endangered species such as Chacoan peccaries. Additionally, some villagers harvest large numbers of armadillos (up to 200 per weekend) to sell in nearby cities.

Consumptive value

The consumption value of meat was high in comparison with minimum daily wages. If the amount of wild meat consumed were to be replaced by buying meat it would represent a consumption value of US$ 223 per family per year, equivalent to 2 months of minimum wages. For the entire region, considering only the rural area, the amount of meat consumed was estimated to be around 59,700 kg per year, representing US $79,600 (at the 2003 conversion rate of dollar-Argentinean peso 1:3). This estimate considers only the consumption of meat by rural inhabitants. The value would be higher considering the amount of meat consumed by non-local loggers, villagers and sport hunters from cities. For example, it was estimated that village hunters from the seven villages killed about a fourth of the numbers of peccaries killed by rural hunters in the same area. If this were representative of hunting of all species, villagers would be harvesting an additional 14,000 kg of wild meat, adding US$ 18,600 more to the consumptive value of wildlife in the study area.

Economic value

Hunting peccaries was an economically advantageous strategy in 2001, when considering the average daily wage and the price of meat in local markets. Hunting a collared peccary takes less than 1 day and provides approximately 15 kg of edible meat, representing US$ 10. To replace this meat with purchased meat, the hunter would have to work for 3 days to earn US$ 10 (average daily wage $ 3). When compared with logging, hunting was similarly advantageous in economic terms. One experienced man cutting fence posts could earn in 1 day the price equivalent to 15 kg of meat.

With the national economic changes in 2001 (devaluation of the Argentine currency), hunting became more advantageous than in previous years in comparison with prices of domestic meat, but less in comparison with prices of wood. In 2003, the cost of 15 kg of meat was twice as much as before the devaluation. Prices of food increased proportionally more than wages, such that a man had to work 4 days instead of 3 to buy 15 kg of meat. Prices of fence posts also increased such that a man cutting wood in 1 day could earn the equivalent to 25 kg of meat. These values, however, would vary among households depending on the number of young males who could work making posts and on the time they need to dedicate to other activities such as agriculture and livestock ranching.

Discussion

Small species constitute the main source of wild meat in the *Impenetrable* in terms of frequency and biomass. This result differs from others in the Neotropics, where large mammals are the most important game species (Hill and Hawkes 1983; Vickers 1984; Alvard 1993; Bodmer 1995; Stearman and Redford 1995). This result also differs from the Bolivian Chaco, where Izoceño Communities, although harvesting a larger number of armadillos than of other species, obtain most of their meat from brocket deer and collared peccary (Noss 1998; Cuéllar 2000). Naranjo et al. (2004) found that harvest rates by indigenous and mestizo communities in the Lacandon Forest were positively correlated with the intrinsic rate of natural increase of species. In the *Impenetrable* however, higher harvest rate of small species may reflect depletion of large prey near settlements. Previous studies in this region have shown that white-lipped and Chacoan peccaries have diminished or disappeared in association with settlement age (Barbarán and Saravia-Toledo 2000; Altrichter and Boaglio 2004; Altrichter 2005). Depletion of large species near human habitations is a commonly observed phenomenon in Latin America (Smith 1976; Hill and Padwe 2000; Lopes and Ferrari 2000; Peres 2001). In the *Impenetrable*, preference for small species may also result from the fact that local people are not depending on wild meat sales. However, when sale of hides was one of the main sources of income for local people (before 1990), harvest composition was probably very different. Concentration of harvest in large species in other regions has been explained as a way to maximize economic gains from wild meat sales (Bodmer 1995).

Illegal commercialization of wild meat in the *Impenetrable* is uncommon and irrelevant as a source of income for the majority of the population. This pattern is similar to that found in the Lacandon forest (Naranjo et al. 2004), but different from most other Latin America sites where commercialization of wild meat generates important economic revenues for rural communities (Redford 1993; Bodmer et al. 1994; Bodmer 1995; Loibooki et al. 2002; Ortiz von Halle 2002). Although trade of wild meat is not important, its consumptive value is significant in comparison with local wages. If the average amount of wild meat consumed in rural households were replaced by purchasing meat, this would represent 2 months worth of minimum salary. Thus, for some rural communities that are not engaged on commercialization of wildlife, hunting can be an important subsistence activity (Cuéllar 2000; Naranjo et al. 2004). Other uses of wild animals, such as pets, medicine and adornment do not seem to have important implications for conservation in this region. Medicinal and ornamental uses of wildlife in the *Impenetrable*, unlike other Latin American regions (Redford and Robinson 1991; Thomsen and Brautigam 1991; Cuéllar 2000), are limited and do not motivate hunting. However, the illegal trade of wild animals by village dwellers is probably impacting wild populations, because it affects some of the most vulnerable species such as jaguars, Chacoan peccary and giant armadillo.

The species consumed in the *Impenetrable* and the proportion of each in the diet of local people differs from other Latin American mestizo communities and from indigenous communities in other regions of the Chaco (Noss 1999; Cuéllar 2000). Whereas in several mestizo communities in Latin America, it was found that mammals composed 60% and birds 30% of their diet (Redford and Robinson 1987), in the *Impenetrable* mammals alone constitute 92% of the consumed biomass and birds only 3.1%. Ojasti (1996) found that tortoises, peccaries and birds were numerically the major hunted groups (around 18% each group) in mestizo communities in Latin America. This result contrast with the *Impenetrable*, where Chacoan cavies alone constitute 42% of the total number of animals harvested, indicating that peasants concentrate on a few species. Although concentration on few species seems to be characteristic of mestizo hunters (Vickers 1984; Redford and Robinson 1987), the number of species used in the *Impenetrable* is smaller than reported for other mestizo communities in Latin America (Ojasti 1996, Naranjo et al. 2004), and indigenous groups in the Bolivian Chaco (Noss 1999; Cuéllar 2000).

The range of species consumed and the seasonal patterns of hunting respond to preferences for quality of meat, cultural practices of hunting and behavior of the species. Hunters in the Paraguayan Chaco consider the meat of Chacoan peccaries to be the tastiest of all Chacoan fauna (Sowls 1984; Brooks 1996), whereas in the *Impenetrable* this species was not among the most preferred. Several species such as anteaters, parrots, and carnivores that are relatively abundant in the region and are appreciated as a source of meat by other mestizo communities (Ojasti 1996; Bennet and Robinson 2000; Ortiz von Halle 2002) and indigenous people of the Bolivian Chaco (Cuéllar 2000) are not consumed in the *Impenetrable*, because the meat is considered to taste bad. The nocturnal Brazilian rabbit is consumed by Latin American mestizo communities (Ojasti 1996), but not in the *Impenetrable*, even when it is abundant, because local people prefer not to hunt at night. Some species such as peccaries are available all year, but are mainly consumed seasonally when hunters believe their meat has higher fat content. Seasonal changes of hunting activity and species consumed observed in other regions responds generally to climatic conditions such as seasonal floods (Behrens 1981; Bodmer 1990), or because hunters are occupied in planting crops (Smith 1976) or in seasonal jobs (Cuéllar 2000). Seasonal patterns of hunting based on preferences for content of fat do not seem to be common (Souza-Mazurek et al. 2000), although it has been observed in Indigenous people of the Bolivian Chaco (Noss and Cuéllar 2001). Although, for armadillos, it is difficult to discern between preferences for meat quality and availability, I observed that when hunters encountered armadillos during the hotter months they rarely killed them. Seasonality of hunting in the *Impenetrable* is also affected by species behavior, such as activity patterns. The effects of seasonal hunting in terms of sustainability should be studied. For example, hunting season coincides with the breeding season of peccaries in this region (Noss et al. 2003) and tegus (Fitzgerald et al. 1991), but the effects of this overlap on the populations are poorly understood (Fitzgerald et al. 1991).

Rural hunters in the *Impenetrable* use hunting methods similar to other mestizo hunters (Ojasti 1996), with some differences. Hunting only during the day, alone and almost always with dogs, is not common among mestizo peasants (Smith 1976; Ojasti 1996). This practice probably results from the spread out spatial disposition of settlements that precludes working collaboratively. Villagers however, by having more access to technological improvements, have modified their hunting methods, as it has been observed in many other Latin American cases (Stearman 2000; Ortiz von Halle 2002). Incorporation of other elements such as spotlights and vehicles has improved their hunting effectiveness. Village hunters harvest larger number of peccaries (per hunter) than rural hunters (Altrichter 2005). It is possible that with the increased economic gains from forest exploitation, rural hunters will also incorporate the technology used by village hunters, which may influence game selection as it has been observed in other Latin America mestizo communities (Vickers 1984).

Whether wild meat is a significant source of food for local people in the *Impenetrable* does not have a simple answer. On the one hand, wild meat seems important, because it constitutes one third of the total amount of meat consumed, and provides fresh food during the hotter months when it is difficult to store meat. Wild meat also represents a considerable consumptive value, especially for rural peasants without a regular source of income. On the other hand, rural peasants have ready access to domestic meat and total consumption of meat is high (almost 90% of the meals have meat) in comparison with other mestizo in Latin America (Ojasti 1996) and indigenous communities in the Bolivian Chaco (Cuéllar 2000). The total amount of meat consumed was roughly constant throughout the year, indicating that people want to maintain a certain level of meat consumption and they reach this level by modifying the types of meat they consume. Other indications that local people do not depend on wild meat can be deduced from hunters' behavior.

Hunters behave in ways that suggest selective rather than opportunistic hunting, in contrast to the findings of Redford and Robinson (1987) who say that mestizo hunters will take whatever game they encounter, within their range of acceptable species. Ortiz von Halle (2002) also asserts that people hunt whatever they must to meet their needs when the favorite species are exhausted. In the *Impenetrable* however, hunters harvest species according to preferences for taste, meat quality, accessibility and availability of preys, and concentrate on a few species disregarding others that are abundant and consumed in other regions. These findings suggest that peasants could decrease, but probably not eliminate, their consumption of wild meat and their nutritional condition would not be adversely affected by a shortage of protein. However, other aspects, such as the cultural importance of hunting for local people need to be addressed. Decreasing hunting of some vulnerable species, such as peccaries, may not be acceptable by local people, as it has been observed in rural communities in the Bolivian Chaco (Noss and Cuéllar 2001). Other measures that do not directly involve a change of behavior of local people should be considered. For example, controlling illegal commercial hunting and hunting by outsiders seems to be a type of measure more supported by local people (Noss and Cuéllar 2001). The fact that hunting in the rural areas of the *Impenetrable* remains common despite the existence of alternative sources of meat calls for more research about the cultural factors related to the hunting activity itself, and the cultural value associated with the possession of livestock.

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References

Altrichter M. 2005. Factors underlying the interactions between people and wildlife in the Argentine Chaco. Ph.D. dissertation, School of natural Resources, University of Arizona.

Altrichter M. and Boaglio G. 2004. Distribution and relative abundance of peccaries in the Argentine Chaco: associations with human factors. Biol. Conserv. 116: 217–225.

Alvard M. 1993. A test of the 'ecologically noble savage hypothesis': Interspecific prey choice by neotropical hunters. Hum. Ecol. 21: 355–387.

Barbarán F.R. 2001. Evaluación de sostenibilidad del uso comercial de la fauna Chaqueña: dimensiones ecológica, económica, social e institucional. Actas del V Congreso Internacional de Manejo de Fauna en Amazonia y Latinoamérica. Cartagena de Indias, Colombia.

Barabarán F.R. and Saravia-Toledo C.J. 2000. Caza de subsistencia en la provincia de Salta: su importancia en la economía de los aborígenes y criollos del Chaco semiárido. In: Bertonatti C. and Corchera J. (eds), Situación ambiental Argentina 2000. Fundación Vida Silvestre Argentina, Buenos Aires, pp. 193–206.

Behrens C.A. 1981. Time allocation and meat procurement among the Shipibo Indians of Eastern Peru. Hum. Ecol. 9: 189–220.

Bennet E.L. and Robinson J.G. 2000. Hunting for the Snark. In: Robinson J. and Bennett E. (eds), Hunting for Sustainability in Tropical Forests. Columbia University Press, Columbia, pp. 1–9.

Bodmer R.E. 1990. Responses of ungulates to seasonal inundations in the Amazon Floodplain. J. Trop. Ecol. 6: 191–201.

Bodmer R. 1995. Managing Amazonian wildlife: biological correlates of game choice by detribalized hunters. Ecol. Appl? 5: 872–877.

Bodmer R.E., Fang T.G., Moya L. and Gill R. 1994. Managing wildlife to conserve Amazonian forests: population biology and economic considerations of game hunting. Biol. Conserv. 67: 29–35.

Bodmer R.E., Einsberg J.F. and Redford K.H. 1997. Hunting and the likelihood of extinction of Amazonian Mammals. Conserv. Biol. 11: 460–466.

Bolkovic M.L. 1999. Usos de fauna silvestre por pobladores de las cercanías de la Reserva Provincial Copo, Santiago del Estero, Argentina. In: Fang T.G., Montenegro O.L. and Bodmer R.E. (eds), Manejo y Conservación de Fauna Silvestre en América Latina. Instituto de Ecología, La Paz, Bolivia, pp. 117–124.

Brooks D.M. 1996. Herd interactions of chacoan peccaries (*Catagonus wagneri*) costs and benefits. Anim. K. Forum 23: 123–134.

Bucher E.H. 1982. Chaco and Caatinga: South American arid savannas, woodlands and thickets. In: Huntley B. and Walker B. (eds), Ecology of Tropical Savannas. Ecological Studies 42, Springer-Verlag, Berlin, pp. 48–79.

Bucher E.H. and Huszar P.C. 1999. Sustainable management of the Gran Chaco of South America: ecological promise and economic constraints. J. Environ. Manage. 57: 99–108.

Cuéllar R.L. 2000. Uso de los animals silvestres por pobladores Izoceños. In: Cabrera E., Mercolli C. and Resquin R. (eds), Manejo de fauna silvestre en Amazonía y Latinoamérica. CITES Paraguay, Fundación Moises Bertoni, Unviersity of Florida.

Cullen L., Bodmer R.E., Valladares-Padua C. and Ballau J.D. 2004. mammalian densities and species extinctions in Atlantic forest fragments: the need for population management. In: Silvius K.M., Bodmer R.E. and Fragoso J.M.V. (eds), in People in Nature. Columbia University Press, New York, pp. 211–226.

Fang T.G., Montenegro O.L. and Bodmer R.E. 1999. Manejo y conservación de fauna silvestre en America Latina. Instituto de Ecología, La Paz, Bolivia.

Fitzgerald L.A., Chani J.M. and Donadio O.E. 1991. Tupinambis lizards in Argentina: Implementing Management of a traditionally exploited resource. In Robinson J. and Redford K. (eds), Neotropical Wildlife Use and Conservation. University of Chicago Press, Chicago, pp. 303–316.

Fragoso J.M.V., Bodmer R.E. and Silvius K.M. 2004. Introduction Wildlife conservation and management in South and Central America: Multiple pressures and innovative solutions. In: Silvius K.M., Bodmer R.E. and Fragoso J.M.V. (eds), in People in Nature. Columbia University Press, New York, pp. 1–8.

Hill K. and Hawkes K. 1983. Neotropical hunting among the Ache of Paraguay. In: Redford K.H. and Mansour J.A. (eds), Traditional Peoples and Biodiversity Conservation in Large Tropical Landscapes. The Nature Conservancy, Arlington, VA, pp. 159–196.

Hill K. and Padwe J. 2000. Sustainability of Ache hunting in the Mbaracayu Reserve, Paraguay. In: Robinson J. and Bennet E. (eds), Hunting for Sustainability in Tropical Forests. Columbia University Press, pp. 79–105.

Loibooki M., Heribert H., Kenneth L. and Marion L. 2002. Bushmeat hunting by communities adjacent to the Serengeti National Park, Tanzania: The importance of livestock ownership and alternative sources of protein and income. Environ. Conserv. 29: 391–398.

Lopes M.A. and Ferrari S.F. 2000. Effects of human colonization on the abundance and diversity of mammals in eastern Brazilian Amazonia. Conserv. Biol. 14: 1658–1665.

Mares M.A. 1992. Neotropical mammals and the myth of Amazonian biodiversity. Science 255: 976–979.

Mares M., Ojeda R.A. and Barquez R.M. 1989. Guide to the Mammals of Salta Province, Argentina. University of Oklahoma Press, London.

Martin G.H.B. 1985. Carcass composition and palatability of some wild animals commonly used as food. World Anim. Rev. 53: 40–44.

Morello J. and Adamoli J. 1968. Las grandes unidades de vegetación y ambiente del Chaco Argentino. Primera parte: Objetivos y metodología. Instituto Nacional de Tecnología Agropecuaria (Argentina), Serie Fitogeografica, No 10.

Naranjo E.J., Guerra M.M, Bodmer R.E. and Bolaños L.E. 2004. Subsistence hunting by three ethnic groups of the Lacandon Forest, Mexico. J. Ethnobiol. 24: 233–253.

Noss A. 1998. El monitoreo comunitario de cacería en el Izozog: datos preliminaries. Ecología en Bolivia 31: 53–66.

Noss A. 1999. Manejo de fauna comunitario en el Gran Chaco, Bolivia. In: Fang T.G., Montenegro O.L. and Bodmer R.E. (eds), Manejo y conservación de fauna silveste en América Latina. Instituto de Ecología, la Paz, Bolivia, pp. 109–116.

Noss A. and Cuéllar R.L. 2001. Community attitudes towards wildlife management in the Bolivian Chaco. Oryx 35: 292–300.

Noss A., Cuéllar J.E. and Cuéllar R.L. 2003. Hunter self-monitoring as a basis for biological research: data from the Bolivian Chaco. Mastozoología Neotropical 10: 49–67.

Ojasti J. 1996. Wildlife Utilization in Latin America: Current situation and prospects for sustainable management. FAO Conservation, FAO, Rome.

Ortiz von Halle B. 2002. Preliminary assessment of the environmental and socio-economic impacts of wild meat harvesting in South America. In Mainka S. and Trivedi M. (eds), Links between biodiversity conservation, livelihoods and food security. The sustainable use of wild meat. IUCN, Gland, Switzerland and Cambridge, pp. 61–69.

Peres A.C. 2001. Synergistic effects of subsistence hunting and habitat fragmentation on Amazonian forest vertebrates. Conserv. Biol. 15: 1490–1505.

Prescott-Allen R. and Prescott-Allen C. 1982. What's wildlife worth?. International Institute for Environment and Development, Washington, D.C.

Redford K.H. 1993. Hunting in neotropical forests: a subsidy from nature. In: Hladik C.M., Hladik A., Linares O.F., Pagezy H., Semple A. and Hadley M. (eds), Tropical Forests, People and Food. Man and the Biosphere Series Vol. 13. UNESCO, Paris, pp. 227–246.

Redford K.H. and Robinson J.G. 1987. The game of choice: patterns of Indian and colonist hunting in the neotropics. Am. Anthropol. 89: 650–666.

Redford K.H. and Robinson J.G. 1991. Subsistence and commercial uses of wildlife in Latin America. In: Robinson J. and Redford K. (eds), Neotropical Wildlife Use and Conservation. University of Chicago Press, Chicago, pp. 6–23.

Robinson J. and Bennet E. (eds) 2000a. Hunting for Sustainability in Tropical Forests. Columbia University Press, New York.

Robinson J. and Bennet E. 2000b. Carrying capacity limits to sustainable hunting in tropical forest. In: Robinson J. and Bennet E. (eds), Hunting for Sustainability in Tropical Forests. Columbia University Press, New York, pp. 13–30.

Silvius K.M., Bodmer R.E. and Fragoso J.M.V. (eds) 2004. People in Nature. Columbia University Press, New York.

Smith N.J. 1976. Utilization of game along Brazil's transamazon higway. Acta Amazonica 6: 455–466.

Sowls L.K. 1984. The Peccaries. The University of Arizona Press, Tucson, Arizona.

Souza-Mazurek R.R., Pedrinho T., Feliciano X., Hilario W., Geroncio S. and Marcelo E. 2000. Subsistence hunting among the Wimiri Atroari Indians in central Amazonia, Brazil. Biodivers. Conserv. 9: 579–596.

Stearman A.M. 2000. A pound of flesh: Social changes and modernization as factors in hunting sustainability. In: Robinson J. and Bennet E. (eds), Hunting for Sustainability in Tropical Forests. Columbia University Press, pp. 233–250.

Stearman A.M. and Redford K.H. 1995. Game management and cultural survival: the Yuqui ethnodevelopment project in lowland Bolivia. Oryx 29: 29–34.

Thomsen J.B. and Brautigam A. 1991. Sustainable use of neotropical parrots. In: Robinson J. and Redford K. (eds), Neotropical Wildlife Use and Conservation. University of Chicago Press, Chicago, pp. 359–379.

Vickers W.T. 1984. The faunal components of lowland South American hunting kills. Interciencia 9: 366–376.

Zak M.R., Cabido M. and Hodgson J.G. 2004. Do subtropical seasonal forests in the Gran Chaco, Argentina, have a future?. Biol. Conserv. 120: 589–598.

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An ethnobiological assessment of *Rumohra adiantiformis* (samambaia-preta) extractivism in Southern Brazil

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Abstract. The fronds of *Rumohra adiantiformis*, also known as '7-weeks-fern,' 'leatherleaf' or 'samambaia-preta,' are used worldwide as florists' greenery. Costa Rica and the USA cultivate and export *R. adiantiformis*, whereas in South Africa and Brazil this trade is based on extractivism. In Brazil, *R. adiantiformis* is harvested in the Atlantic Forest biome; 50% of the production comes from the slopes of the 'Serra Geral' (state of Rio Grande do Sul), where some 2000 families harvest and trade *R. adiantiformis* as their main source of revenue. However, harvesting, trading and transporting wild ornamental species is illegal in the Atlantic Forest, This study evaluates *R. adiantiformis* extractivism in hilly areas of Rio Grande do Sul, from an ethnobotanical/ethnoecological perspective. The study reveals that emic perceptions on the sustainability of *R. adiantiformis* extractivism are in agreement with relevant ecological data. The regeneration areas on the slopes of the Serra Geral have the highest plant density ever reported for *R. adiantiformis*; its extractivism has low environment impact and generates significant income for local communities. Further studies of these areas are important in order to support neoextractivism as a suitable form of use of the state's biodiversity.

Introduction

Rumohra adiantiformis (G. Forest) Ching fronds are very popular in the international flower market, because they maintain their appearance well after harvesting. This species, known as 7-weeks-fern and leatherleaf in the international trade, and samambaia or samambaia-preta (black-fern) in Brazil, is distributed widely in Australasia, South and Central America, southern Africa and some Indian Ocean islands (Geldenhuys and van der Merwe 1988). In the late 1930s, *R. adiantiformis* was adapted to cultivation in irrigated shaded nurseries in the State of Florida (USA), and has since become very popular worldwide as florists' greenery. Currently, Florida and Costa Rica are the major producers; Florida trades with American and European markets (Mathur et al. 1983), while Costa Rica exports to America, Europe and Japan. Abundant natural populations of *R. adiantiformis* are found in South Africa and Brazil, where it is economically exploited though extractivism (Milton 1987; Geldenhuys 1994; Miguel et al. 2005).

In Brazil, *R. adiantiformis* extractivism takes place in Atlantic Forest biome in the South and Southeast regions (Conte et al. 2000; Hanazaki 2001; Coelho de Souza 2003), especially in the state of Rio Grande do Sul. *R. adiantiformis* can be found throughout the state, but is particularly abundant on the slopes of the 'Serra Geral,' a part of the Atlantic Forest included in the Mata, Atlântica Biosphere Reserve. It is estimated that more than 50% of the *R. adiantiformis* traded in Brazil comes from Rio Grande do Sul (Anama/PGDR-UFRGS 2003; Miguel et al. 2005). According to Gerhardt (2002), *R. adiantiformis* extractivism was established in the 1970s as a major survival strategy for small-scale agriculturists in these steeply sloping areas. This activity played a crucial role in avoiding economically induced rural exodus, and for preserving the social organization associated with traditional family economic patterns. *R. adiantiformis* extractivism became increasingly intensive in the following decades, attracting an increasing number of families prevented from cultivating in their own land due to environment legislation (Brazil 1993), by the limited availability of appropriate areas for harvesting, or due to rural exodus of the majority of youngsters. It is currently estimated that some 2000 agricultural families in the Northeast region of Rio Grande do Sul are involved with harvesting and trading *R. adiantiformis* fronds as their major source of income. Unfortunately, agriculturists do not have control of the complete trade network, a situation that renders them extremely dependent on middlemen.

Although *R. adiantiformis* extractivism is currently of great importance in the municipal economies in the Northeast region of Rio Grande do Sul, it is illegal under the State Forest Law (Rio Grande do Sul 1992). According to Ribas et al. (2002), the trade (trading activity SCharles) of *R. adiantiformis* is unstructured, both in terms of the organization of the actors and the lack of information about the extractivism itself, this situation is related to both the illegality and the informality that characterize this trade. The purpose of this study was to evaluate the extractivism of *R. adiantiformis* in the Atlantic Forest slopes in Rio Grande do Sul from an ethnoecological perspective.

Methodology

The survey was done between 2000 and 2002 (bimonthly visits of 3–4 days each) in the municipalities of Osório, Caraá and Maquiné. The main focus was the extractive community of 'Fundos da Solidão' in Maquiné. Confirmation of *R. adiantiformis* correct identity was done by botanists at the Universidade Federal do Rio Grande do Sul (voucher number ICN122597, Herbarium of the UFRGS).

At ‘Fundos da Solidão,’ 22 families were identified as belonging to profiles I and II of the production system typology, as proposed by the social economic diagnosis conducted at Maquiné (Anama/PGDR-UFRGS 2000). The profiles I and II are characterized by family agriculturists who live on the slopes of the steep valley and possess small land holdings unsuited for commercial plantations. The major economic activity of these families is *R. adiantiformis* extractivism and is complemented by non-mechanized subsistence agriculture. At Fundos da Solidão, 60% of the families are associated with extractivism to some degree, and 47% have *R. adiantiformis* extractivism as their main source of income (followed by rural pensions, 33%) (Anama/PGDR-UFRGS 2003; Miguel et al. 2005).

These 22 families were accompanied by participant observation (Amorozo 1996; Etkin 1993). Open and semi-structured interviews (Viertler 2002) were also used with families members to elicit information on *R. adiantiformis* extractivism, biology, and management. Based on the interviews, key informants were identified as being knowledgeable and active in harvesting and trading activities; participant observation was conducted with these key informants during *R. adiantiformis* harvest, transporting and processing.

Results

Extractivism

Based upon the preliminary interviews, five families were selected as key informants. Each family was accompanied twice during *R. adiantiformis* harvest, transporting and processing. Collection of *R. adiantiformis* fronds is done as a family activity (usually, husband and wife), and has four steps: (1) extracting on slope areas; (2) transporting to storage sites; (3) preparing the ‘mala’ (*R. adiantiformis* trading unit, consisting of approximately 60 fronds); and (4) delivering the produce to the middlemen. In order to obtain 100 ‘malas,’ the family’s work requires three to four 3-h shifts: two or three shifts for selecting, cutting and transporting fronds to the storage site, and one more to prepare the ‘malas.’ A ‘mala’ is worth US$ 0.12; on average, weekly revenue derived from *R. adiantiformis* varies from US$ 12.50–25.00 (for contrast, the current Brazilian minimum wage fluctuates around US$ 85.00 per month). The family quota is decided beforehand by the middlemen, varying from 50 to 100 ‘malas’ per order, with 1–2 orders per week.

Collection areas are assigned to families; a family either has ‘possession’ of or rents a given collection area. Collection areas are usually located along the trails in second-growth forest towards the hilltops. The collection is manual, generally with the aid of a knife. The following characteristics are used to select fronds: (a) color (dark green); (b) texture (stiffness characteristic of the mature frond); and (c) sori (preferably absent). In the wintertime, sori are acceptable given the scarcity of mature fronds.

After collecting the fronds and tying up the bundles, the harvesters carry them over their shoulders (Figure 1) towards the storage areas, sometimes making use of a horse. This activity demands transporting very heavy loads (an average of 25 kg for 50 'malas'). Storage sites are close to the rivers in order to facilitate conservation of frond freshness, or by roads close to the middlemen's trucks. The 'malas' are arranged in a big pile, splashed with water and covered with *Hedychium coronarium* L. leaves or plastic canvas (Figure 2), where it stays for 3 days. On the third day the 'malas' (Figure 3) are tied up with pieces of rope, previously provided by the middlemen, and the load is finally delivered on the fourth day.

Ethnoecology

Table 1 presents ethnoecological information on *R. adiantiformis* management obtained through the interviews conducted throughout this study, as well as from a previously conducted project ('Projeto Samambaia Preta') that specifically aimed to obtain data on *R. adiantiformis* biology, management and production, as well as a socio-economic profile of the harvesting communities (Anama 2002; Anama/PGDR-UFRGS 2003; Miguel et al. 2005). During the 'Projeto Samambaia Preta' standard biology inventories were made in order to evaluate the species' stocks and to determine if extractivism had a significant impact on the species' natural populations, a set of data relevant to this discussion. The project revealed that this particular stage of forest regeneration allows for the continuous growth of the species, as this second growth forest provides appropriate amounts of light and shade.

It is common sense among harvesters that 'the more you take the "samambaia," the more it grows...' (Table 1), which can be explained by the fact that this is a rhizomatous species demanding moderate shade. The species' growth is favored by the additional light reaching the plant after harvesting of mature fronds, as well as from removing surrounding vegetation. According to Homma (1996), the extraction of a plant part characterizes extractivism collection, since the plant's growth matrix is preserved. The extractivits also state '...in 10 or 15 years the "samambaia" will be finished.' This perception is in accordance with the fact that *R. adiantiformis* occurs in second-growth forest during its early and medium regeneration stages; as the natural succession progresses, with increasing shade, the area suitable for the species growth decreases. Therefore, the biological data obtained by the Projeto Samabaia Preta is in agreement with the traditional (emic) view on the sustainability of *R. adiantiformis* frond extractivism, both pointing to its viability.

Based on interviews and participant observation, it is estimated that an average family collects as much as 576,000 fronds/year (200 'malas'/week). According to Miguel et al. (2005), the second-growth areas studied present

Table 1. Ethnoecological information of *R. adiantiformis* management in south Brazil.

Parameters	Indigenous perception (as close as possible to original phrasing)	Biological data (from Miguel et al. 2005)
Extractive sites	'capoeira sparse or dense' 'samambaia' fronds become apparent after 3–4 years in areas free of management ('pousio') or cleared by fire 'samambaia likes best areas that were previously used to cultivate sugar cane and were subsequently burned'	Occurrence on initial (11,36% of relative value of cover) to medium (44,14% of relative value of cover) regeneration stages
Features of fronds from areas of early regeneraion stage	'samambaia comes more in sparse capoeira' 'samambaia from sparse capoeira comes with more fronds and is more seedy'	Fronds are more stiff, therefore more durable; smaller sizes and greater quantities
Features of fronds from areas of medium regeneration stage	'on dense capoeira the fronds are smoother, has no seeds and lasts less'	Fronds are smoother, therefore in its more marketable shape, but less durable and in smaller quantities
Extration units (areas with denser occurrence of *R. adiantiformis* fronds)	'bolas or malhas'	Places with *R. ndinntiformis* high density between 13.76 a 86.8 fronds/m^2 Although denser areas do exist it is not clear why they occur or even if it refers to a single or many individuals
Criteria for frond selection	'it must be in good conditions, it can not be over dried ('sapecada', it can not have seeds'	The adult fronds in good conservation conditions are collected, preferentially without sori
Harvest periodicity	'Twice or three times per year' 'the more you take the "samambaia," the more it grows' when it is cut, one has to take it all out, so that it sprouts again and fronds will then be symmetrical. It is like banana, one collects, cuts and it comes again strong'	In experiments on 5×5 m plots to compare fronds from non-management (no cuts) areas with areas where cuts were done twice a year (as in traditional management) with adult fronds with more than 30 cm revealed no significant differences regarding number of fronds or average size of fronds
Seasons	'The summer is the best period to extract samambaia'	No differences were found for availability or frond size through the year. Young fronds are less abundant in late winter and early spring

Table 1. Continued

Parameters	Indigenous perception (as close as possible to original phrasing)	Biological data (from Miguel et al. 2005)
Sprouting	2 periods of buds growing are identified, corresponding to early spring and late summer, when greater care is needed in order to avoid stepping on new sprouts	The number of sprouts decrease in the fall and increase in early spring
Area needed for a year harvesting	'it is hard to tell because the areas are very different… 3 areas could be enough for a year harvesting… if the areas are good, more or less 4 or 5 hectares'	The productivity of areas varies from 7 to 66 fronds/m^2. In average 56% of fronds were found to be collectable adults in most areas, an estimated 16.8 collectable fronds/m^2 in an area with 30 frond/m^2.
Availability	*'in 10 or 15 years the 'samambaia' will* be finished' 'what will finish with the ''samambaia'' is the capoeira'	Forest regeneration diminishes *R. adiantiformis* availability *R. adiantiformis* extractive areas) due to excessive shadow. The intensive extraction in rented areas is another significant factor that may contribute to diminishing resources over time

considerable variation, producing from 6.7 up to 137.5 fronds/m^2 (average of 51 [±49.6] fronds/m^2), of which 11% are harvestable (mature) fronds in these areas. Based on this data, and considering that both traditional information and biological data suggest that a given area can be harvested twice a year in a sustainable manner, an average extraction of 5.8 (±5.2) mature fronds/m^2 can be estimated. Based on this estimation, the minimum area needed for a family earning US$ 96.00/month (US$ 11 in excess of the minimum wage) can be estimated as 5 ha of second growth Atlantic Forest in early to medium stages of regeneration. Again, this estimate is in accordance with the traditional information obtained from the interviews (Table 1).

Discussion

According to Miguel et al. (2005), the slopes of the Solidão valley were occupied at the end of the XIX century by small holder farmers (the forefathers of the current residents) coming from the coast and southern cities. Up to the 1960s, the local agricultural economy was essentially based on family units, principally subsistence farming complemented by some degree of trading (e.g., beans, pigs, corn, sugar cane, tobacco). Between the 1950s and 1970s, the valley was increasingly occupied; according to current residents, all areas currently occupied by second growth were once occupied by sugar cane. From the 1970s on, sugar cane and tobacco cultivation became prohibitive for small farmers, due to decreased soil fertility and an ever increasing population, with consequent demand for housing areas, As a result, vegetable cropping became increasingly common in flat areas. Subsequently, the modernization of vegetable cropping rapidly increased the value of land in the flat areas suitable for machinery, leaving few alternatives for traditional local communities and stimulating rural exodus. According to Gerhardt (2002), this socio-economic history has greatly influenced forest regeneration. The key factors of this process include: rural exodus, migration of remaining labor from slopes to flat areas, restricted availability of flat areas, problems with land management associated with forest legislation, and replacement of agriculture by extractivism (in this case, stimulated by an increasing national demand for *R. adiantiformis*). The fact that *R. adiantiformis* is an abundant species on second growth slopes greatly facilitated the consolidation of this pattern of extractivism.

In 1970s the growing national market for *R. adiantiformis* attracted traders from São Paulo to this region, acting as intermediaries for other Brazilian states. Local middlemen started to organize the transport of *R. adiantiformis* fronds to sites closer to federal highways, and in time *R. adiantiformis* collection became one of the few economic activities for the remaining communities.

The fact that the slopes of the Atlantic Forest in Rio Grande do Sul are regarded as a major production center of *R. adiantiformis* must be considered in terms of the abundance of *R. adiantiformis* as a stage in natural forest succession. Although *R. adiantiformis* is abundant in anthropic areas, its stocks are currently diminishing. Likewise, studies of *R. adiantiformis* in African Cape forests show that fern density and performance must be considered relative to its temporary phase in the regrowth and development of the forest towards maturity (Geldenhuys 1994). In Rio Grande do Sul, the last 30 years have been characterized by forest regeneration following the end of agricultural use and a significant arboreal stratum is emerging (Nodari et al. 2000). It is not rare to hear the harvesters comment that 'in 10 or 15 years the ''samambaia'' will be finished' and 'what will finish with the 'samambaia' is the capoeira' (Table 1). It is also stated that 10 years ago *R. adiantiformis* fronds were harvested three or four times as easily as nowadays.

The density of *R. adiantiformis* fronds vary widely. In southern African Cape forests the density of the *R. adiantiformis* varies from 0.1 to 9 fronds/m^2, depending on its location in cool moist mountain forests, warmer river valley forests, and coastal scarp (Milton and Moll, 1988; Geldenhuys 1994). At Ilha Comprida (São Paulo, Brazil) the density varies from 0.3 in forested areas to 5 fronds/m^2 in more open areas (Conte et al. 2000). In Maquiné, the density varies from 7 to 66 fronds/m^2 (Table 1, Miguel et al. 2005); to our knowledge this is the highest *R. adiantiformis* density so far reported.

Based on this data, we suggest that *R. adiantiformis* could be sustainable managed in Atlantic Forest slope areas by managing the second growth to avoid excessive shade. This apparently viable alternative is jeopardized by the legal impossibility of clear-cutting vegetation taller than 3 m (Rio Grande do Sul 1998), a condition easily and quickly attained under local ecological conditions. To comply with the current law one is obliged to bring to a halt the natural succession, a necessary condition to maximize *R. adiantiformis* production. Moreover, current law limits family harvesting to the short term and with limited areas, preventing medium and long term planning.

According to Kageyama and Reis (2002), *R. adiantiformis* extractivism is a typical activity of communities using natural resources in an environmentally friendly way. The management of *R. adiantiformis* comprises with the Brazilian legislation for areas of permanent preservation, and also conforms to the aims established by the State forest legislation for the development of municipalities in the sloping areas of Rio Grande do Sul (Fepam 2000), since it is an activity that allows the selective sustainable harvesting of native vegetation. This study suggests that a family must be able manage 4–5 ha of areas containing *R. adiantiformis* to earn relevant revenue. Ideally, studies should be carried out to evaluate the socioeconomic viability of managing such areas in association with subsistence cultivation and complementary economic activities. Although the biology of this species suggests that its extractivism is indeed sustainable from an environmental perspective, the resolution of social and economical questions is necessary.

Conclusion

This study revealed that regeneration areas on the slopes of the Serra Geral in the State of Rio Grande do Sul have the highest density ever reported for *Rumohra adiantiformis*. Further studies of these areas are important to support neoextractivism as a suitable form of using the biodiversity in Rio Grande do Sul. In this context, the legalization of *R. adiantiformis* extractivism should be regarded as a conservation investment for the Atlantic Forest at Rio Grande do Sul.

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References

Amorozo M.C.M. 1996. A abordagem etnobotânica na pesquisa de plantas medicinais. In: Di Stasi L.C. (org.), Plantas medicinais: arte e ciência. Um guia de estudo interdisciplinar. Editora da Universidade Estadual Paulista, São Paulo, pp. 47–68.

Anama 2002. Avaliação etnobiológica e ecológica da samambaia-preta *(Rumohra adiantiformis*(G.Forest.) Ching) no município de Maquiné. Relatório Final Secretaria Estadual do Meio Ambiente, Porto Alegre.

Anama and PGDR-UFRGS 2000. Diagnóstico socioeconômico e ambiental do município de Maquiné - RS: perspectivas para um desenvolvimento rural sustentável. Relatório de Pesquisa, Fapergs, Porto Alegre.

Anama and PGDR-UFRGS 2003. Avaliação etnobiológica e socioeconômica da samambaia preta *(Rumohra adiantiformis* (G.Forest.) Ching) na região da Encosta Atlântica do Estado. Relatório Final, Pesquisa por Demanda - RS RURAL. Secretaria de Agricultura e Abastecimento do Estado do Rio Grande do Sul, Porto Alegre.

Brazil 1993. Decreto Federal n° 750. de 10 de fevereiro de, 1993. www.cprh.pe.gov.br/downloads/decreto-750-93.doc.

Coelho de Souza G. 2003. Extrativismo em áreas de Reserva da Biosfera da Mata Atlântica no Rio Grande do Sul: estudo etnobiológico em Maquiné. Doctor thesis, Universidade Federal do Rio Grande do Sul, Porto Alegre.

Conte R., Reis M.S. and Ribeiro J.R. 2000. Estudo de parâmetros técnicos para o manejo sustentado da samambaia silvestre *(Rumohra adiantiformis)*. In: Diegues A.C. and Viana V.M. (orgs.), Comunidades tradicionais e manejo dos recursos naturais da Mata Atlântica. Provográfica, São Paulo, pp. 29–42.

Etkin N.L. 1993. Anthropological methods in ethnopharmacology. J. Ethnopharmacol. 38: 93–104.

Fepam 2000. Diretrizes ambientais para o desenvolvimento do Litoral Norte. Cadernos de planejamento e gestão do litoral ambiental, Vol. 1. Fepam (org), Porto Alegre, 96 pp.

Geldenhuys C.J. 1994. Review of studies of the fern *Rumohra adiantiformis* in the southern Cape forests: implications for sustained management. Report FOR-DEA 758, Division of Forest Science and Technology, CSIR, Pretoria, 14 pp.

Geldenhuys C.J. and van der Merwe C.J. 1988. Population structure and growth of the fern *Rumohra adiantiformis* in relation to frond harvesting in the southern Cape forest. S. Afr. J. Bot. 54(4): 351–362.

Gerhardt C. 2002. Agricultores familiares, mediadores sociais e meio ambiente: a construção da "problemática ambiental" em agro-eco-sistemas. Master dissertation PGDR-UFRGS, Porto Alegre, RS.

Hanazaki N. 2001. Ecologia de caicaras: uso de recursos e dieta. Doctor thesis, Unicamp, Campinas, SP.

Homma A.K.O. 1996. Extrativismo vegetal na Amazônia: limites e possibilidades. In: Clüsener-Godt M. and Sachs I. (eds), Extrativismo na Amazônia brasileira: perspectivas sobre o desenvolvimento regional. Compêndio Mab 18 - UNESCO, Montevideo, Uruguai, pp. 35–61.

Kageyama P. and Reis A. Resumo de campo sobre samambaia-preta em Maquiné – 02/02/2002. In: Anama (ed.), Avaliação etnobiológica e ecológica da samambaia - preta *(Rumohra adiantiformis* (G.Forest) Ching) no município de Maquiné. Relatório Final, Secretaria Estadual do Meio Ambiente, Porto Alegre, pp. 104–105.

Mathur D.D., Stamps R.H. and Conover C.A. 1983. Response of *Rumohra adiantiformis* to water application level and nitrogen form. HortScience 18: 759–760.

Miguel L.A., Coelho de Souza G. and Kubo R. 2005. Extrativismo da Samambaia-preta *(Rumohra adiantiformis* (G.Forest) Ching) no Rio Grande do Sul. Série do IEPE. Editora da Universidade Federal do Rio Grande do Sul, Porto Alegre, RS.

Milton S.J. 1987. Effects of harvesting on four species of forest ferns in South Africa. Biol. Conserv. 41: 133–146.

Milton S.J. and Moll E.J. 1988. Effect of harvesting on frond production of *Rumohra adiantiformis* (Pteridophyta: Aspidiaceae) in South Africa. J. Appl. Ecol. 25: 725–743.

Nodari R.O., Fantini A.C., Reis A. and Reis M.S. 2000. Restauração de populações de *Euterpe edulis Martius*(Arecaceae) na Mata Atlântica. In: Reis M.S. and Reis A. (eds), *Euterpe edulis* Martius (palmiteiro). Biologia, conservação e manejo Herbario Barbosa Rodrigues, Itajai, SC, pp. 189–201.

Rêgo J.F. 2000. Amazônia: do extrativismo ao neoextrativismo. Ciência Hoje 25(147): 62–65.

Ribas R.P., Dourado A.C.B., Miguel L.A., Guimarães L.A., Kubo R.R. and de Souza G. 2002. Aspectos econômicos e sociais da cadeia produtiva da samambaia-preta *(Rumohra adiantiformis* (G. Forest) Ching) na região da Encosta Atlântica do Estado do RS. Redes 7(2): 153–166.

RioGrande do Sul 1992. Lei 9.519 – Código Florestal Estadual de 21 de janeiro de 1992 www.sema.rs.gov.br/sema/html/lei_9519.htm.

RioGrande do Sul 1998. Decreto Estadual n° 38.355 de 1° de abril de 1998. www.sema.rs.gov.br/sema/html/dec_38355.htm.

Viertler R.B. 2002. Métodos antropológicos como ferramenta para estudos em etnobiologia e etnoecologia. In: Amorozo M.C.M., Ming L.C. and Silva S.P. (eds), Métodos de coleta e análise de dados em etnobiologia, etnoecologia e disciplinas correlatas. Divisa Gráfica Editora, Rio Claro, SP, pp. 11–30.

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Urban areas and isolated remnants of natural habitats: an action proposal for botanical gardens

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Abstract. The International Union for Conservation of Nature and Natural Resources (IUCN) and the World Wide Fund for Nature (WWF) advocates an increase of the number of botanical gardens throughout the world as one of the measures that can help to preserve the world's biodiversity. To implement this strategy, the present work brings forward a suggestion particularly suited to tropical regions: establishing municipal botanical gardens. It refers to the experience of a newly opened municipal botanical garden in Brazil, comparing its attractive power on visitors to that of other botanical gardens included in the Brazilian network of Botanical Gardens. It also presents considerations on *in situ* conservation in small remnants and on the importance of urban reserves to preserve the regional biodiversity and spread the conservationist philosophy. The present proposal promotes the participation of local communities making the public opinion more aware and active, besides being able to counterbalance proposals that support protecting the world biodiversity through interventionist actions. It assumes that, through actions planned and coordinated by regional and national botanical garden networks, the measure proposed can mitigate the anthropic actions exerted on important natural reserves all over the world.

Introduction

The quick destruction of the natural vegetation cover throughout the world has been among the main topics of the debates on the need for conservation of biodiversity, and sustained development (Myers 1980; Raven 1987; Santos and Câmara 2002). One of the strategies suggested by the International Union for Conservation of Nature and Natural Resources (IUCN) and the World Wide Fund for Nature (WWF) is to create botanical gardens, especially in countries with a rich tropical flora (IUCN 1989). According to the World Conservation Strategy (IUCN 1987), in these countries, botanical gardens would help to maintain essential ecological processes and life-supporting systems and preserve genetic diversity (Given 1987; Hamann 1987; Tilman 2000). Furthermore, through environmental education programs, they would raise the local community awareness of the importance of using the natural resources in a responsible and sustainable way (Given 1987; Hamann 1987; Forero 1989; IUCN 1989), and favor the establishment and management of natural reserves (Meffe and Carroll 1997).

The best way to preserve endangered animal and vegetal species is to protect their ecosystems, that is, conserving these species *in situ* (Hamann 1987; Primack and Rodrigues 2001). This practice allows the environmental phenomena involved in the evolutionary mechanisms to continue exerting their influence not only on the endangered or economically interesting species, but on the whole community (Frankel and Soulé 1981; Ashton 1987; Hoyt 1992; Spellerberg and Hardes 1995). It is thus advisable that the botanical gardens of the whole world, especially in regions with high plant diversity, put their efforts into the *in situ* conservation of the regional flora, while the protection of the most endangered species of these habitats (Williams and Creech 1987; IUCN 1989) is often associated to *ex situ* conservation (Maunder et al. 2001a).

Good examples of institutions dealing with *in situ* conservation are the so-called natural or woodland botanical gardens (Conselho Nacional do Meio Ambiente et al. 2001), more common in tropical countries. An interesting case is that of the Adolpho Ducke Botanical Garden, in Manaus (Brazil), and its efforts aimed at *in situ* conservation ever since it was created (Primack and Rodrigues 2001). In addition, some botanical gardens are classified as municipal *in situ* conservation, i.e. municipalities that protect both the natural plant communities and their fauna found within their limits, or maintain biological reserves which they manage (IUCN 1989).

If maintained and managed by botanical gardens, small remnants of natural vegetation will help to increase the area covered by conservation programs and systematize the preservation of biological diversity in the scale of different towns and cities (Margules and Pressey 2000).

No country has so far protected its biodiversity in an effective way. Therefore, establishing natural reserves in remnants of different sizes, even in the smallest and least representative ones in terms of local diversity, would represent an attempt to preserve the different remaining regional habitats and species (Margules and Pressey 2000), threatened by the intense destruction rhythm of the natural vegetation cover, all over the world (McCann 2000; Myers et al. 2000).

This work aims at highlighting the importance of preserving small urban and suburban remnants, in addition to those inserted in the rural landscape. Based on the experience of a recent Brazilian botanical garden and on their concern to promote the increase in number of botanical gardens all over the world, the authors suggest establishing municipal reserves. This may represent a remarkable socio-economical effort to improve the quality of life in the cities of tropical and subtropical regions. It would also contribute to preserve animals and vegetal species they shelter, and to raise the awareness of the public opinion on the importance of the conservationist practices and of a better use of the regional natural resources. The present work considers as small remnants those that have up to few hundreds of hectares, dimensions usually regarded as inadequate to preserve different animal and plant populations (Turner 1996; Chiarello 1999; Gonzáles-Solis et al. 2001; Marsden et al. 2001), although the definition of an area as insufficient for conservation may vary according to species (Henle and Mühlenberg 1996).

The authors do not argue the importance and urgency of creating large reserves for wildlife all over the world, nor the necessary efforts to establish them (Terborgh and van Schaik 2002). However, they acknowledge the importance of complementing these large-scale efforts with regional action, and suggest moderate cost actions on resources little or not at all considered in conservation and environmental education activities: isolated remnants of natural habitats pertaining to towns or cities, especially in regions of the world where conservationist actions have become urgent.

A few considerations on *in situ* conservation

Reduced and isolated remnants and in situ conservation

Remnants of natural vegetation, especially small ones (Collinge 1996), are seldom considered as priority for environmental conservation or management because they are not self-sustainable (Viana and Tabanez 1996); they cannot guarantee the effective protection of their biological diversity; and are always prone to perturbations that may affect them in all extension (Meffe and Carroll 1997). In addition, they present low populational densities (Caldecott 1996), low species heterogeneity and little or no contact with other natural areas (Meffe and Carroll 1997). Priority is usually given to large extensions of lands that shelter endemic, endangered or economically important species (Primack and Rodrigues 2001).

Nevertheless, because of the expansion of agricultural frontiers, demographic growth and chronic poverty, many tropical countries do not have such large natural remnants to preserve (Murphy 1988; Turner 1996). They usually present highly fragmented environments, with natural vegetation remnants smaller than 100 ha, isolated in an altered landscape (Turner and Corlett 1996), like the areas of the Brazilian Atlantic forest (Caldecott 1996) and the savanna formations close to towns and cities in Southeastern Brazil (Kronka et al. 1998).

Remnants a little smaller than 100 ha can maintain a relatively high biological diversity for decades, after isolation (Turner and Corlett 1996), before their genetic diversity begins to erode (Meffe and Carroll 1997). Nevertheless, they do need such appropriate management practices as the establishment of corridors linking different remnants (May 1975; Saunders et al. 1991; Collinge 1996; Meffe and Carroll 1997; Primack and Rodrigues 2001), the introduction of new individuals of endangered species (Turner 1996) and the creation of buffer zones (Götmark et al. 2000) to prevent their invasions by foreign organisms and edge effect (Ledig 1986; Saunders et al. 1991), which can affect even the large and long-lasting tropical trees (Laurence et al. 2000).

In very troubled regions, maintaining small remnants of natural vegetation, a little larger than 1 ha (Kemper et al. 1999; Pither and Kellman 2002), can offer benefits to the ecosystem in which they are inserted. Islands of biodiversity in altered landscapes may help recover lost or degraded ecosystems through restoration ecology (Jordan 1988), introducing specimens in areas where they occur in low density or have been extinct (Viana and Tabanez 1996) and allowing the expansion of remnants and the transit of animals (Janzen 1988; Kattan and Alvarez-López 1996). These, as dispersing agents of diaspores, will favor the advance of these natural plant formations to areas they used to occupy (Turner and Corlett 1996).

Small remnants made up of secondary plant formations are important to maintain physical and biological processes, since they function as shelters for pollinators, dispersing agents of propagules, offer temporary shelter for nutrition and nesting to migratory birds, and help to maintain the quality of edaphic water (Brown and Lugo 1990; Turner and Corlett 1996; Viana and Tabanez 1996).

In situ conservation in urban reserves

In the third world, mainly in big cities, the urbanization process has been characterized by migratory fluxes in search of better conditions of life. This demographic explosion has provoked a deterioration of the urban environment (Gnaneshwar 1995) and the loss of habitats and species (McGeoch and Chown 1997; Hardy and Dennis 1999) in tropical regions. Yet, some of the more tolerant species, as some small mammals (Vuorisalo et al. 2001) and birds (Fernández-Juricic and Jokimäki 2001), have survived to the urban pressure (Spellerberg and Hardes 1995) and have found shelter in isolated remnants (Turner and Corlett 1996).

Conservation areas within cities or towns or in areas close to their perimeter not only improve the quality of urban life, but they also provide a contact with natural habitats to city dwellers, important spaces for recreation, and scenic beauty (Vuorisalo et al. 2001). They also favor the environmental balance providing, e.g., thermal comfort through the micro-climate generated (Evans and Schiller 1996), protection of valley bottoms and of springs against erosion and drying of the soil (Murphy 1988), and spaces to study the functioning of wildlife in urban environments (Fernández-Juricic and Jokimäki 2001). They can also provide important information for the development of appropriate techniques and strategies of management and conservation for small remnants (Turner 1996), which is still extremely scarce (Henle and Mühlenberg 1996).

This strategy of increasing the spreading of natural reserves (Margules and Pressey 2000) multiplying the conservation sites that contain habitats with similar features is as important as the most common management procedures

(Frankel and Soulé 1981). It actually multiplies the efforts to preserve remnants (Hamann 1987) and therefore contributes to minimize the impact of environmental changes, e.g., the global climatic change (Scott et al. 2001; Thiollay 2002). It also reduces the probability of population and/or whole community extinction (Caldecott 1996) in different places of the world (Hamann 1987).

A recent Neotropical botanical garden and *in situ* conservation

A brief analysis of the Municipal Botanical Garden of Bauru

Located in the city of Bauru, State of São Paulo, Southeastern Brazil (Figure 1), the Municipal Botanical Garden of Bauru (JBMB) was created and included in the Brazilian Network of Botanical Gardens in 1994. Its trajectory, although brief, is very similar to that of other botanical gardens in developing countries.

It covers 321.70 ha in the outskirts of Bauru (Figure 2), in an area which was bought in the beginning of the XXth century to preserve the spring of the *Vargem Limpa* creek, which was destined to supply water to the city (Mello 1917), the JBMB began working with six employees and two trainees and was mainly aimed at trying to guarantee the conservation of one the biggest urban remnants of natural vegetation in the Center-West of the State of São Paulo (Pinheiro 2000).

An important characteristic of the natural vegetation remnant protected by the JBMB is the fact that it is not isolated, but inserted in a set of nearby remnants. Sympathizer and political actions of support were decisive for the creation, in 1996, of a municipal Area of Environmental Protection (APA) (Bauru 1997). After a recent expansion due to the inclusion of other remnants, this APA now amounts to 1145.42 ha of natural vegetal cover, consisting of semideciduous seasonal forest, swamp forest and forested savanna.

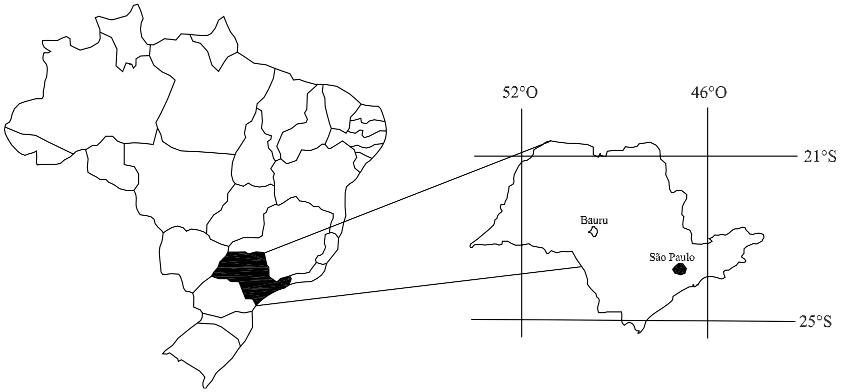

Figure 1. Localization of the State of São Paulo and of the city of Bauru.

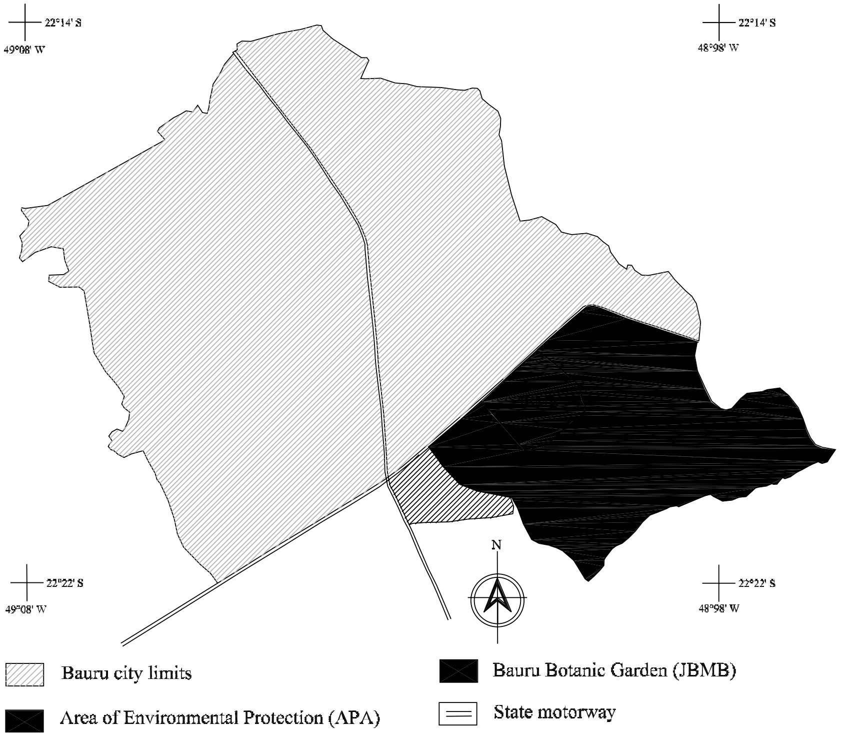

Figure 2. Localization of the municipal botanical garden in Bauru in relation to the urban perimeter. Modified from Bauru (1997).

At first, its infrastructure was limited and included only administrative headquarters, a storeroom, a native sapling nursery, a 1000 m ecological footpath through the semideciduous seasonal forest and the forested savanna, and a 450 m^2 orchidarium, sheltering 2094 examples of native and exotic orchids of different origins, some of which are included in the list of endangered taxa in the state of São Paulo, e.g., *Bifrenaria tyrianthina* (Loudon) Rchb.f. and *Laelia purpurata* Lindl. & Paxton. Still, 3707 people from Bauru and region visited the JBMB the first year, through its Environmental Education Program (Figure 3), whose goals have always been to inform the public of the importance of biodiversity and of the need to preserve the regional biocenose (Tunnicliffe 2001).

After some structural improvements along the years, e.g., the building of a visit center, herbarium, a cultivated plot with medicinal plants beds, and a green house, it now employs 18 staff, comprising technicians, trainees, and maintenance, vigilance and fire brigade employees. The number of visitors in search of environmental education activities has steadily increased, now totaling 9651 students (Figure 3) in 1 year period. On the other hand, the mean

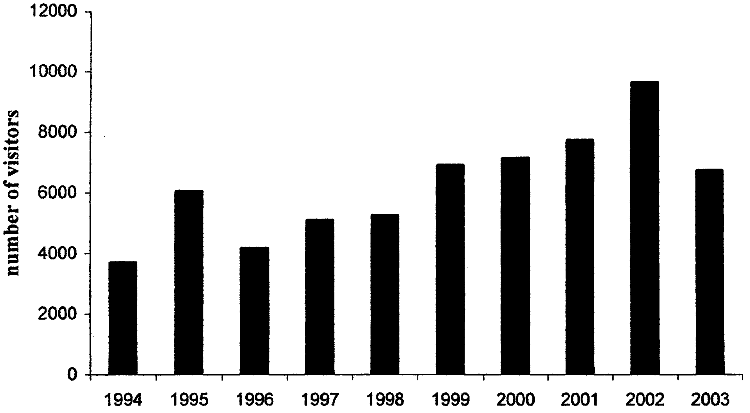

Figure 3. Total of visitors programmed visits received by the program of environmental education of the JBMB between the years of 1994 and 2003.

number of annual spontaneous visitors, i.e., those who made no appointment, was 20,795, for the period 2000 through 2002.

An analysis showing the attractive power of the JBMB, and that of other botanical gardens, is based on the ratio between the estimated number of people who annually visit these institutions (Diretório dos Jardins Botânicos Brasileiros 2000) and the total population of the towns and cities in which they are located (Instituto Brasileiro de Geografia e Estatística 2001). It is thus estimated that the São Paulo Botanical Garden, one of the largest and popular in Brazil, located in a city with 10,434,252 inhabitants, attracts ca. 80,000 visitors every year. In comparison, the JBMB, located in a city with 316,064 inhabitants, attracted ca. 20,000 spontaneous visitors. Such numbers indicate that in Bauru, in 2002, one out of each 15 dwellers visited the JBMB, that is, 1:15, while in São Paulo, one dweller out of each 130 went to the São Paulo Botanical Garden, a 1:130 ratio (Table 1). This analysis considered problems inherent to each botanical garden, such as its reputation among the public and the physical space destined to the visits, as factors influencing the results.

The ratio above cited is not far from the one found for the botanical gardens of Caucaia, Lajeado, Paulínia and Santos, for those of Porto Alegre, Rio de Janeiro and of the Federal University of Minas Gerais (UFMG), located in big Brazilian cities (Table 1). As for the Museu de Biologia Professor Mello Leitão, located in Santa Tereza, State of Espirito Santo, its estimated number of annual visitors (Diretório dos Jardins Botânicos Brasileiros 2000) exceeded the number of the city inhabitants, respectively, 35,000 and 20,622 (Instituto Brasileiro de Geografia e Estatística 2001).

Different research activities were developed at the JBMB (Cavassan et al. 1995; Paschoal and Corrêa 1996; Garcia et al. 1997; Pinheiro 2000; Pinheiro et al. 2002) and in nearby sites, mainly within the municipal APA in which the

Table 1. Brazilian botanical gardens part of the Brazilian Network of Botanical Gardens that reported their estimated annual visits to the Diretório dos Jardins Botânicos Brasileiros (2000) and some of their features.

Botanical gardens	Total area (ha)	City/Brazilian region	Estimated visitors/year	Population of the city/town[a]	Ratio[b]
Museu Paraense Emílio Goeldi	5.2	Belém/NO	200,000	1,280,614	1:6
Jardim Botânico de Pipa	60	Timbau do Sul/NE	5,000	7,749	1:1.5
Parque Botânico do Ceará	190	Caucaia/NE	20,000	250,479	1:12
Jardim Botânico de João Pessoa	515	João Pessoa/NE	1,800	597,934	1:332
Jardim Botânico de Recife	10.7	Recife/NE	9,184	1,422,905	1:155
Jardim Botânico ‘Amália Hermano Teixeira’	100	Goiânia/CE	4,000	1,093,007	1:273
Jardim Botânico de Brasília	5,000	Brasília/CE	24,000	2,051,146	1:85
Jardim Botânico da Fundação Zoobotânica do Rio Grande do Sul	43	Porto Alegre/SU	90,000	1,360,590	1:15
Jardim Botânico de Caxias do Sul	60	Caxias do Sul/SU	300	360,419	1:1201
Jardim Botânico do Lajeado	24.8	Lajeado/SU	3,000	64,133	1:21
Jardim Botânico Municipal ‘Francisca Maria Garfunkel Rischbieter’	17.8	Curitiba/SU	576,000	1,587,315	1:3
Jardim Botânico da Universidade Federal de Santa Maria	13	Santa Maria/SU	300	243,611	1:812
Jardim Botânico da Fundação Zoobotânica de Belo Horizonte	10.3	Belo Horizonte/SE	19,000	2,238,526	1:118
Museu de História Natural e Jardim Botânico da UFMG	60	Belo Horizonte/SE	60,000	2,238,526	1:37
Jardim Botânico da Universidade Federal Rural do Rio de Janeiro	16.5	Seropédica/SE	300	65,260	1:217
Instituto de Pesquisa Jardim Botânico do Rio de Janeiro	137	Rio de Janeiro/SE	600,000	5,857,904	1:10
Jardim Botânico Municipal ‘Adelelmo Piva Júnior’	8.6	Paulínia/SE	2,000	51,326	1:25
Jardim Botânico de São Paulo	143	São Paulo/SE	80,000	10,434,252	1:130
Jardim Botânico da UNESP	11	Botucatu/SE	3,000	108,306	1:36
Jardim Botânico Municipal ‘Chico Mendes’	9	Santos/SE	50,000	417,983	1:8
Jardim Botânico Municipal de Bauru	321.7	Bauru/SE	20,000	316,064	1:15

The acronyms for the Brazilian regions are: NO – north; NE – Northeast; CE – Center-West; SE – Southeast, SU – South.

[a] 2000 Populational census carried out by the Instituto Brasileiro de Geografia e Estatísticas (2001).

[b] Ration between the estimated visits to the different botanical gardens and the population of their respective cities.

botanical garden is located (Cavassan 1990). Some actions are currently being taken to increase the research activities at the JBMB, such as the diversification of partnerships with universities and research institutes; the creation of the JBMB Research Council, agency of scientific advisory services composed by researchers from different institutions; and the creation of the project 'Friends of the Botanical Garden,' created by a municipal law to provide independent funds from the private initiative to develop research activities, acquire equipment and consumption material.

Studies carried out in two of the phytocenoses protected by the JBMB give an idea of the importance of municipal botanical gardens for the *in situ* conservation of the flora of the regions where they are located. In a phytosociological survey on 26 (twenty-six) 10 m × 10 m plots (total area = 0.26 ha) within the 12 ha area of a remnant of semideciduous seasonal forest, the Shannon-Weaver Diversity Index was 3.79, very close to the highest values ever found in other phytosociological studies performed in the State of São Paulo (Pinheiro 2000; Pinheiro et al. 2002). This value may be explained by both the different microhabitats found in the forested area analyzed, due to its proximity to the forested savanna and the swamp forest, and the inclusion criterion adopted, which considered all tree and shrub individuals over 1.5 m high and boles of at least 1.30 m (Pinheiro et al. 2002).

In a floristic analysis, which also included a plot of forested savanna contiguous to this seasonal forest studied (Pinheiro 2000), five of the shrub and tree species identified: *Bowdichia virgilioides* Kunth, *Maytenus floribunda* Reissek, *Myroxylon peruiferum* L.f., *Pseudobombax tomentosum* (Mart. & Zucc.) A.Robyns and *Psychotria capitata* Ruiz & Pav., were on the list of endangered species of the flora of the State of São Paulo, published as Resolution SMA 48, by the State Department of Environmental Conservation. Such list was elaborated on the bases of guidelines defined by the Convention on Biological Diversity and Agenda 21, and on criteria adopted by the IUCN. Out of these species, only *Maytenus floribunda* and *Myroxylon peruiferum* were reported in the above-mentioned phytosociological study, with a small number of sampled individuals, respectively, 5 and 6, in a total list of 1,947 shrub and tree individuals. *Bowdichia virgilioides*, a savanna species, was only found in the area of the contiguous forested savanna. As for the populations of *Pseudobombax tomentosum* and *Psychotria capitata* they were possibly composed by a small number of individuals or presented aggregated distribution. This phytosociological survey also reported that the mean height of *Maytenus floribunda* individuals sampled was 2.3 m, (max. = 5 m, min. = 1.5 m) and that of the *Myroxylon peruiferum* individuals was 4.8 m, (max. = 13 m, min. = 2 m). Since the populations of *M. floribunda* and of *M. peruiferum* are represented by adult and young individuals, such feature may indicate that they are suited to restore their respective populations.

Although, in Brazil, municipal botanical gardens are only beginning their *in situ* conservation activities, it is worth mentioning that the Botanical Garden of the Fundação Zoobotânica de Belo Horizonte, State of Minas Gerais, has directed its research towards implementing conservation practices of the regional flora. It is thus adopting measures to preserve endangered species, which have culminated in the reintroduction of species in their original sites (Mendonça and Lins 2000). Such action includes the conservation and management of the Leguminosae *Dimorphandra wilsonii* Rizzini, a Cerrado species endemic to the region of Paraopeba, State of Minas Gerais; and the study of the ecology of *Cipocereus laniflorus* N.P. Taylor & Zappi, a Cactaceae endemic to the *Parque do Caraça* (Rego, personal communication). Both species are placed on the list of endangered species of the flora of the State of Minas Gerais (Mendonça and Lins 2000).

Proposal to increase the conservationist efforts

With their specialized technical body offering teaching and leisure activities related to conservation to the communities (Ashton 1988; Murphy 1988; Forero 1989) and their vocation to conciliate research and conservation of plant communities, the botanical gardens are one of the most important institutions to spread conservationist values around the world.

Nevertheless, the great concentration of botanical gardens in temperate countries and/or regions with temperate climate, in comparison to those with higher biodiversity (such as those in the tropics – Spellerberg and Hardes 1995), is a situation that must be changed (Forero 1987; IUCN 1989). Until 2000, Brazil, e.g., had 26 botanical gardens which composed the Brazilian Network of Botanical Gardens, 17 of which were located in the South and Southeastern regions, against only two in the Amazon region, but none in the Pantanal, a complex, annually flooded biome, located in the Center-West region of the country (Diretório dos Jardins Botânicos Brasileiros 2000). In addition, such numbers are inexpressive of the biological diversity existing in this country. Germany and France possess 74 and 66 botanical gardens, respectively . Europe as a whole totals 527 (Maunder et al. 2001b) and North America, until the 1980s, had 262 botanical gardens (Heywood 1987).

We do believe that preserving municipal remnants, e.g., urban forests (Konijnendijk 2000) and valley bottoms with natural vegetation (Baschak and Brown 1995; McGuckin and Brown 1995; Ehrenfeld 2000; Burkart 2001) could help to reverse this situation.

In many Brazilian cities, and possibly around the world, remnants of natural vegetation of the most varied dimensions have been spared to guarantee the preservation of springs to supply public water. They could shelter botanical gardens aimed at *in situ* conservation and at environmental education practices. The São Paulo Botanical Garden (Hoehne et al. 1941) and the JBMB (Pinheiro et al. 2002) were created in forest remnants originally protected to that end.

The elaborating of a plan that allows to increase the number of municipal botanical gardens for *in situ* conservation in tropical countries (IUCN 1989), with the financial help of government and international institutions, seems to be consistent with and meet the objectives of the Botanical Gardens Conservation Strategy (IUCN 1987, 1989). Actually, the priority of botanical gardens is to preserve the regional biodiversity, interfering in a coordinate way through a national or regional network of botanical gardens (Forero 1989; IUCN 1989), based on established criteria and goals. On the other hand, they are not only aimed at recreation, as most of the municipal botanical gardens in South Africa, as reported by Elloff (1987).

The urban and suburban municipal botanical gardens may be categorized, which will allow the division of work and the definition of different forms of action for each category according to established criteria. The network of botanical gardens of each country could carry out the coordination, based on the understanding of the needs and the elaboration of goals.

For the conservation of the biota present in the region where the proposed botanical gardens are located, research and management activities could be performed through cooperation among botanical gardens (Forero 1987; Simmons and Beyer 1987), research institutions and universities. And *ex situ* conservation practices could also take place when the structure and interaction capacity of these institutions allow it.

Based on the high number of visitors that botanical gardens can receive annually (Elloff 1987; IUCN 1989), municipal gardens including and managing small and biologically impoverished remnants would be of great importance if they concentrated their efforts in educational activities for the public in general, which are necessary to develop an informed public opinion that could support the conservationist efforts.

Increasing the number of botanical gardens mainly dedicated to environmental education, for local communities, as the XIXth century North America private botanical gardens (Heywood 1987), may represent an important measure to raise the regional public opinion awareness and to spread conservationist projects and activities (Caldecott 1996). Such increase would thus complete the effort spent in huge reserves close to these botanical gardens, in regions considered as *biodiversity hotspots* (Myers et al. 2000), entailing major sympathy and acceptance of the public opinion for such projects (Danielsen et al. 2000; Huber 2001). Furthermore, they may offer a series of services to the local communities, which could culminate in the sustainable use of the natural resources.

Botanical gardens should consider the possibility of including disconnected areas of natural vegetation as associated reserves to form a mosaic of protected areas. Such a measure would increase the chances of preserving a higher number of different populations of the same species (Margules 1996; Purvis and Hector 2000), i.e., the effective protection of different ecotypes (Stace 1991) thanks to small, but representative natural reserves in a wide geographical extension along distinct environmental gradients (Kunin 1997).

The funding of these municipal botanical garden activities would depend on the socio-economical reality of the different countries located in the regions of interest, most of which are found in tropical regions sheltering a rich flora and fauna (IUCN 1989; Myers et al. 2000). These countries do not usually have adequate financial resources to maintain conservation activities, so they will need the cooperation of the international community.

Conclusions

An important issue raised by Jepson and Canney (2001) on conservation projects in regions of the world with high endemism, diversity and richness of species, is that such projects underrate the human action on a local scale. Since these regions are geographically wide, the bases for conservation actions should consider the regional cultural differences and promote conservation strategies adapted to the cultural diversity through the transparent policy actions of public institutions and non-governmental organizations.

In Brazil, studies to define conservation strategies recognize a need to inform and raise the public awareness in the local sphere, involve segments of the society in decision-making and widen the scientific knowledge on the conservation of different biomes. However, no details are given on how such goals should be attained (Alho and Martins 1995; Pinto et al. 1996; São Paulo 1997; Avaliação 2000). The present work proposes a way out of these impasses multiplying the centers of *in situ* conservation and of environmental education through the creation of municipal botanical gardens organized in regional and national networks (Forero 1989).

On the other hand, any program aimed at increasing the regional participation in the effort of *in situ* conservation in different parts of the world, and also at multiplying and aggregating municipal botanical gardens, trusting the towns and cities willing to act as partners in this effort, should consider that even in developed countries, the current effectiveness of conservation programs in many botanical gardens is lower than desired. Such programs should be widened stressing *in situ* conservation, among other measures (Maunder et al. 2001b).

The preference for municipal botanical gardens is easy to explain since they are urban institutions with a great potential to form the public opinion, not to mention that the local public politics is naturally committed with issues involving social welfare, especially in the third world (Gnaneshwar 1995). Furthermore, in Brazil, although the different conservation unities defined by the Sistema Nacional de Unidades de Conservação (National System of Conservation Unities) provide activities of environmental education, leisure and ecological tourism (SNUC 2000), they are not accessible to most of the population, they suffer from serious financial restrictions and do not have the necessary infrastructure to perform such activities.

On the other hand, municipal botanical gardens can offer city dwellers an easy opportunity to understand the importance of preserving the natural resources. In addition, since they are nearby, they can continuously attract numerous visitors along the year (Ellof 1987). Their structure should not be very costly if we consider they could only offer, initially, ecological footpaths, even in very small urban remnants, usually discarded for practices of *in situ* conservation.

Based on sharp, defined goals, the municipal botanical gardens organized in national and regional networks would be able to mitigate the anthropic pressures on areas of importance for conservation. Thus, through environmental education actions and activities directed to the communities, mainly those living on resources extracted directly from nature, such pressures could sensibly diminish. For the success of conservation practices this measure should be grounded on awareness raising and the participation of local society (Caldecott 1996).

The establishment costs of a network of municipal botanical gardens in small remnants could be low if the involved towns and cities have public areas dedicated to this goal, in addition to having their own facilities and labor. The latter could be trained with the help of other botanical gardens. Nevertheless, most of the cases will need basic infrastructure, e.g., electric system, water-sewer network, toilets, etc. The establishment of botanical gardens, especially in countries in bad economical situation, will thus demand external financial help, which could be awarded according to criteria defined by the national or regional botanical gardens networks. Such criteria should be based on the ecological importance of the remnants and the need to establish environmental education programs in the region of the future botanical gardens, especially in *biodiversity hotspots*.

Although all the activities of the municipal botanical gardens should ideally be in charge of the city itself, this will probably not always be possible, especially for research activities that demand equipment and inputs. It is thus advisable that these botanical gardens find complementary income sources, such as selling certified plantlets, and allowing the development of ecotourism activities (Caldecott 1996). Furthermore, they could share a common financing fund through a nationwide network.

Although the establishment of a network of municipal botanical gardens cannot be considered as a panacea for the problems facing the whole world, owing to the increasing loss of species and vegetal ecosystems, it would represent a way to delegate to the local communities the responsibility of conserving their natural goods, which they often fail to recognize. It would also allow to widen the ca. 400 botanical gardens that have taken upon themselves, together with to the Botanic Garden Conservation International, the practice of *in situ* conservation (Conselho Nacional do Meio Ambiente et al. 2001). It thus represents an alternative to the interventionist proposals advocated for regions of the world that are in a more critical economical and political situation (Terborgh and Boza 2002). In fact, in these regions, the direct or indirect involvement of the citizen in the regional efforts of conservation would be preponderant, if backed by a logistical planning and support.

The JBMB has features that qualify it as an important spreader of the conservationist cause. Not only is it located close to the marginal savanna formations of Southeastern Brazilian, but it shelters savanna forest and seasonal forest, and savannas are one of the most endangered biomes in Brazil (Alho and Martins 1995; São Paulo 1997; Kronka et al. 1998).

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References

Alho C.J.R. and Martins E.S. 1995. De Grão em Grão, o Cerrado Perde Espaço. Cerrado: Impactos do Processo de Ocupação. WWF – Fundo Mundial para a Natureza, Brasília, Distrito Federal.

Ashton P.S. 1987. Biological considerations in *in situ* vs *ex situ* plant conservation. Proceedings of an International Conference Botanic Gardens and the World Conservation Strategy 3–18.

Ashton P.S. 1988. Conservation of biological diversity in botanical gardens. In: Wilson E.O. (ed.), Biodiversity. National Academy Press, Washington, pp. 269–278.

Avaliação e Ações Prioritárias para a Conservação da Biodiversidade da Mata Atlântica e Campos Sulinos 2000. Brasília: Ministério do Meio Ambiente. Secretaria de Biodiversidade e Florestas, São Paulo, São Paulo.

Baschak L.A. and Brown R.D. 1995. An ecological framework for the planning, design and management of urban river greenways. Landscape Urban Plan. 33: 211–225.

Bauru 1997. Plano Diretor de Bauru 1996: Cadernos de Dados, Levantamentos, Diagnósticos, Lei No. 4126/1996. Prefeitura Municipal de Bauru, Secretaria Municipal do Planejamento, Bauru, São Paulo.

Brown S. and Lugo A.E. 1990. Tropical secondary forests. J. Trop. Ecol. 6: 1–32.

Burkart M. 2001. River corridor plants (Stromtalpflanzen) in Central European lowland: a river of a poorly understood plant distribution pattern. Global Ecol. Biogeogr. 10: 449–468.

Caldecott J.O. 1996. Designing Conservation Projects. Cambridge University Press, Cambridge, England.

Cavassan O. 1990 Florística e fitossociologia da vegetação lenhosa de um hectare de cerrado no Parque Ecológico Municipal de Bauru (SP). Ph.D. Thesis, Instituto de Biologia, Universidade Estadual de Campinas, Campinas.

Cavassan O., Paschoal M.E.S., Azevedo A.M.G., Barbosa A.V.G. and Dias N.M 1995. Avaliação do desenvolvimento de essências nativas introduzidas em uma área degradada. Salusvita 13: 15–24.

Chiarello A.G. 1999. Effects of fragmentation of the atlantic forest on mamad communities in south-eastern Brazil. Biol. Conserv. 89: 71–82.

Collinge S.K. 1996. Ecological consequences of habitat fragmentation: implications for landscape architecture and planning. Landscape Urban Plan. 36: 59–77.

Conselho Nacional do Meio Ambiente, Rede Brasileira de Jardins Botânicos, Instituto de Pesquisas Jardim Botânico do Rio de Janeiro, Botanic Gardens Conservation International 2001.

Normas internacionais de conservação para jardins botânicos. EMC, Rio de Janeiro, Rio de Janeiro.

Danielsen F., Balete D.S., Poulsen M.K., Enghoff M., Nozawa C.M. and Jensen A.E. 2000. A simple system for monitoring biodiversity in protected areas of a developing country. Biodivers. Conserv. 9: 1671–1705.

Diretório dos Jardins Botânicos Brasileiros 2000. Expressão e Cultura, Rede Brasileira de Jardins Botânicos, Rio de Janeiro. Rio de Janeiro.

Ehrenfeld J.G. 2000. Evaluating wetlands within an urban context. Ecol. Eng. 15: 253–265.

Elloff J.N. 1987. Botanic gardens and education in South Africa. Proceedings of an International Conference Botanic Gardens and the World Conservation Strategy 85–100.

Evans J.M. and Schiller S. 1996. Application of microclimate studies in town planning: a new capital city, an existing urban district and urban river front development. Atmos. Environ. 30: 361–364.

Fernández-Juricic E. and Jokimäki J. 2001. A habitat island approach to conserving birds in urban landscapes: case studies from southern and northern Europe. Biodivers. Conserv. 10: 2023–2043.

Forero E. 1987. 80,000 plants in South America: the case for creating more botanic gardens. Proceedings of an International Conference Botanic Gardens and the World Conservation Strategy, 227–37.

Forero E. 1989. Los jardines botanicos y la conservacion de la naturaleza. Acta Bot. Brasil. 3: 315–322.

Frankel O.H. and Soulé M.E. 1981. Conservation and Evolution. Cambridge University Press, Cambridge, England.

Garcia M.J., Pinheiro M.H.O., Rueda J., Monteiro R., Cesar O. and Mune S.E. 1997. Considerações preliminares sobre a microflora quaternária proveniente de um solo do Jardim Botânico Municipal de Bauru, São Paulo Brasil. Revista Universidade de Guarulhos – Geociências 2: 242.

Given D.R. 1987. What the conservation requires of *ex situ* collections. Proceedings of an International Conference Botanic Gardens and the World Conservation Strategy, 103–116.

Gnaneshwar V. 1995. Urban policies in India: paradoxes and predicaments. Habitat Int. 19: 293–316.

Gonzáles-Solis J., Guix J.C., Mateos E. and Llorens L. 2001. Population density of primates in a large fragment of the Brazilian atlantic rainforest. Biodivers. Conserv. 10: 1267–1282.

Götmark F., Söderlundh H. and Thorell M. 2000. Buffer zones for forest reserves: opinions of land owners and conservation value of the forest around nature reserves in southern Sweden. Biodivers. Conserv. 9: 1390–1390.

Hamann O. 1987. The IUCN/WWF plants conservation programme. Proceedings of an International Conference Botanic Gardens and the World Conservation Strategy 31–43.

Hardy P.B. and Dennis R.L.H. 1999. The impact of urban development on butterflies within a city region. Biodivers. Conserv. 8: 1261–1279.

Henle K. and Mühlenberg M. 1996. Areas requirement and isolation: conservation concepts and application in Central Europe. In: Settele J., Margules C., Poschlod P. and Henle K. (eds), Species Survival in Fragmented Landscapes. Kluwer Academic Publishers, Dordrecht, pp. 111–122.

Heywood V. 1987. The change role of the botanic gardens. Proceedings of an International Conference Botanic Gardens and the World Conservation Strategy 3–18.

Hoehne F.C., Kuhlmann M. and Handro O. 1941. O Jardim Botânico de São Paulo. Departamento de Botânica do Estado, São Paulo, São Paulo.

Hoyt E. 1992. Conservando los Parientes Silvestres de las Plantas Cultivadas. Addison-Wesley Iberoamericana, Wilmington.

Huber O. 2001. Conservation and environmental concerns in the Venezuelan Amazon. Biodivers. Conserv. 10: 1627–1643.

Instituto Brasileiro de Geografia e Estatística 2001. Censo Demográfico 2000: Características da População e dos Domicílios. Resultados do Universo, Instituto Brasileiro de Geografia e Estatística, Rio de Janeiro.

IUCN 1987. The IUCN Botanic Gardens Conservation Strategy: a summary. Proceedings of an International Conference Botanic Gardens and the World Conservation Strategy xxxvii–xxxix.

IUCN 1989. The Botanic Gardens Conservation Strategy. IUCN Botanic Gardens Conservation Secretariat. World Wide Fund for Nature, Gland.

Janzen D.H. 1988. Management of habitat fragments in a tropical dry forest: growth. Ann. Missouri Bot. Gard. 75: 105–116.

Jepson P. and Canney S. 2001. Biodiversity hotspots: hot for what? Global Ecol. Biogeogr. 10: 225–227.

Jordan W.R.III 1988. Ecological restoration: reflections on a half-century of experience at the University of Wisconsin-Madison Arboretum. In: Wilson E.O. (ed.), Biodiversity. National Academy Press, Washington, pp. 311–316.

Kattan G.H. and Alvarez-López H. 1996. Preservation and management of biodiversity in fragmented landscapes in the Colombian Anden. In: Schelhas J. and Greenberg R. (eds), Forest Patches in Tropical Landscapes. Island Press, Washington, pp. 3–18.

Kemper J., Cowling R.M. and Richardson D.M. 1999. Fragmentation of South African renosterveld shrublands: effects on plant community structure and conservation implications. Biol. Conserv. 90: 103–111.

Konijnendijk C.C. 2000. Adapting forestry to urban demands – role of communication in urban forestry in Europe. Landscape Urban Plan. 52: 89–100.

Kronka F.J.N., Nalon M.A., Matsukuma C.K., Pavão M., Guillaumon J.R. and Cavalli A.C. et al. 1998. Áreas de Domínio do Cerrado no Estado de São Paulo. Secretaria do Meio Ambiente, São Paulo, São Paulo.

Kunin W.E. 1997. Sample shape, spatial scale and species counts: implications for reserve design. Biol. Conserv. 82: 369–377.

Laurence W.L., Delamônica P., Laurence S.G., Vasconcelos H.L. and Lovejoy T.E. 2000. Rainforest fragmentation kills big trees. Nature 404: 836.

Ledig F.T. 1986. Heterozygosity, heterosis, and fitness in outbreeding plants. In: Soulé M.E. (ed.), Conservation Biology: The Science of Scarcity and Diversity. Sinauer Associates, Sunderland, pp. 77–104.

Margules C. 1996. Experimental fragmentation. In: Settele J., Margules C., Poschlod P. and Henle K. (eds), Species Survival in Fragmented Landscapes. Kluwer Academic Publishers, Dordrecht, pp. 128–137.

Margules C.R. and Pressey R.L. 2000. Systematic conservation planning. Nature 405: 243–253.

Marsden S.J., Whiffin M. and Galetti M. 2001. Bird diversity and abundance in forest fragments and *Eucalyptus* plantation around an Atlantic forest. Biodivers. Conserv. 10: 737–751.

Maunder M., Lyle B., Dransfield J. and Baker W. 2001a. The conservation value of botanic garden palm collections. Biol. Conserv. 98: 259–271.

Maunder M., Higgens S. and Culham A. 2001b. The effectiveness of botanic gardens collections in supporting plant conservation: a European case study. Biodivers. Conserv. 10: 383–401.

May R.M. 1975. Island biogeography and the desing of wildlife preserves. Nature 254: 177–178.

McCann K.S. 2000. The diversity–stability debate. Nature 405: 228–233.

McGeoch M.A. and Chown S.L. 1997. Impact of urbanization on a gall-inhabiting Lepidoptera assemblage: the importance of reserves in urban areas. Biodivers. Conserv. 6: 979–993.

McGuckin C.P. and Brown R.D. 1995. A landscape ecological model for wildlife enhancement of stormwater management practices in urban greenways. Landscape Urban Plan. 33: 227–246.

Meffe G.K. and Carroll C.R. 1997. Conservation reserves in heterogeneous landscapes. In: Meffe G.K. and Carroll C.R. (eds), Principles of Conservation Biology. Sinauer Associates, Sunderland, pp. 305–343.

Mello L.V.F. 1917. Câmara Municipal de Bauru. Relatório da Administração do Município, durante o ano de 1917. O Estado de São Paulo, São Paulo, São Paulo.

Mendonça M.P. and Lins L.V. (org). 2000. Lista vermelha das espécies ameaçadas de extinção da flora de Minas Gerais. Fundação Biodiversitas, Fundação ZooBotânica de Belo Horizonte, Belo Horizonte.

Murphy D.D. 1988. Challenges to biological diversity in urban areas. In: Wilson E.O. (ed.), Biodiversity. National Academy Press, Washington, pp. 71–76.

Myers N. 1980. Conversion of Tropical Moist Forests. A report prepared for the Committee on Research Priorities in Tropical Biology of the National Research Priorities in Tropical Biology of the National Council. National Academy of Sciences, Washington.

Myers N., Mittermeier R.A., Mittermeier C.G., Fonseca G.A.B. and Kent J. 2000. Biodiversity hotspots for conservation priorities. Nature 403: 853–858.

Paschoal M.E.S. and Corrêa P.L. 1996. Pelas Trilhas do Jardim Botânico de Bauru. EDUSC, Bauru, São Paulo.

Pinheiro M.H.O. 2000. Levantamento florístico e fitossociológico da floresta estacional semidecidual do Jardim Botânico Municipal de Bauru, São Paulo. MSc Thesis, Universidade Estadual de Campinas, Campinas.

Pinheiro M.H.O., Monteiro R. and Cesar O. 2002. Levantamento fitossociológico da floresta estacional semidecidual do Jardim Botânico de Bauru, São Paulo. Naturalia 27: 145–164.

Pinto L.P.S., Costa J.P.O., Fonseca G.A.B. and Costa C.M.R. (eds) 1996. Mata Atlântica: Ciência, Conservação e Políticas. Workshop científico sobre a Mata Atlântica. Secretaria de Estado do Meio Ambiente, São Paulo, São Paulo.

Pither R. and Kellman M. 2002. Tree species diversity in small, tropical riparian forest fragments in Belize, Central America. Biodivers. Conserv. 11: 1623–1636.

Primack R.B. and Rodrigues E. 2001. Biologia da Conservação. E. Rodrigues, Londrina, Paraná.

Purvis A. and Hector A. 2000. Getting the measure of biodiversity. Nature 405: 212–219.

Raven P. 1987. The scope of the plant conservation problem world-wide. Proceedings of an International Conference Botanic Gardens and the World Conservation Strategy 19–29.

Santos T.C.C. and Câmara J.B.D. 2002. Geo Brasil 2002: Perspectivas do Meio Ambiente no Brasil. Edições IBAMA, Brasília, Distrito Federal.

São Paulo. Secretaria de Estado do Meio Ambiente 1997. Cerrado: bases para conservação e uso sustentável das áreas de cerrado do estado de São Paulo. Secretaria de Estado do Meio Ambiente, São Paulo, São Paulo.

Saunders D.A., Hobbs R.J. and Margules C.R. 1991. Biological consequences of ecosystem fragmentation: a review. Conserv. Biol. 5: 18–32.

Scott J.M., Murray M., Wright R.G., Csuti B., Morgan P. and Pressey R.L. 2001. Representation of natural vegetation in protected areas: capturing the geographic range. Biodivers. Conserv. 10: 1297–1301.

Simmons J.B.E. and Beyer R.I. 1987. Cooperation in training and technical liaison between botanic gardens. Proceedings of an International Conference Botanic Gardens and the World Conservation Strategy 263–270.

SNUC 2000. Sistema Nacional de Unidades de Conservação da Natureza: Lei 9.985 de 18 de julho de 2000. Ministério do Meio Ambiente, Secretaria de Biodivesidade e Florestas, Brasília, Distrito Federal.

Spellerberg I.F. and Hardes S.H. 1995. Biological Conservation. Cambridge University Press, Cambridge, England.

Stace C.A. 1991. Plant Taxonomy and Biosystematics. Edward Arnold, London.

Terborgh J. and Boza M.A. 2002. Internacionalização da conservação da natureza. In: Terborgh J., van Schaik C., Davenport L. and Rao M. (orgs) (eds), Tornando os Parques Eficientes: Estratégias para Conservação da Natureza nos Trópicos. Editora UFPR, Curitiba, Paraná, pp. 414–425.

Terborgh J. and van Schaik C. 2002. Por que o mundo necessita de parques. In: Terborg J., van Schaik C., Davenport L. and Rao M. (org) (eds), Tornando os Parques Eficientes: Estratégias para a Conservação da Natureza nos Trópicos. Editora UFPR, Curitiba, Paraná, pp. 25–36.

Thiollay J.M. 2002. Bird diversity and selection of protected areas in a large neotropical forest tract. Biodivers. Conserv. 11: 1377–1395.

Tilman D. 2000. Causes, consequences and ethics of biodiversity. Nature 405: 208–211.

Tunnicliffe E.D. 2001. Talking about plants – comments of primary school groups looking at plant exhibits in a botanical garden. J. Biol. Educ. 36: 27–34.

Turner I.M. 1996. Species loss in fragments of tropical rain forest: a review of the evidence. J. Appl. Ecol. 33: 200–209.

Turner I.M. and Corlett R.T. 1996. The conservation value of small, isolated fragments of lowland tropical rain forest. Trends Ecol. Evol. 11: 330–333.

Viana V.M. and Tabanez A.J. 1996. Biology and conservation of forest fragments in the Brazilian atlantic Moist Forest. In: Schelhas J. and Greenberg R. (eds), Forest Patches in Tropical Landscapes. Island Press, Washington, pp. 151–167.

Vuorisalo T., Lahtinen R. and Laaksonen H. 2001. Urban biodiversity in local newspapers: a historical perspective. Biodivers. Conserv. 10: 1739–1756.

Williams J.T. and Creech J.L. 1987. Genetic conservation and the role of botanic garden. Proceedings of an International Conference Botanic Gardens and the World Conservation Strategy 161–173.

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Impacts of community-based conservation on local communities in the Annapurna Conservation Area, Nepal

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Abstract. Approaches to the management of protected areas that involve the participation of local communities are now being widely promoted. However, the impacts of such community-based conservation initiatives on local communities remain poorly defined. This research examines the socio-economic impacts of community-based conservation within the Annapurna Conservation Area (ACA), Nepal, through semi-structured interviews and a questionnaire survey with local residents, situated both within and outside the protected area. Results indicate that local communities have received a number of benefits from conservation, including improvements in access to forest resources, improved basic infrastructure such as drinking water, trails and bridges, and improvements in health, sanitation and social services. However, relatively few people (14.9%) within ACA receive direct financial income from tourism. Local communities also experience a number of costs of being involved in conservation, the most significant of which is increased crop damage by wildlife. Eighty-four percent of respondents within ACA have experienced problems of crop damage, accounting for 6% (rice) to 23% (maize) of total production. Depredation of livestock by wildlife is also experienced; mean losses per household being the equivalent of £3.9 (Rs. 479.70) each year. However, 66% of respondents within ACA reported that they had never experienced this problem. These results indicate that the socio-economic benefits of community-based approaches to conservation can outweigh the costs, even though the latter are significant. However, a participatory approach to management of problematic animal species will need to be developed within ACA, if conflicts between local communities and protected area management are to be avoided in future.

Introduction

The designation and management of protected areas has become one of the main instruments for the conservation of biodiversity, and now constitutes a principal element of development planning in many countries (Pimbert and Pretty 1997). However, many protected areas were originally established by either displacing local communities or without giving sufficient consideration to their livelihoods (Ghimire and Pimbert 1997). Designation of protected areas can result in a variety of negative consequences for rural communities such as the restriction of access to traditionally used resources (Mishra 1982b), the disruption of local cultures and economies by tourists (Hough 1988), increased depredation of crops and livestock by wild animals (Mishra 1982b) and displacement of people from their traditional lands, leading to social and cultural disruption and enforced poverty (Calhour 1972 and Lusigi 1984 cited in Hough 1988). Many protected areas consequently suffer from poaching, logging, agricultural encroachment or other forms of degradation (Wells and Brandon 1992; Terborgh and Schaik 2002).

Such concerns have led to a growing recognition that for protected areas to be effective, local people need to be closely involved in their management (Brandon and Wells 1992; Wells and Brandon 1992; DNPWC 1996; Oviedo and Brown 1999; Rao et al. 2002b). Approaches are required that effectively engage local people in management and decision-making, and that enable their livelihood needs to be adequately met. The concept of linking conservation with development has resulted in a major shift in conservation management, based on the assumption that if local communities derive some benefits from conservation, they will be more likely to contribute to conservation of biodiversity (Mishra 1982a; Sherpa et al. 1986; Lehmkuhl et al. 1988; Brandon and Wells 1992; Wells and Brandon 1992; IUCN 1998; Dudley et al. 1999; Stolton and Dudley 1999; Salafsky and Wollenberg 2000). The need to recognise and guarantee the rights of local communities in relation to natural resources and biodiversity conservation is also now widely appreciated (IUCN 2003).

Local people are increasingly being accepted as ‘partners’ in wider efforts towards sustainable management, an approach generally termed ‘community-based conservation’ (Mehta and Kellert 1998). The approach is based on the principle that conservation strategies should emphasise the role of local communities in decision-making (Adams and Hulme 1998). By definition, the conservation should be of, by and for communities (Murphree 1994), with the communities involved as active partners in protected area management (Songorwa et al. 2000). Community-based conservation programmes achieve their goals by: (1) allowing people living in and around protected areas to participate in land-use policy and management decisions; (2) giving people proprietorship or ownership over wildlife resources; and (3) providing local people with economic benefits from wildlife conservation (Hackel 1998).

Community-based approaches to protected area management have now been established in many areas, most notably in Africa, such as the CAMPFIRE, ADMADE and LIRDP programs. These initiatives have reported decreases in poaching, improved conservation through an increase in wildlife game scouts, provision of direct economic benefits from trophy hunting and implementation of development schemes (Metcalfe 1994; Lewis and Alpert 1997; Wainwright and Wehrmeyer 1998). Experience from these schemes has shown a degree of success, at least where big game animals are present (Hackel 1998). However, there are growing concerns that these schemes have succeeded in protecting some of the larger mammals not by their ability to distribute socio-economic benefits but by virtue of their increased enforcement levels (Gibson and Marks 1995). In some cases, it has been reported that there has been no decrease in wildlife poaching as a result of the programmes, as poachers have shifted their tactics and prey selection (Gibson and Marks 1995). In many initiatives, communities are apparently not actively participating in planning and management (Metcalfe 1994; Wainwright and Wehrmeyer 1998; Songorwa et al. 2000). Local level institutions are also sometimes lacking, and as a result, management decisions are controlled by district- or state-owned institutions (Metcalfe 1994). There is also evidence of conflicts between rural peoples' economic needs and the implementation of community-based conservation (Hackel 1998). It has even been suggested that community-based conservation has rarely improved the standard of living of local communities (Wainwright and Wehrmeyer 1998).

Information on the effectiveness of the conservation-based approach is generally lacking (Hackel 1998), and therefore it is difficult to define under which situations the approach is most likely to be successful. Despite a lack of evidence regarding its effectiveness, the community-based approach is increasingly being promoted in many areas, including countries throughout Asia. In Nepal, most of the protected areas were originally established following a strict protectionist approach enforced by the armed forces. Despite the success achieved in protection of certain flagship species, a number of problems have emerged, including displacement of local communities, poaching of protected species, and confrontation between protected area guards and local communities. To address these problems, the Nepal government has recently introduced community-based approaches to protected area management.

The aim of this research was to examine the impact of the community-based approach on local communities within a protected area in Nepal. The research was undertaken in the Annapurna Conservation Area (ACA), the first conservation area declared in Nepal that involves the local communities directly in conservation. The overall responsibility for managing ACA lies with the King Mahendra Trust for Nature Conservation (KMTNC), a Nepali non-governmental organisation, but at a local level, natural resource management is the responsibility of local communities, whose activities are monitored by the Trust. Communities are involved in conservation planning and management, as well as being permitted to continue their traditional land use practices. Communities within ACA are also responsible for the implementation of integrated conservation and development programmes that are supported financially by income derived from tourist revenues (KMTNC-ACAP 1997, 1999). The objective of the research was to analyse the key factors that encourage local people to become involved in conservation and the costs and benefits of conservation to the local communities. Analyses were based on semi-structured interviews and a questionnaire survey with local communities situated both within and outside the protected area.

Study area

The Annapurna Conservation Area (ACA) is the largest protected area in Nepal, covering 7629 km^2, and is located in hills and mountains of west-central Nepal (83°57′ E, 28°50′ N), covering five districts (Nepal being divided into political units such as Zone, District and Village; District is the second largest political unit with more than one Village Development Committee. There are 14 zones and 75 Districts in Nepal). The area is bounded to the north by the dry alpine deserts of Dolpo and Tibet, to the west by the Dhaulagiri Himal and the Kaligandaki Valley, to the east by the Marshyangdi Valley and to the south by the valleys and foothills surrounding the town of Pokhara. ACA is well known both nationally and internationally for its scenic beauty, unique ecology and rich cultural heritage, including within its boundaries some of the world's highest mountains and the world's deepest river valley. The geology, physiography and climate all vary markedly across ACA, owing to the high altitudinal range and dissected topography, providing a wide range of different habitats and environments. Surveys of biodiversity within the area have been very limited to date, but more than 472 bird species, 21 species of amphibians, 32 species of reptiles and more than 101 species of mammals have so far been recorded (Inskipp and Inskipp 2001; KMTNC 1997). ACA is inhabited by approximately 120,000 people from five major ethnic and other tribal groups. Traditionally, the people of the region are highly dependent on natural resources, particularly native forests.

The present research focused on the southern slopes of the Annapurna range (Figure 1), which is the area most affected by ACA management policies. Study sites were selected on the basis of existing information and preliminary field visits, following consultation with conservation area management and district development committee members. Care was taken to select study communities that are characteristic of ACA on the basis of ethnic composition, resource use patterns, topography, climate, altitude and vegetation type. The study areas lie within the subtropical to temperate climatic zones, with a mean annual temperature of 16.3 °C and a mean annual rainfall of approximately 5000 mm. The study sites were divided between two areas, surrounding the villages of Ghandruk (Kaski district) and Bhujung (Lamjung district), respectively. Within both of these areas, villages inside and outside ACA were selected, with 14 villages selected in total. These were (with districts in parentheses) (i) inside ACA: Baghum (Lamjung), Bhujung (Lamjung), Chhomrong (Kaski), Dangsing (Kaski), Ghandrung (Kaski), Landrung (Kaski), Sabet (Kaski); (ii) outside ACA: Aantighar (Kaski), Bhulbhule (Lamjung), Maling (Lamjung), Mauja (Kaski), Ngadi (Lamjung), Sarangkot (Kaski), Taksar (Lamjung).

The study villages lie between 820 and 2100 m a.s.l., with most lying between 1600 and 1800 m a.s.l., and were between 3 and 8 h walking distance from the nearest road passable to motorised vehicles. The mean number of households per village was 92 ± 11.3, with a mean of 6.5 individuals per household. The

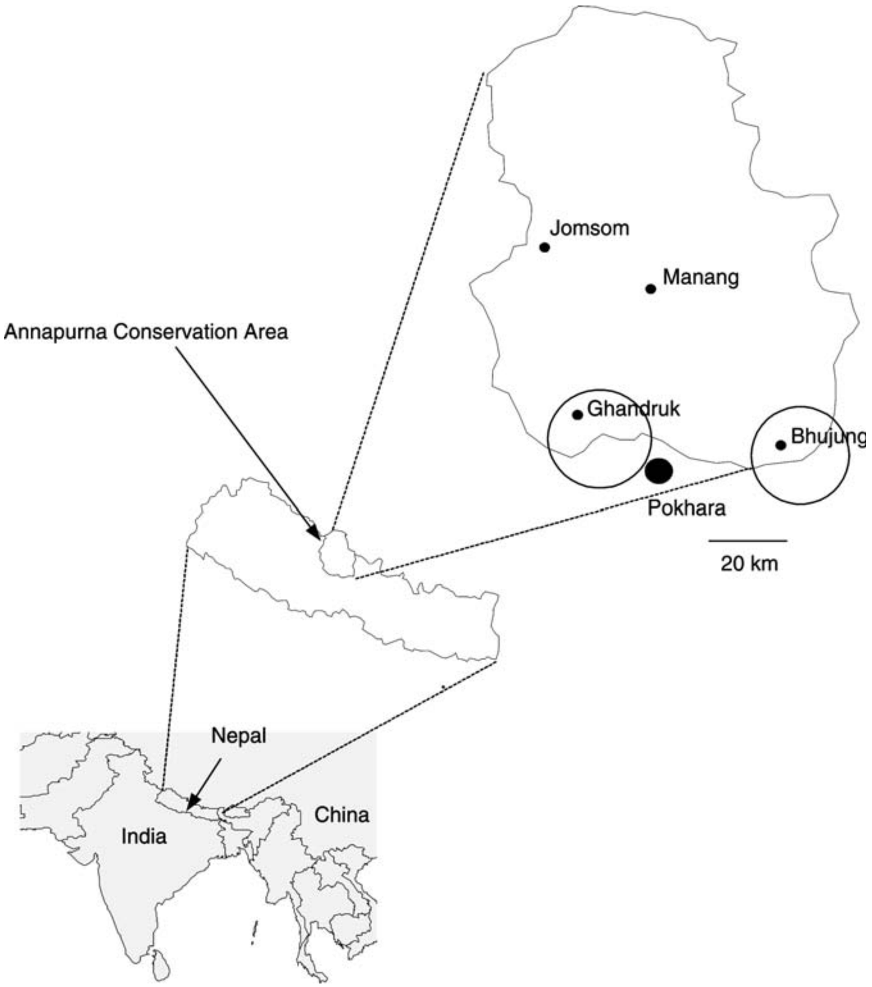

Figure 1. Location of the Annapurna Conservation Area.

main ethnic group in all cases was Gurung, but Magar, Brahman and Chhetri groups were also present. In addition, the Damais, Kamis and Sarki caste groups were present in all villages; many providing agricultural labour but typically owning little land themselves. All of these village communities are dependent on wild resources for fuelwood, fodder and timber. Natural forests are a common property resource, accessible to all members of the community. Agricultural land is always privately owned, but may include woodlots of planted trees. Agriculture is practised on terraced hill slopes. The principal crops grown are maize, millet and rice. Livestock farming (principally buffalo and cattle) is also carried out in all of the villages.

Before its declaration as a protected area, the resources within the ACA were managed by the government's District Forest Office. Although a few communities continued a traditional common property management system, in practice, the government did not have any control over the resources of the area. To improve the livelihood of local communities and to conserve the resource-rich mountain ecosystems, the government declared the area as a protected area with a new category. The 1973 National Parks and Wildlife Conservation Act was amended in 1989 to provide a legal basis for establishing multiple use conservation areas. The local communities of the protected area were encouraged to conserve and use the resources as part of this process.

The villages within ACA are currently the focus of integrated conservation and development programmes being implemented by the ACA Project (ACAP), which is managed by the KMTNC. Financial support is received from tourism revenues and international donors such as DFID (the UK government), WWF (USA), CIDA (Canada), SNV (the Netherlands), GEO and DSW (Germany). Study villages outside ACA also receive financial support for development, primarily from the national government and some donors such as the British Gurkha Welfare Office, HELVETAS (the Swiss government) and JICA/JOVC (the Japanese government). The ACA management helped local communities to reduce pressure on the natural forests by providing alternatives such as development of community and private woodlots for fodder and fuel wood and the provision of alternative energy sources. As a result of the conservation policy adopted by ACA, communities were made more responsible for the management of their resources, and benefited from improved availability of and access to natural forest resources.

Data collection and analysis

Social survey methods involved a combination of participatory research methods followed by structured interviews and a questionnaire survey of a sample village from each site. A structured questionnaire was developed during a pilot survey in conjunction with park staff. The issues raised in the pilot sessions were also incorporated in the questionnaire, which was tested and modified during the pilot survey. The information generated from participatory rural appraisal (PRA) was validated by results from other surveys. A variety of participatory tools was used (following Chambers 1997). Information on perceived costs and benefits to local communities was obtained by drawing an interactive cost-benefits chart. General patterns of forest resource use were obtained by using a participatory pie chart tool. Different locally available materials such as grains and stones were used to facilitate this tool.

Semi-structured interviews were applied to gather information on rationale for involvement in conservation, conservation benefits and costs of conservation. The interviews were conducted from November 2001 to February 2002 based on a pre-designed questionnaire (full details are provided by Bajracharya 2004). Respondents were asked a series of pre-established questions with pre-set response categories (Punch 1998). The questions were presented in an informal way to establish greater trust and dialogue, and to increase opportunities for other information to emerge. The interview team consisted of three persons experienced in questionnaire surveys, able to develop an appropriate rapport with the respondents. The interviews were conducted in Nepali or in local Gurung dialect. The structured questionnaires included both fixed-response and open-ended questions. In some cases, the respondents were invited to score the extent to which they agreed with the statement offered. A five-point Likert scale was used in this context, with 1 = strongly disagree, 2 = disagree, 3 = neutral, 4 = agree, and 5 = strongly agree. The questions were written in Nepali.

Random stratified sampling was carried out within each village, stratifying households according to different social groups such as conservation leaders, elected leaders, tourism entrepreneurs, women and occupational groups, as defined by the park office and Village Development Committee (VDC) office. Households in each stratum were then selected randomly such that 15% of the total households in each village were interviewed (Sah and Heinen 2001). In each survey village, interviews purposely included at least two chairpersons from among various functional local institutions such as village development committee (local village government), conservation area management committee, mother's group, tourism management group and youth group identified during the PRA exercises.

An assessment of impact of wildlife conservation on communities was undertaken by conducting household interviews in the sampled villages. A structured questionnaire was posed orally to an adult individual in 150 households selected by stratified random sampling to ensure representative proportions of households from different geographical areas and across the main ethnic groups. It should be noted that the study areas were relatively homogeneous both in terms of the environment (forest cover) and population (ethnic groups). The survey covered 10% of all households in the sampled villages; this represented around 1% of the total number of households and 10% of the villages throughout ACA and in those areas studied outside. Information was collected on socio-economic issues such as crops grown and yields; livestock ownership; damage caused by wildlife on each major crop and livestock; species causing damage; percentage losses and protection measures adopted and attitudes toward wildlife conservation.

The data were analysed using SPSS v. 10.0 (SPSS Inc., Chicago, Illinois, USA). χ^2 tests were used to analyse frequencies. A *t*-test was used to compare means. Normality of the data was tested using the Anderson–Darling test. If the observations were not normally distributed, the data were log transformed prior to analysis. Nonparametric tests (Mann–Whitney *U*-tests) were used if the data were not normal even after transformation.

Results

Rationale for involvement in conservation

The semi-structured interviews indicated that the main reasons given by the respondents in ACA (n = 114) for their involvement in conservation were sustainable use of wild resources (72%), conservation education and awareness (65%), integration of local needs with conservation (50%) and infrastructure development (42.1%). The percentage of respondents citing these reasons for involvement in conservation were significantly lower outside ACA (n = 85, $p < 0.01$ in each case, χ^2-test). Devolution of management authority to the local communities (27.2%), involvement of women in conservation and development (23.7%) and community ownership of resources (22.8%) were also cited by ACA residents as important reasons to be involved in conservation activities, the former two reasons again being cited by a significantly higher percentage of respondents inside ACA than outside ($p < 0.001$ in each case, χ^2-test). Income from tourism was cited by a relatively low percentage of respondents (14.9 vs. 1.2% within and outside ACA respectively; $p = 0.001$, χ^2-test).

Benefits of conservation policy

The principal benefits of the conservation policy have been the reduced depletion of natural resources and increased wildlife, achieved by providing alternative fuelwood, fodder and other energy supplies. As a result of conservation policy, there has been an increase in fodder and fuelwood trees on private woodlots, regeneration of trees on degraded land, greatly increased local institutional development, an increase in forest cover, easier availability of fodder and fuelwood in the forest, improved water resources, an increase in wildlife populations, infrastructure development, and improvements in health and sanitation. These were all reported as benefits by the PRA participants. Results from PRA indicated that local communities in ACA depend on natural forests for '*Nigalo*' (a non-timber forest product, *Arudinaria* spp.), wild vegetables, timber, fodder and fuelwood, the latter two products being quantitatively the most important. The ACA management has also facilitated the restoration or strengthening of traditional resource management systems.

A majority of the respondents believed that access to major resources such as fuelwood and fodder has improved since involvement in ACAP. More than three quarters of the respondents in ACA (89.5%) compared to 36.5% outside strongly agreed with the statement that they have easy access to fuelwood and fodder. Support for social services through improvement in infrastructures in the villages was a further perceived benefit of involvement in conservation. The overwhelming majority of respondents in ACA (94%) either strongly agreed or agreed with the statement regarding satisfaction of village development activities, whereas 78% of respondents reported that basic infrastructure such as drinking water, trails, bridges and health facilities had improved following the conservation intervention. Respondents outside ACA similarly reported that they have received support for infrastructure development through various government agencies and other sources. However χ^2 tests indicated that a greater proportion of ACA respondents perceived livelihood benefits compared to those outside ACA with respect to improvement of access to the village ($\chi^2 = 14.3$, $p < 0.0001$); bridge improvement ($\chi^2 = 44.3$, $p < 0.0001$), village sanitation improvement ($\chi^2 = 28.11$, $p < 0.0001$), and electricity provision ($\chi^2 = 21.67$, $p < 0.0001$). However, no significant differences were found with respect to drinking water improvement ($\chi^2 = 0.53$, $p = 0.47$), provision of health facilities ($\chi^2 = 0.44$, $p = 0.51$) or support for school improvements ($\chi^2 = 2.20$, $p = 0.14$).

Agriculture is the major economic activity in the area. More than half of the respondents (66.7%) in ACA reported that they had received support for agricultural development such as training in sustainable farming, access to vegetable seeds and seedlings, and technical help to establish a vegetable nursery. Only 36.5% of respondents outside ACA reported the same. A higher proportion of respondents in ACA reported that they received support than those outside ($\chi^2 = 17.86$, $p < 0.0001$), 13.2% reporting that they received improved varieties of cereal crop seeds and 38.6% receiving support for seasonal vegetable seeds and seedlings. Overall, within ACA, 81.6% reported that the number of economic opportunities in villages has increased. In contrast, only 34.3% outside reported this. ACA has also provided direct employment opportunities; among 242 ACA staff, almost half of them (49.6%) are local staff from the area.

Costs of conservation

The participatory research revealed that the major costs of conservation were an increase in crop damage by wildlife, a decrease in fodder grass species in forests, a decrease in wild mushroom availability in forests and a decrease in crop production as a result of shading by the on-farm plantations of trees.

More than a quarter of respondents (28.9%) in ACA reported that they have encountered livelihood difficulties since 1989, when ACA was declared. However, a χ^2-test revealed that this value was significantly lower inside than outside ACA ($p = 0.005$). Almost half of the respondents outside ACA (48.2%) reported that they have encountered difficulties as a result of the Government's forest conservation programme, principally the restriction of forest utilisation and a lack of grazing land (Table 1). Forest areas outside ACA do not have any legal designation but are generally under government control through the activities of the District Forest Offices. The government has recently been promoting community forestry to protect forest areas in the vicinity of settlements, which aims to manage and utilise forest resources for

Table 1. Potential difficulties experienced by local communities following introduction of conservation measures, identified through semi-structured interviews.

Difficulties	Inside ACA (%) (n = 114)	Outside ACA (%) (n = 85)	χ^2	p-Value
1. Restriction of forest utilisation	10.5	32.9	15.23	< 0.0001
2. Control of hunting	7.0	10.6	0.80	0.375
3. Lack of grazing land	3.5	27.1	23.03	< 0.0001
4. Restriction of commercial harvesting	3.5	4.7	0.18	0.671
5. Frequent intervention by conservation authorities	0.9	0	0.75	0.387
6. Decrease in forest-based small-scale industry	0.9	3.5	1.74	0.187
7. Crop damage and livestock depredation	15.8	12.9	0.317	0.573

and by the community but there are no integrated conservation efforts outside ACA. The results illustrated in Table 1, experienced outside ACA, may therefore reflect perceptions of community forestry initiatives. These difficulties were perceived to be significantly less of a problem within ACA ($p < 0.001$). However, crop damage and livestock depredation were reported as significant problems by the respondents in ACA (15.8%).

Most respondents in ACA (84%, $n = 89$) reported that they have experienced problems of crop damage by wildlife such as monkeys, deer, etc. at least some of the time. In general, the incidence of crop losses appeared to be more severe inside ACA than outside (Figure 2), where 28% reported that crop damage was either rarely or never experienced, compared to only 2% within ACA. Generally, perceptions of crop losses by wildlife varied considerably among study villages (Figure 3). This evidence suggests that crop damage by wildlife has intensified as a result of ACA. The incidence of crop damage also differed between villages; in six villages, 100% of respondents stated that they experienced crop damage at least some of the time.

Millet (*Sorghum* spp.), paddy rice (*Oryza sativa*), maize (*Zea mays*) and potato (*Solanum tubersum*) were the key crops damaged by wildlife, which are the main crops grown in ACA. Among the respondents in ACA, more than 97% ($n = 89$) reported that they cultivated maize and millet, and 51% cultivated potatoes. Of the total respondents, almost three quarters (74%) reported loss of maize by wild animals, whereas 38 and 42% reported loss of rice and millet, respectively. Crop losses were also estimated as a proportion of total production, based on the difference between reported yield and possible yield in the absence of crop damage on individual plots as reported by the respondents (Studsrod and Wegge 1995). Losses inside ACA ranged from 6% (rice) to 23% (maize) of total production (Figure 3). In the case of maize, millet and potatoes, the proportional losses were significantly higher inside ACA than outside ($p = 0.001$, 0.005 and 0.008, respectively, Mann–Whitney *U*-tests).

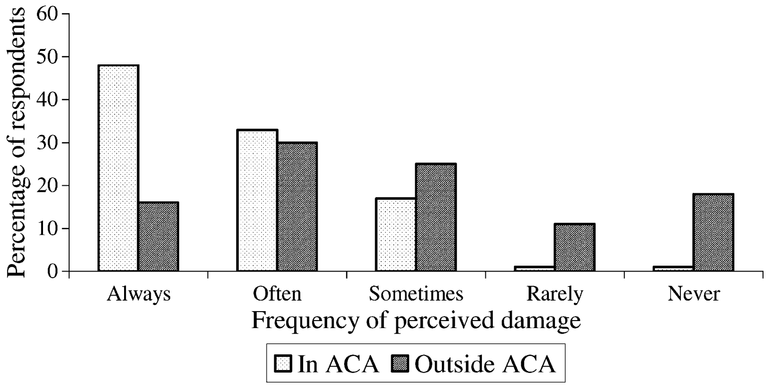

Figure 2. Frequency of perceived damage of crops by wildlife based on a questionnaire survey.

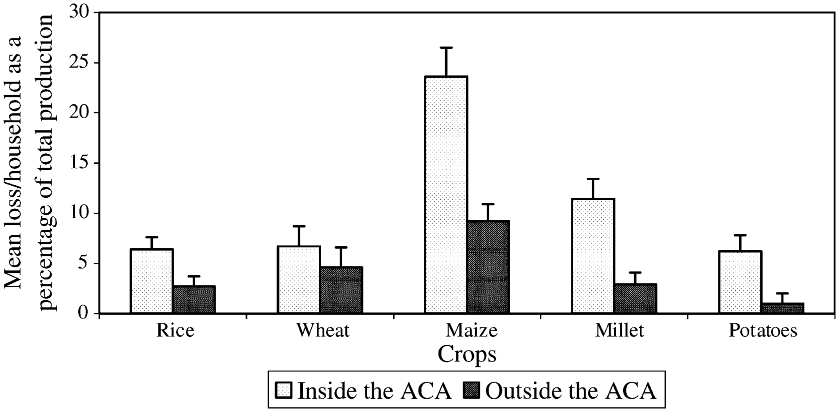

Figure 3. Estimated mean crop losses by each household in the study area based on a questionnaire survey.

Five species of animal were reported as significant causes of crop damage, both within and outside ACA (Figure 4). The Rhesus macaque (*Macaca mulatto*) and porcupine (*Hystrix indica*) were reported to be the most important causes of crop damage by respondents within ACA (87 and 72% respondents, respectively). These animals are difficult to drive away and often damaged substantial quantities of crops. The barking deer (*Muntiacus muntjak*), Himalayan black bear (*Ursus thibetanus*) and Common langur (*Semnopithecus entellus*) were also considered to be significant causes of crop damage by respondents (Figure 4). Approximately three quarters of the respondents within ACA either strongly agreed or agreed with the statement that pest wildlife species, especially the rhesus monkey and porcupine should be culled, while more than half of the total respondents outside ACA either strongly agreed or agreed with this statement. A Mann–Whitney *U*-test showed that the

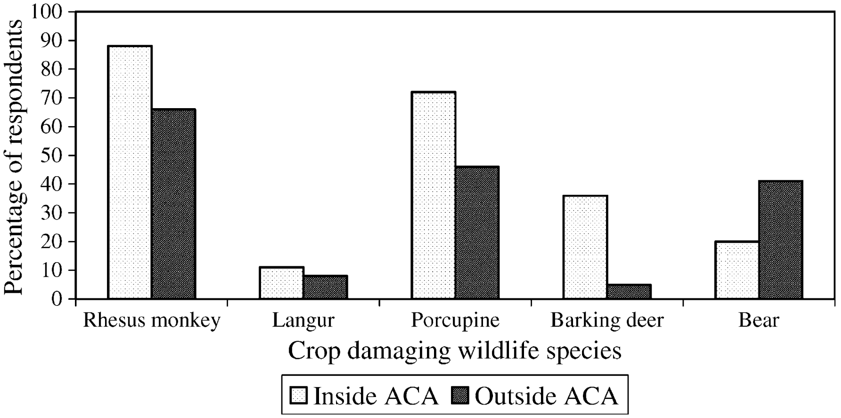

Figure 4. Respondent's ranking of the major crop damaging wildlife species as indicated in a questionnaire survey.

proportion that agreed was significantly higher in ACA (U = 1904.5, p = 0.001). The results show that there is a clear perception of wildlife damage within ACA and that this view is substantiated by physical evidence of crop loss, affecting a significant proportion of crop production.

Results indicated that the problem of livestock depredation by wild predators exists in ACA, but was not perceived to be serious by respondents, with a majority (66% within ACA, 64% outside) reporting that they had never experienced livestock depredation incidents (Figure 5). During discussions forming part of the PRA exercises within ACA, participants reflected that livestock depredation had decreased over the past two decades.

The majority of respondents both inside (94.4%) and outside ACA (97%) indicated that they raised livestock. Buffaloes were the main animals in both within and outside ACA. The mean (± SE) livestock unit (LSU), which is calculated as a buffalo = 1.5 LSU; cattle = 1 LSU and goat and sheep = 0.20 LSU (source: Sekhar 1998), was 6.5 ± 1.0 and 4.1 ± 0.42 LSU per household within and outside ACA, respectively. There was no significant difference in livestock-holding inside and outside ACA. Despite buffaloes being the main livestock in the study area, none of the respondents either within or outside ACA reported killings by wild animals during the past three years. However, respondents in both areas reported occasional killing of cattle, goats and sheep. The establishment of the conservation area therefore appears not to have affected wildlife-livestock conflicts. The mean number of cattle, goats and sheep killed by wild animals was found to be no different within and outside ACA (Table 2).

On average, a household within ACA lost total animals valued at the equivalent of £3.9 (Rs. 479.70) each year. Similarly, a household outside ACA lost the equivalent of £3.6 (Rs. 442.80) each year. These estimates are based on prices provided by the respondents and the ACA Natural Resources Conservation section (Buffalo = £131.1; Cow = £12.2; Ox = £65.0; Goat = £24.4

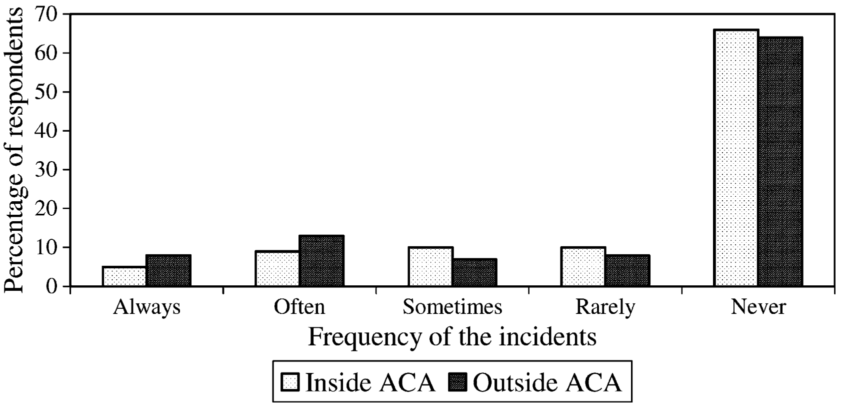

Figure 5. Frequency of livestock depredation by wild predators perceived by local communities as indicated in a questionnaire survey.

Table 2. Estimated livestock killing by wildlife over a three-year period (1999–2001), based on results from a questionnaire survey.

Households	Inside ACA (*n* = 89)	Outside ACA (*n* = 61)
Mean Livestock unit (LSU)	6.5	4.1
Livestock killed		
Buffaloes	0	0
Cattle	9	2
Goats and sheep	30	24
Total kills	39	26
Total kill in LSU	15	6.8
Average LSU loss (mean ± SE)	0.16 ± 0.04	0.12 ± 0.04

Livestock unit (LSU) is calculated as a buffalo = 1.5 LSU; cattle = 1 LSU and goats and sheep = 0.20 LSU. *Source*: Sekhar (1998).

and Sheep = £28.5; and 1 pound = Rs. 123.00). The common leopard (*Panthera pardus*) is the only carnivorous species held responsible for killing livestock in the area.

A further factor mentioned by respondents with respect to crop losses was the impact of shade from tree plantations. The local communities in ACA reported during the PRA exercises that crop yields decreased by a quarter in the farms adjacent to private or community woodlots. This was not a concern outside ACA as there are no such woodlots. It was also reported that the effects of tree-shade were more significant for small landholders.

Discussion

It is generally believed that local communities are more likely to support conservation initiatives if they receive direct benefits from them (McNeely

1995). The cost-benefit ratio of conserving a protected area must ultimately be positive for the local communities if conservation is to be effective in the long term (McNeely 1995). The results presented here show that local communities in ACA have received various direct and indirect benefits from their involvement in the protected area, which can be broadly categorised into consumptive use benefits, benefits from improved social services, and benefits from increased economic opportunities. In general, most of the benefits received by local communities in ACA were non-monetary and for subsistence purposes.

Fuelwood, fodder, timber, wild vegetables and other non-timber forest products, particularly *nigalo* (*Arudinaria* sps.), are major consumptive uses of natural forests in ACA. Among these products, fuelwood and fodder are the most important resources for subsistence use by local communities. The communities in ACA considered the implementation of un-bureaucratic and self-governing local management of the resources and improved rights of access to wild forest resources were the major consumptive use benefits of ACA. Imposition of the protected area regulations has not prohibited subsistence use of these resources. This is very different from other protected areas in Nepal where resource management and protection are carried out directly by the government without formal involvement of local communities (Sharma and Wells 1996; Nepal 2002). The current results also contrast with many communities living within or outside protected areas in other areas, where access to wild resources is often possible only under strict licenses or through illegal actions (Mishra 1982a; Sharma 1990; Hough 1991; Abbot and Mace 1999; Fortin and Gagnon 1999; Straede and Helles 2000). Bajracharya et al. (2005) indicate that as a result of introduction of community-based conservation approaches in ACA, fuelwood harvesting has declined, which can be attributed to measures such as the introduction of alternative forms of energy, conservation education and the development of fuelwood in private woodlots.

Improvements in basic social services such as sanitation and drinking water, primary healthcare and basic education, improve human development outcomes and also help to reduce poverty by raising human capability levels (UNDP 2002). Social development services with a strong system of local management are major visible and important benefits received by local communities within ACA. The present findings were broadly consistent with those of Mehta and Heinen (2001), indicating that the majority of ACA villages have adequate sanitation and drinking water facilities, trails, bridges, primary healthcare, primary education both for children and adults, provision of electricity and most importantly a system of community management of these services. The community-based approach to conservation has therefore helped to improve the living standards of local communities within ACA.

The majority of village infrastructure development projects are either financed through the revenue from park entry fees or from the support of international donors. A substantial proportion of the annual funding for conservation activities in ACA was, until the recent Maoist action, financed through tourist revenues (Gurung 2005). Similar infrastructural development benefits have been reported from other community-based projects elsewhere (Metcalfe 1994; Pearl 1994; Wainwright and Wehrmeyer 1998; Infield and Namara 2001; Kangwana and Mako 2001). An overwhelming majority of respondents in the conservation area expressed satisfaction with social service developments. Services such as trails, schools, bridges, health-posts, water and electricity were either nonexistent or were highly seasonal before the inception of ACA. The official records of ACA also support these results (KMTNC-ACAP 1997, 1999, 2001; Kim and Karky 2001). ACAP has insisted on community participation, in cash or labour, in these social development projects to avoid investing as 'gifts' (Feldmann 1994). Community involvement in social services has been reported as insignificant elsewhere in Nepal (UNDP 2002). On the other hand, some infrastructure developments such as drinking water schemes, health facilities and school development were reported also to have improved outside ACA. Various donor agencies and some government agencies are actively working on delivering development programmes outside ACA. However, the majority of the study villages outside ACA do not currently have access to adequate health and educational facilities.

The major economic benefits received by local people within ACA were the investments made to improve social services, agriculture and livestock improvement, development of employment opportunities and provision of various training schemes. ACAP's annual investment in conservation and development, which is financed either through sharing revenue from the entry fee levied on tourists or from the support of international donors, is a major economic benefit to local communities. Unlike most national park entry fees (Metcalfe 1994; Lewis and Alpert 1997), these fees do not to go to national government treasury but are retained by KMTNC for conservation projects in ACA. This arrangement is unique in Nepal and is little-known elsewhere (Sharma and Wells 1996). Over the last 13 years (1989/90 to 2000/01), slightly more than £3.8 million (NRs. 471 million) revenue was collected from visitors and about £2.7 million (NRs. 330 million) was received from international donors. Of the total income during the period, £5.8 million was invested in conservation and development programmes. However, although agriculture and livestock farming are the major economic activities in the conservation area, it is clear that support to local communities regarding these activities is still a weak aspect of the ACA programme.

It has been reported that with the exception of lodge operation and other tourism businesses, many community members in ACA have not yet been able to benefit financially from conservation (Nepal et al. 2002). The current results also indicated that the majority of residents in ACA, with the exception of tourism entrepreneurs, have not received direct monetary benefits from conservation. However, evidence suggests that economic opportunities such as horticulture, poultry, bakery, and employment opportunities for skilled persons have been increased within the ACA villages. Nepal et al. (2002) reported that more than 1500 local people are employed by lodges alone in the southern slopes of the Annapurna area. Employment of the local communities within the ACA management was also found to be significant. Of the total 242 ACA staff, 49.6% are locally hired. In contrast, it has been reported that local employment has been entirely neglected in management of protected areas in some other countries such as China (Ghimire 1997).

Despite the many important benefits of protected areas, local communities often have to bear a variety of different costs after an area is declared as a protected area, as a number of different negative consequences may ensue (McNeely 1995; Ghimire and Pimbert 1997; Lusigi 1982; Mishra 1982a; Hough 1988; McNeely 1995; Spergel 1997). The community-based conservation approach is designed to mitigate these costs by providing compensation or appropriate substitutions to reduce the need of local communities to exploit wild resources within protected areas. A surprisingly high proportion of the respondents within ACA reported that they have not encountered any major difficulty as a result of the protected area designation, although crop damage by wildlife in ACA was found to be a significant problem. This result needs to be treated cautiously, as respondents may have been reluctant to speak against the conservation programme. Nevertheless, it is possible that strengthened access to wild resources such as fuelwood and fodder, and tangible improvements in basic social services supplemented by increased conservation awareness have outweighed any difficulties encountered. This suggests that if local communities perceive direct benefits from conservation of wild resources, they may be more likely to accept a degree of crop damage (Naughton-Treves 1997).

Recent studies have reported similar crop losses in protected areas elsewhere (Studsrod and Wegge 1995; Naughton-Treves 1997; Sekhar 1998; Mehta and Heinen 2001; Miah et al. 2001; Rao et al. 2002a; Madhusudan 2003). The current results show that there is a clear perception of wildlife damage to crops within ACA and that this view is substantiated by physical evidence of crop loss, representing a significant part of income. The situation is significantly worse within ACA than outside, presumably as a result of conservation measures having resulted in increased populations of those species responsible for crop damage. The extent and intensity of crop damage may vary, depending on the cropping patterns (Rao et al. 2002a). The evidence suggests that crop damage has affected food security of the local communities, because staple food grains such as maize, millet and potatoes were the worst affected. The current results indicate that on average a household in ACA loses about a quarter of the annual maize production owing to wildlife damage, in an area where 18% of households were reported to be not able to meet their basic food needs (Banskota and Sharma 1995). The majority of local communities in ACA are at or below subsistence level (Gurung and DeCoursey 1994). Losses of crops to wildlife are therefore very significant to local communities. Discussions with the local communities indicated that the problem of crop damage has increased since the inception of ACA.

Studies have shown that crop damage by wild animals is one of the main reasons for park-people conflicts (Mishra 1982a; Sharma 1990; Osborn and Parker 2003; Weladji and Tchamba 2003). Despite the acute problem of crop damage in ACA, local communities have not demanded compensation. However, during discussions local communities reported that an application for permission to kill crop-damaging animals has been made to the ACA management. Some questionnaire survey respondents expressed their frustration by criticising the ACA management for not giving proper attention to the issue. Therefore, crop damage could potentially be a major source of conflict between local communities and ACA management in future, if it is not properly addressed.

In contrast to reports from elsewhere (Studsrod and Wegge 1995; Sekhar 1998), only a few animal species were responsible for crop damage, particularly the Rhesus macaque and porcupine. However, respondents in Ghandruk, Landruk and Chhomrong villages also reported barking deer as a problem animal. Discussions with local communities indicated that the problem with the Rhesus macaque and porcupine existed before establishment of the conservation area, and they also reported a traditional system of controlling these animals, involving driving away or killing some of these animals annually. Trapping and killing of a few rhesus macaques was reported to be enough to keep away other animals from farmlands for a year. However, the legal prohibitions on killing of crop damaging animals appear to have resulted in increased crop damage. A high proportion of the respondents expressed the opinion that these crop-damaging animal species should be culled. This is not a surprising result and is a reflection of concerns over the present situation. Other recent studies have also shown a similar pattern of response from local communities (Mehta and Heinen 2001; see also Songorwa et al. 2000; Weladji and Tchamba 2003). Studies have shown that crop damage by wildlife is one of the main reasons for a negative attitude among local communities towards conservation even though they receive benefits from conservation (Parry and Campbell 1992; Heinen 1993; Newmark et al. 1993; Akama et al. 1995; Fiallo and Jacobson 1995; Studsrod and Wegge 1995).

It is important to note that according to 2002 IUCN Red List of Threatened Species (IUCN 2002), Rhesus macaque is in the lower risk category and Himalayan Black bear is classified as Vulnerable. Barking deer, leopard and porcupine are not considered threatened. However, present conservation regulations do not allow any wildlife to be controlled. According to the Conservation Area Management Guidelines, the ownership of wildlife remains with the government; hence permission from the government is generally required to control such problem animals. Discussions with PRA participants suggest that occasionally porcupine, Rhesus macaque, barking deer and Himalayan black bear are killed illegally when there are severe threats from these animals. The primary reason for these illegal actions is the protection of farm productivity and not direct monetary or subsistence benefits from the wildlife. Similar actions by local communities have also been reported from protected areas in India (Rao et al. 2002a).

In contrast, livestock losses either within or outside ACA were not found to be so significant; within ACA, the incidence of livestock depredation was reported by less than a quarter of the respondents. Although it was reported previously that an increase in wildlife has in turn led to livestock depredation in ACA (Banskota and Sharma 1995), no evidence was found during the current research. In contrast, a study in Royal Bardia National Park, Nepal reported that about half of the households lost livestock to predators each year (Studsrod and Wegge 1995). However, in monetary terms, losses of domestic animals per household per year is higher in ACA than as reported by Studsrod and Wegge (1995), but lower than that reported by Sekhar (1998) in Sariska Tiger Reserve, India. A majority of the PRA participants in ACA believed that an increase in the population of ungulates, particularly barking deer, has reduced livestock depredation. They mentioned that in the past local people use to hunt barking deer, therefore leopards used to kill livestock. One explanation for a decrease in livestock depredation in ACA, therefore, could be that the prey–predator balance in ACA has altered.

However, there are other potential reasons for the results observed. Free grazing of domestic stock in forests has decreased considerably. As a result, competition between livestock and ungulates for grazing in the forest has been reduced. Evidence also suggests that there has also been a reduction in the number of small-bodied livestock such as goats and sheep thereby reducing the likelihood of depredation. Studsrod et al. (1995) reported that leopards kill small-sized animals such as goats and sheep. The common leopard is the only carnivore species held responsible for killing of livestock either in ACA or outside. In contrast, it has been reported from other protected areas that an increase in livestock population densities has also increased conflict with wildlife (Sekhar 1998). For example, Parry and Campbell (1992) reported that 59% of the households with livestock in Botswana complained of livestock losses during a year. The present evidence also does not support the suggestion that conflict with rural communities in ACA as a result of livestock depredation by large carnivores has increased in recent years.

Conclusions

The 1973 National Parks and Wildlife Conservation Act of Nepal was amended in 1989 to provide a legal basis for establishing multiple use conservation areas. With this amendment, conservation is not just limited to protection, but explicitly refers to protection and/or sustainable use of species and ecosystems. As a result of implementation of this policy in ACA, local communities have been given greater access to forest resources, and alternative sources of energy and fodder have been developed, which have reduced the impact of local communities on natural forest resources and associated biodiversity. The community-based approach to protected area management as implemented in ACA has also succeeded in delivering a range of benefits to local communities. These include consumptive use benefits, benefits from social services and increased economic opportunities. These improvements to the life of local communities are associated with increasingly effective conservation of biodiversity within ACA. This is substantiated by a range of indicators such as reduced forest loss and increases in wildlife abundance (Bajracharya et al. 2005). However, local communities have also incurred significant costs, the most important of which is crop damage by wildlife. This implies that the management policy for ACA will need reviewing or modifying in future. One possible solution is to give more authority and responsibility to local communities to manage wildlife for their crop protection. However, this issue is controversial (Infield and Namara 2001), especially where some of the animals concerned are threatened with extinction. It has been argued that the future success of conservation in Nepal depends on the ability to provide local villagers with sufficient and varied resources to secure their livelihoods (Studsrod and Wegge 1995). The results of the current research suggest that if this is to be achieved, a participatory approach to management of problematic animal species will need to be developed.

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References

Abbot J.I.O. and Mace R. 1999. Managing protected woodlands: fuelwood collection and law enforcement in Lake Malawi National Park. Conserv. Biol. 13: 418–421.

Adams B. and Hulme D. 1998. Conservation and Communities: Changing Narratives, Policies and Practices in African Conservation. Working Paper No. 4. IDPM, University of Manchester, Manchester, 31 pp.

Akama J.S., Lant C.L. and Burnett G.W. 1995. Conflicting attitudes towards state wildlife conservation programmes in Kenya. Society Nat. Resour. 8: 133–144.

Bajracharya S.B. 2004. Community Involvement in Conservation: An Assessment of Impacts and Implications in the Annapurna Conservation Area, Nepal. PhD Thesis, University of Edinburgh, Edinburgh, Scotland, 314 pp.

Bajracharya S.B., Furley P.A. and Newton A.C. 2005. Effectiveness of community involvement in delivering conservation benefits to the Annapurna Conservation Area, Nepal. Environ. Conserv. (in press).

Banskota K. and Sharma B. 1995. Tourism for Mountain Community Development: Case Study Report on the Annapurna and Gorkha Regions of Nepal. International Centre for Integrated Mountain Development, Kathmandu, 233 pp.

Brandon K.E. and Wells M. 1992. Planning for people and parks: design dilemmas. World Develop. 20: 557–576.

Chambers R. 1997. Whose Reality Counts? Putting the First Last. Intermediate Technology Publications, London, pp. xx + 297.

DNPWC 1996. Annual Progress Report for Fiscal Year 2052–53. Department of National Parks and Wildlife Conservation/HMG, Kathmandu, Nepal.annexes + 34 pp.

Dudley N., Gujja B., Jackson B., Jeanrenaud J., Oviedo G., Phillips A., Rosable P., Stolton S. and Wells S. 1999. Challenges for protected areas in 21st century. In: Stolton S. and Dudley N. (eds), Partnerships for Protection. WWF, IUCN and Earthscan Publications Ltd, London, UK, pp. 3–12.

Feldmann F. 1994. Community environmental action: the national policy context. In: Western D., Wright M.R. and Strum S. (eds), Natural Connection: Perspectives in Community-based Conservation. Island Press, Washington, DC, pp. 393–402.

Fiallo E.A. and Jacobson S.K. 1995. Local communities and protected areas: attitudes of rural residents towards conservation and Machalilla National Park, Ecuador. Environ. Conserv. 22: 241–249.

Fortin M.J. and Gagnon C. 1999. An assessment of social impacts of national parks on communities in Quebec, Canada. Environ. Conserv. 26: 200–211.

Ghimire K.B. 1997. Conservation and social development: an assessment of Wolong and other reserves in China. In: Ghimire K.B. and Pimbert M.P. (eds), Social Change and Conservation. Earthscan Publications Limited, London, pp. 187–213.

Ghimire K.B. and Pimbert M.P. 1997. Social change and conservation: an overview of issues and concepts. In: Ghimire K.B. and Pimbert M.P. (eds), Social Change and Conservation: Environmental Politics and Impacts of National Parks and Protected Areas. Earthscan Publications Limited, London, pp. 1–45.

Gibson C.C. and Marks S.A. 1995. Transferring rural hunters into conservationists: an assessment of community-based wildlife management in Africa. World Develop. 23: 941–957.

Gurung G. 2005. Securing financial sustainability for Annapurna Conservation Area. In: Sharma U.R. and Yonzon P.B. (eds), People and Protected Areas in South Asia. IUCN South Asia and Resources Himalaya Foundation, Kathmandu, Nepal, pp. 86–89.

Gurung C.P. and DeCoursey M.A. 1994. The Annapurna Conservation Area Project: a pioneering example of sustainable tourism?. In: Cater E. and Lowman G. (eds), Ecotourism: A Sustainable Option?. John Wiley and Sons, New York, pp. 177–194.

Hackel J.D. 1998. Community conservation and the future of Africa's wildlife. Conserv. Biol. 13: 726–734.

Heinen J.T. 1993. Park people relations in Kosi Tappu Wildlife Reserve, Nepal – a socio-economic analysis. Environ. Conserv. 20: 25–34.

Hough J.L. 1988. Obstacles to effective management of conflicts between national parks and surrounding human communities in developing countries. Environ. Conserv. 15: 129–136.

Hough J. 1991. Michiru Mountain Conservation Area: integrating conservation with human needs. In: West P.C. and Brechin S.R. (eds), Resident Peoples and National Parks: Social Dilemmas and Strategies in International Conservation. The University of Arizona Press, Tucson, pp. 130–137.

Infield M. and Namara A. 2001. Community attitudes and behaviour towards conservation: an assessment of a community conservation programme in around Lake Mburo National Park, Uganda. Oryx 35: 48–60.

Inskipp C. and Inskipp T. 2001. A popular guide to the birds and mammals of the Annapurna Conservation Area. KMTNC-Annapurna Conservation Area Project. Pokhara, Nepal, x + 41 pp.

IUCN 1998. Towards Participatory Management of Protected Areas in Asia Region. IUCN.

IUCN 2002. 2002 IUCN Red List of Threatened Species. IUCN, www.redlist.org.

IUCN 2003. Durban Action Plan. In: The Vth IUCN World Park Congress Available from www.iucn.org/themes/wcpa/wpc2003/. IUCN, Durban, South Africa.

Kangwana K. and Mako R.F. 2001. Conservation, livelihoods and the intrinsic value of wildlife: Tarangire National Park, Tanzania. In: Humle D. and Murphree M.W. (eds), African Wildlife and Livelihoods: the Promise and Performance of Community Conservation. James Currey Limited, Oxford.

Kim E. and Karky B.S. 2001. Water Resource Use in the Annapurna Conservation Area: Assessment of Micro-Hydropower Management in Sikles and Chhomrong. KMTNC-Annapurna Conservation Area Project, Pokhara, Nepal, 34 pp.

KMTNC-ACAP 1997. A new approach in protected area management. KMTNC-Annapurna Conservation Area Project, Pokhara, Nepal, 39 pp.

KMTNC-ACAP 1999. Two Years Retrospective Report: 1996/97 & 1997/98. Published Report. KMTNC-Annapurna Conservation Area Project, Pokhara, 30 pp.

KMTNC-ACAP 2001. Two Years Retrospective Report July 1998–July 2000. Published Report. KMTNC-Annapurna Conservation Area Project, Pokhara, 44 pp.

Lehmkuhl J.F., Upreti R.K. and Sharma U.R. 1988. National parks and local development: grasses and people in Royal Chitwan National Park, Nepal. Environ. Conserv. 15: 143–148.

Lewis D.M. and Alpert P. 1997. Trophy hunting and wildlife conservation in Zambia. Conserv. Biol. 11: 59–68.

Lusigi W.J. 1982. Future directions for the Afrotropical realm. In: McNeely J.A. and Miller K.R. (eds), The Third World Congress on National Parks and Protected Areas. Bali, Indonesia, 1984. Smithsonian Institute Press, Washington, DC, pp. 137–146.

Madhusudan M.D. 2003. Living amidst large wildlife: livestock and crop depredation by large mammals in the interior villages of Bhadra Tiger Reserve, south India. Environ. Manage. 31: 466–475.

McNeely J.A. 1995. Partnerships for conservation: an introduction. In: McNeely J.A. (ed.), Expanding Partnerships in Conservation. Island Press, Washington, DC, pp. 1–10.

Mehta J.N. and Heinen J.T. 2001. Does community-based conservation shape favourable attitudes among locals? An empirical study from Nepal. Environ. Manage. 28: 165–177.

Mehta J.N. and Kellert S.R. 1998. Local attitudes toward community-based conservation policy and programmes in Nepal: a case study in the Makalu-Barun Conservation Area. Environ. Conserv. 25: 320–333.

Metcalfe S. 1994. The Zimbabwe Communal Areas Management Programme for Indigenous Resources (CAMPFIRE). In: Western D. and Wright R.M. (eds), Natural Connections: Perspectives in Community-based Conservation. Island Press, Washington, DC, pp. 161–192.

Miah D., Rahman L. and Ashan F. 2001. Assessment of crop damage by wildlife in Chunati Wildlife Sanctuary, Bangladesh. Tigerpaper 28: 22–28.

Mishra H. 1982a. Balancing human needs and conservation in Nepal's Royal Chitwan National Park. Ambio 11: 246–251.

Mishra H.R. 1982b. A delicate balance: tigers, rhinoceros, tourists and park management vs. the needs of local people in Royal Chitwan National Park, Nepal. In: McNeely J.A. and Miller K.R. (eds), The Third World Congress on National Parks and Protected Areas. Bali, Indonesia, 1984. Smithsonian Institute Press, Washington, DC, pp. 197–205.

Murphree M.W. 1994. The role of institutions in community-based conservation. In: Western D., Wright R.M. and Strum S.C. (eds), in Community-based Conservation. Island Press, Washington, DC, pp. 403–427.

Naughton-Treves L. 1997. Predicting patterns of crop damage by wildlife around Kibale National Park, Uganda. Conserv. Biol. 12: 156–168.

Nepal S. 2002. Linking parks and people: Nepal's experience in resolving conflicts in parks and protected areas. Int. J. Sustain. Develop. World Ecol. 9: 75–90.

Nepal S.K., Kohler T. and Banzhaf B.R. 2002. Great Himalayas: Tourism and the Dynamics of Changes in Nepal. Swiss Foundation for Alpine Research in collaboration with the Centre for Development and Environment, University of Berne, Zurich, 92pp.

Newmark W.D., Leonard N.L., Sariko H.I. and Gamassa D.G.M. 1993. Conservation attitudes of local people living adjacent to protected areas in Tanzania. Biol. Conserv. 63: 177–183.

Osborn F.V. and Parker G.E. 2003. Towards an integrated approach for reducing the conflict between elephants and people: a review of current research. Oryx 37: 80–84.

Oviedo G. and Brown J. 1999. Building alliances with indigenous peoples to establish and manage protected areas. In: Stolton S. and Dudley N. (eds), Partnerships for Protection. WWF, IUCN and Earthscan Publications Ltd, London, pp. 98–108.

Parry D. and Campbell B. 1992. Attitudes of rural communities to animal wildlife and its utilisation in Chobe Enclave and Mababe Depression, Bostwana. Environ. Conserv. 19: 245–252.

Pearl M.C. 1994. Local initiatives and rewards for biodiversity conservation: Crater Mountain Wildlife Management Area, Papua New Guinea. In: Western D. and Wright M.R. (eds), in Community-based Conservation. Island Press, Washington, DC, pp. 193–214.

Pimbert M.P. and Pretty J.N. 1997. Parks, people and professionals: putting 'participation' protected-area management. In: Ghimire K. and Pimbert M.P. (eds), Social Change and Conservation. Earthscan Publication Limited, UK, pp. 297–330.

Punch K.F. 1998. Introduction to Social Research: Quantitative and Qualitative Approaches. SAGE Publications, London, pp. xv + 319.

Rao K.S., Maikhuri R.K., Nautiyal S. and Saxena K.G. 2002a. Crop damage and livestock depredation by wildlife: a case study from Nanda Devi Biosphere Reserve, India. J. Environ. Manage. 66: 317–327.

Rao M., Rabinowitz A. and Khaing S.T. 2002b. Status review of the protected area system in Myanmar, with recommendations for conservation. Conserv. Biol. 16: 360–368.

Sah J.P. and Heinen J.T. 2001. Wetland resource use and conservation attitudes among indigenous and migrant peoples in Ghodaghodi Lake area, Nepal. Environ. Conserv. 28: 345–356.

Salafsky N. and Wollenberg E. 2000. Linking livelihood and conservation: a conceptual framework and scale for assessing the integration of human needs and biodiversity. World Develop. 28: 1421–1438.

Sekhar N.U. 1998. Crop and livestock depredation caused by wild animals in protected areas: the case of Sariska Tiger Reserve, Rajasthan, India. Environ. Conserv. 25: 160–171.

Sharma U.R. 1990. An overview of park–people interactions in Royal Chitwan National Park, Nepal. Landscape Urban Plan. 19: 133–144.

Sharma U.R. and Wells M.P. 1996. Nepal. In: Lutz E. and Caldecott J. (eds), Decentralisation and Biodiversity Conservation. The World Bank, New York, pp. 65–76.

Sherpa M.N., Coburn B. and Gurung C.P. 1986. Annapurna Conservation Area, Nepal: Operational Plan. King Mahendra Trust for Nature Conservation and World Wildlife Fund, Kathmandu, xiii + Annexes + 74pp.

Songorwa A.L., Buhrs T. and Hughey K.F.D. 2000. Community-based wildlife management in Africa: a critical assessment of the literature. Nat. Resour. J. 40: 603–643.

Spergel B. 1997. Compensation and substitute programmes. In: Borrini-Feyerbend G. (eds), Seeking Social Sustainability in Conservation. IUCN, Gland, Switzerland, pp. 91–93.

Stolton S. and Dudley N. (eds) 1999. Partnerships for Protection. UK Earthscan Publication Ltd, London, xvii + 283pp.

Straede S. and Helles F. 2000. Park–people conflict resolution in Royal Chitwan National Park, Nepal: buying time at high cost? Environ. Conserv. 27: 368–381.

Studsrod J.E. and Wegge P. 1995. Park–people relationships: the case of damage caused by park animals around the Royal Bardia National Park, Nepal. Environ. Conserv. 22: 133–142.

Terborgh J. and Schaik C.V. 2002. Why the world needs parks. In: Terborgh J., Schaik C.V., Davenport L. and Rao M. (eds), Making Parks Work: Strategies for Preserving Tropical Nature. Island Press, Washington, pp. 3–14.

UNDP 2002. Nepal Human Development Report 2001: Poverty Reduction and Governance. UNDP, Kathmandu, xii + 154pp.

Wainwright C. and Wehrmeyer W. 1998. Success in integrating conservation and development? a study from Zambia World Develop. 26: 933–944.

Weladji R.B. and Tchamba M.N. 2003. Conflict between people and protected areas within the Benoue Wildlife Conservation Area, north Cameroon. Oryx 37: 72–79.

Wells M. and Brandon K. 1992. People and Parks: Linking Protected Area Management with Local Communities. World Bank, World Wildlife Fund and USAID, Washington, DC, xii + 98pp.

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Stakeholder analysis of river restoration activity for eight years in a river channel

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Abstract. From 1998 to 2003, stakeholder analysis was conducted to investigate an origin and continuity of river restoration project by local stakeholders. The project includes introduction of catch-and-release regulation of trout and remaking Sabo dam to slit Sabo dam in a river channel. In the stakeholder analysis, four attributes of stakeholder; such as power, legitimacy, urgency, and position were demonstrated. Then Stakeholder Typology was created to overview stakeholders' characteristic. After that, how the past 8 years project was promoted and how future project should be promoted was described. Network structure was built to arrange these descriptions. Each stakeholder had one or more attributes of power, legitimacy and urgency. Definitive stakeholders, who have three attributes, played a major role to assure the project. Definitive stakeholders were local residents and they first introduced C&R regulation in a local river channel to increase trout population. After that, a definitive stakeholder petitioned to remake Sabo dam to slit Sabo dam to reconnect river continuity and enhance river ecosystem. However, future continuity of the project may be threatened by lack of power of definitive stakeholders.

Abbreviation: FFC – Freshwater Fishery Cooperative; SA – Stakeholder Analysis

Introduction

The project to restore river environment has widely attracted public attention. Streams and rivers have utility for human such as power supply and water supply, and have been variously developed focusing on those purposes. These days, values for ecosystem and recreational use have been increasingly concerned. 'River Law' which incorporated environmental preservation and the citizens' participation for river management was revised in 1997 in Japan.

Streams and rivers enable movement of substances from upstream to downstream and channels should make it possible to pass materials among head stream, upstream, midstream, lower stream, mouth of river and sea. Importance of river basin and river continuity are paid attention to and afforestation to upper river basin by sea fishermen is performed who believe that riparian forest supplies nutrient over sea and help to grow marine product such as fish and shellfish (Yaginuma 1993; Hatai 1999). Reimchen (2001) described, from appearance of nitrogen isotopes in riparian forest, which exists in sea, that salmon for spawn brought nutritive to riparian forest through predatory animals and river basin which salmon run had thick riparian forest compared to river basin which salmon cannot run. In domestic rivers, many fishes such as masu salmon (*Onchorhynchus masou masou*), mountain trout (*Salvelinus leucomaenis pluvius*), Japanese eel (*Anguilla japonica*), and UGUI (*Tribolodon hakonensis*) come and go between sea and upstream and it became clear that supply of nutritive to river basin was made poor by cutting off the river continuity. Recent research pointed out that it is desirable river is not cut-off in pieces as much as possible so that living things can go back and forth from upstream to the sea (Tanaka 1998; Yoshii et al. 2000).

A project now implemented at Sagae River which flows through Yamagata Prefecture, North part of Japan is one of the stimulating and suggesting examples for many organizations who are planning or starting to restore river ecosystem. In this settlement, river restoration project has been viscously, tenaciously implemented from each side of software and hardware project and project was steadily achieved. In the software project, local Freshwater Fishery Cooperative (FFC) asked anglers to release trout after they catch (Catch and Release, C&R) and lucrative trout resource which in the past was severely overharvested was remained alive until spawning season. In the hardware project, river continuity is regained by fishway installation and remaking Sabo dam to slit Sabo dam. These activities made it possible both for fish to spawn to tributary to reproduce and for human being to obtain clean and cold water. These activities (the project, hereafter) have enhanced river environment.

In this article, stakeholder analysis (SA) is applied to analyze the origin and continuity of this project. Secondly, to achieve this objective, the method of network structure being investigated is also proposed.

Materials and methods

Study site

The study site deals closely with C&R regulation since July 1997 (Figure 1) in Sagae River. The river flows through Oisawa district of Nishikawa town, Nishimurayama county, Yamagata prefecture and has been managed by Mogamidaini FFC. The population of Oisawa is about 360 people and the percentage of the older is 46% (as of 2001.4.) which overwhelms the average nationwide number of 18.0% (Ministry of Public Management, Home Affairs, Posts and Telecommunications 2002). The C&R section is located in the domicile and almost half of the section is protected by concrete revetment. The C&R regulation is not prescribed in the FFC regulation but recommended by the local FFC to anglers and it depends on angler's discretion. Now the FFC is

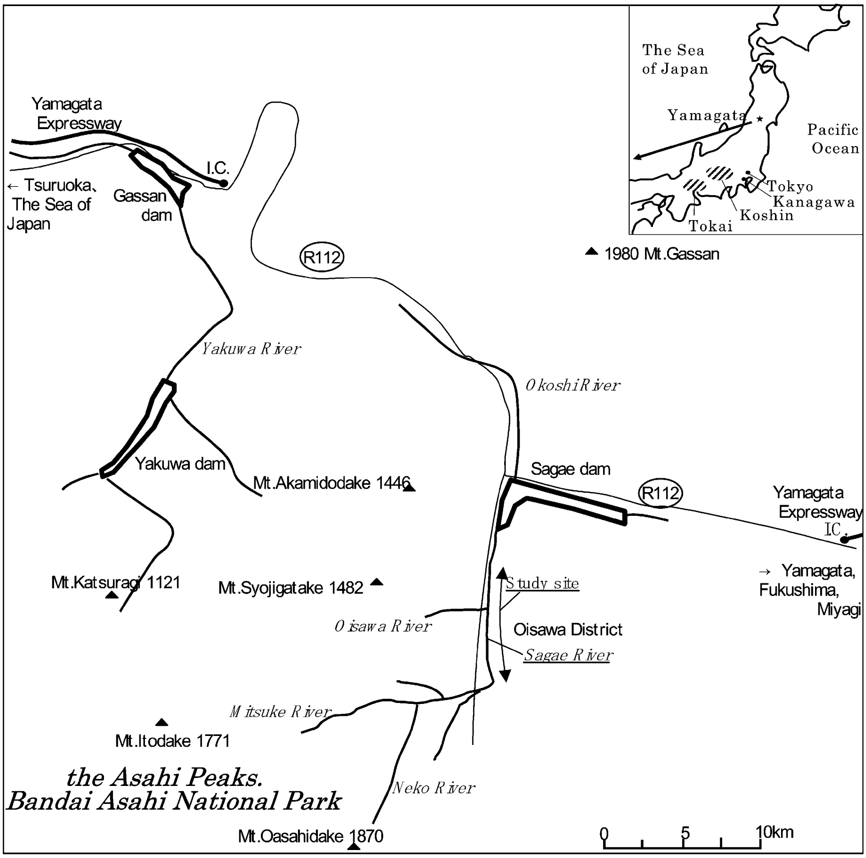

Figure 1. Study site map.

asking prefectural fishery agency to approbate it as a regulation. The section was extended to about 12 km including both tributary and upstream in 2000.

The section had the length of about 7 km, average width of 50 m, deepest depth of 3 m, pool-riffle channel unit, 30 min drive from IC of express way. In the section, Mountain trout (*Salvelinus leucomaenis*), rainbow trout (*Oncorhynchus mykiss*), and masu salmon (*Oncorhynchus masou masou*) are inhabiting. Present regulation of Sagae River do not have restrictions on gear, creel limit, but have size limit under 15 cm. Fishing season is open from March to September. From an economical research of I-O table by Tanaka (unpublished data), many anglers who approve the regulation had come to visit the C&R section from adjacent prefectures and metropolitan areas and economic ripple effect of over 100 million yens to domestic area and over 30 million yens to Yamagata prefecture had been brought from 1999 to 2001. Moreover, large trout exceeding 40 cm have been able to be seen in the section.

Methods

Stakeholder analysis

Stakeholder is defined as an actor who has interest under certain circumstances, have influence on a problem, and have positive or negative impact by policy decision and its enforcement (Varvasovszky and Brugha 2000). There are some definitions of stakeholder (Freeman and Reed 1983; Savage et al. 1991; Brenner 1993, 1995; Freeman 1994; Starik 1994) and some of them are defined only for corporate firm to identify their stakeholders. But stakeholder definition by Freeman (1984) is comprehensive and thus extensively used. He defined it as 'Any group or individual who can affect or is affected by the achievement of the organization's objectives.' SA has started to be applied since 1970s as one of the tools of policy analysis by political scientists and focusing on understanding of power relationship between stakeholders and of roles of stakeholders on the process of policy decision (Brugha and Varvasovszky 2000). Nowadays SA is used as an analytical tool to clarify the differences in the view point between stakeholders who have conflicting interest. Or, SA is used to make alternative strategy to promote sustainable use of natural resources and enhance equality of natural resources' management. Thus, SA clarifies power relationship and decision process between conflicting stakeholders such as groups or individuals under certain condition. SA helps to understand difference of interests and potential common interest between stakeholders and proposes practical mediation for a better natural resource management (Chevalier 2001). SA demonstrates correlation between groups or organizations and focuses on impact assessment to policy under certain relationships (Brugha and Varvasovszky 2000).

SA is also used as a method to analyze how to promote a policy before the policy is conducted, or is used to analyze alternative plans or expansibility of present policy to various directions (Brugha and Varvasovszky 2000). In this article, SA is used to analyze an origin and continuity of the project and to show expected future directions by proposed network structure.

There are some examples of SA. As a conceptual work, Dick (1997) described role for every stakeholder, investigated positions of stakeholders to certain policy (strongly supportive – neutral – strongly opposite), demonstrated influence (+ + ∼ –) and elaborates strategy to implement a policy. Ravnborg and Buerrero (1997) used SA as a tool of solving degradation of land in the hilly country in Colombia. Each group used the subdivided farmland for different purposes because people in this area had different religions by different races. As a result, aggravation of water and erosion of land had happened. At prior interview, respondents were required to mention every problem and list every stakeholder who has different opinion from them. This listing work is called snowball technique (Varvasovszky and Brugha 2000) and useful to collect stakeholders' data and their network (Scott 1991; Wasserman and Faust 1994). After extracting all stakeholders and listing up every problem, resident assembly was held and the cause and the solution of problems were adjusted by discussions. In the management method of SSSI (Sites of Special Scientific Interest) area in Britain, when the traditional agricultural technique which local farmers have long adopted was likely to be excluded by scientist who claims strict ecosystem management, Harrison and Burgess (2000) performed periodical workshops between them by SA analysis and built consensus.

In this study, stakeholder typology (Mitchell et al. 1997) is firstly described to analyze stakeholder's characteristics. Stakeholder typology demonstrates various attributes of stakeholders for every attribute defined beforehand and classifies stakeholders on Ben figure. Mitchell et al. (1997) proposed a method of notional classification of stakeholders in order to enable administrators/managers to be able to pay more attentions to stakeholders' needs and to implement a policy easily. According to Mitchell et al., stakeholders largely have three genre of attributes; power, legitimacy, and urgency (Figure 2).

They used the definition of power from Dahl (1957) and he wrote it as 'A relationship among social actors in which one social actor, A, can get another social actor, B, to do something that B would not have otherwise done.' That means that there is a relationship that a certain stakeholder A can make B do something, and B does not carry out it if A does not have power.

Definition of legitimacy by Suchman (1995) was used to identify legitimacy in this research. He defined legitimacy as 'A generalized perception or assumption that the actions of an entity are desirable, proper, or appropriate within some socially constructed system of norms, values, beliefs, and definitions.' Stakeholders, which have legitimacy, correspond to an individual, an organization, an institute, etc. and they have pragmatic, moral or cognitive

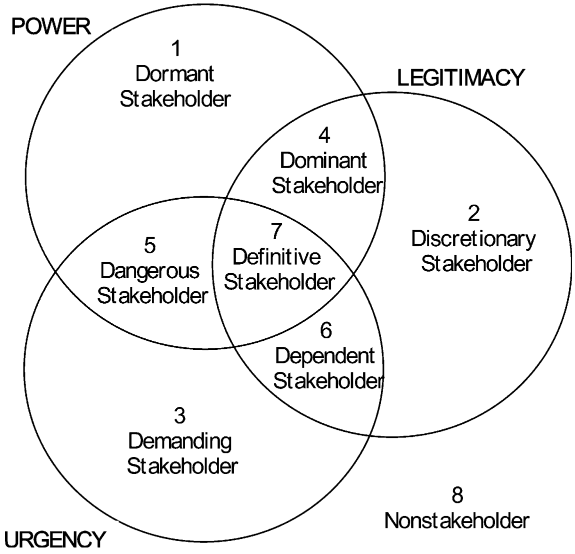

Figure 2. Stakeholder typology by Mitchell et al. (1997).

Table 1. Brief definition of legitimacy (summarized from Suchman 1995).

Primary form	Secondary form	Brief definition
A. Pragmatic legitimacy based on people's self-interest	1. Exchange legitimacy	Legitimacy that stakeholder have support from people based on the policy's expected value
	2. Influence legitimacy	Legitimacy that people support the stakeholder not necessarily because it provides favorable exchanges but because they see it as being responsible to their interests
	3. Dispositional legitimacy	Legitimacy that people treat the stakeholder as morally responsible actors
B. Moral legitimacy based on normative approval	4. Consequential legitimacy	Legitimacy that stakeholder have consequential responsibility such as automobile emission standards
	5. Procedural legitimacy	Legitimacy that stakeholder produce socially valued consequences and embrace socially accepted techniques or procedures
	6. Structural legitimacy	Legitimacy that people see a stakeholder as valuable and worthy support because of socially constructed structure such as educational institutes
	7. Personal legitimacy	Legitimacy that individual 'moral entrepreneurs' play a substantial role in initiating new ones
C. Cognitive legitimacy based on comprehensibility and taken-for-grantedness	8. Comprehensibility	Legitimacy that people merely accept the organization as necessary or inevitable based on some taken-for-granted cultural account
	9. Taken-for-grantedness	Legitimacy that people must struggle to arrange to a rule in coherent, understandable accounts

relation for the interest of a problem. Suchman (1995) defined nine genres of legitimacy (Table 1). Stakeholders which have legitimacy in this research are classified into nine legitimacies. Table 1 shows brief definition of nine legitimacies summarized by author from Suchman (1995).

Mitchell et al. (1997) defined urgency as 'The degree to which stakeholder claims call for immediate attention' and which include cases where it is intolerable for stakeholder to delay implementation of a policy (time sensitivity), and stakeholders can not give up their opinions because an interest collide and tension reached a critical point (criticality). Each stakeholder has more than one attribute covering power, legitimacy and urgency, therefore, it is possible for each stakeholder to be classified to the following Ben figure (Figure 2).

Method

In order to implement SA, interview to all stakeholders was conducted from 1997 to 2003 to describe their power, legitimacy, urgency and position. To demonstrate power of each stakeholder, a method of analyzing each senator's power in a process of a bill enactment in the United States Senate committee (Dahl 1957) is used (after-mentioned).

Whether the stakeholder has legitimacy or not is identified from a point that the stakeholder has administrative responsibility such as river management article prescribed in administrative law, or the stakeholder has support from people about the policy, or people take it natural for stakeholder to engage to solve the problem. These points were considered from administrative documents, local angler's journals and interview from all stakeholders, local people, entrepreneurs and farmers. Then, each stakeholder was classified into one of nine types of legitimacy.

Urgency and position of the stakeholder is judged by answer through interview whether they support or oppose the project, have urgency to support or oppose it and why do they support or oppose it. The interview consists of three stages; namely, general finding, official interview and reconfirmation.

At the general finding stage, snowball technique is used to find all stakeholders. Major stakeholders are firstly identified by random interview to local celebrities, municipalities, local people, local newspapers, and other mass media. In this stage, any person/organization (=informant) who seem to be stakeholder has interview. The Informants are asked to nominate every actor with whom he thinks the project has any relationship. The nominated actors are also asked to nominate other actors with whom he thinks the project has any interconnection. This snowball procedure continues until no one is nominated any more. Informants are also asked to talk every event about the river restoration activity. The interview is conducted by how, what, when, where, with whom, why the assumed stakeholder involves the event. In this study this stage continued from 1997 to 2002. The rather long-term of general finding stage is because in our research new event happened every year in this period until 2002.

Table 2. Stakeholder characteristic of river restoration project.

Stakeholders	Characteristics				
	Involvement in the issue	Power	Legitimacy	Urgency	Position (present)
Branch chief of FFC. Mr.S(BS)	Local fishery management. BS has strong belief to conserve local nature	High	Personal legitimacy	Yes	Supportive
Past member of Fishery Section, Yamagata prefecture. Mr.S(YS)	Political and monetary support from prefecture as trout stock subsidy	High	Personal legitimacy	Yes	Supportive
Executive secretary of C&R Promotetion Conference (ES)	Mediator between BS and OG. He can fix opposed human relations	High	Personal legitimacy	Yes	Supportive
Shinjo Office, Ministry of Land, Insfrastructure and Transport(SO)	Operation of Slit sabo dam and fishway. SO has policy to budget and oparate steam restoration	Medium-high	Consequential legitimacy	Yes	Neutral
Chief of FFC Mr.T(CT)	Enactment of C&R and proclamation among FFC members. FFC has duty to breed fishery resources	High	Consequential legitimacy	Yes	Supportive
Sight-seeing Section, Nishikawa Town. Mr.G(NG)	Support from the town. The section has policy to develop Oisawa sight-seeing	Medium-high	Consequential legitimacy	No	Supportive
Fishery Section, Yamagata prefecture (FY)	As one of concerns, FY comprehend C&R but still does not approbate it because of no antecedent	Medium-high	Consequential legitimacy	No	Neutral
Board of Trade, Oisawa District (BO)	A member of C&R promote conference. The Board expects economical benefit from C&R section (chameleon)	High (chameleon)	Influence legitimacy	Yes	Supportive
Opposite Group (OG)	Intentional resistance to C&R. OG has worried about decline of anglers	Low	Influence legitimacy	No	Opposed
Lyrical Anglers (LA)	Support of human resources. LA wants to recover river environment with plenty of trout	Medium-low	Influence legitimacy	No	Neutral
Trout Forum (TF)	Support by policy planning. Nationwide organization to improve river environment	Medium-low	Influence legitimacy	No	Neutral

Voluntary Anglers (VA)	Human resource support (oversight, making free map, etc.). VA consists of out of local anglers and act to improve river environment	Medium-high	Personal legitimacy	Yes	Supportive
Poachers (PO)	Never purchase fishing ticket, cast fishing net etc. They use any method to keep trout	–	–	–	Opposed
Researcher Mr.T (author) (RT)	RT has written articles in journals and magazines to support the project	Medium-high	Personal legitimacy	Yes	Supportive
Yamagata Newspaper, YTS TV (YY)	YY favorably reports the C&R section and contributes to promote the section among prefectural people	Medium-high	Comprehensibility	No	Supportive

At official interview stage, all stakeholders are asked to confirm what researcher found by interview. The events which stakeholder involved in are list up in a paper. Also current position and urgency of stakeholder is asked directly. The reason to involve in the activity is also asked and legitimacy is considered from the answer.

At reconfirmation stage, some new findings from official interviews are reconfirmed to some stakeholder. This works were done by mail, telephone or direct interview.

Result

Stakeholder analysis through the project

The section has been managed by many people but branch chief of Mogami-daini FFC has played a central role. Related organizations, local people, and many voluntary anglers had supported the section. Management included not only enlightenment activity to anglers about regulation, sales of fishing tickets, surveillance of poaching, but also petition to MLIT (Ministry of Land, Infrastructure and Transport) to remake Sabo dam to slit Sabo dam and installation of fishways.

Table 2 describes stakeholders' descriptive characteristics. 'Involvement in the issue' explain stakeholders' activity in the project. 'Power' expresses influence to the project by the stakeholder and used a method of analyzing each senator's Power exerted on enacting a bill in the United States Senate committee (Dahl 1957). Twenty-five important policy decisions from 1996 to 2002 related to the section was extracted from stakeholder interview and power was calculated based on stakeholders' anti or proposition to the implementation of each policy. Pairwise stakeholders were selected in all combination and the power relationship was judged by whether the policies which the two stakeholders supported or opposed were carried out. As a result, stakeholders were classified into four classes. The class was categorized as High, Medium-high, Medium-low, and Low, respectively. Some of twenty-five policy decisions to analyze power were listed in Table 3. 'Legitimacy' expresses pragmatic, moral, or cognitive attribute of each stakeholder to the project and nine types of legitimacy by Suchman (1995) is used. To find 'Urgency,' stakeholders are asked whether they have urgency to involve in this river restoration project in three levels (high urgency, relative high urgency, in no hurry). If the stakeholder replies they have high or relative high urgency, the stakeholder is considered to have urgency. 'Position' was decided by interview and questionnaire to stakeholders. The researcher asked them whether they support, oppose, or take a neutral stance on the project.

Although stakeholder BO was ranked as one of High Power stakeholders in it, since BO had followed the decision of stakeholder BS, ES and YS, the researcher regarded BO's behavior as satellite behavior (or chameleon behavior)

Table 3. Examples of decision issue from 1996 to 2002 in the project.

Issue (proposal)	Result	Stakeholders														
		BS	YS	ES	SO	CT	NG	FY	BO	OG	LA	TF	VA	PO	RT	YY
1996 Proposal of setting flyfishing area by LA	O	O	O				S				S					
1997 Proposal of setting C&R area by TF	S	S	S			S	S	S		O	S	S	S		S	
2000 Proposal of setting C&R promotion conference by NG	S	S	S			S	S	S	S	O	S				S	
2000 Proposal of extension of C&R area by local people	S	S	S			S	S	S	S	O		O	S		S	
2000 Claim of illegal quarring by Co.A from local people	S	S	S		O								S			
2000 Proposal of holding fishing festival by BS and YS	S	S	S			S	S	S	S		O	O	S		S	
2001 Implementation of slit incision by SO	S	S			S					S					S	
2002 Introduction of barbless hook regulation by CT and BS	S	S	S	S		S							S		S	S

S: support the issue; O: oppose the issue.

(Dahl 1957) and BO was not able to be considered as one of the high power stakeholders. Satellite behavior is also called chameleon behavior. Stakeholder who takes satellite behavior expresses same opinions with other high power stakeholders, do not have own opinion to the policy discussed, and take action together with other high power stakeholders. Stakeholder BO had same actions with BS because increased economic benefit to the section by the project and personable and sincere character of BS. Opinion of BO to the project did not exist. If I dare to say that, the opinion of BO is much likely the same as BS.

The reason of each legitimacy. SO has Mogami river flood control plan based on river law. CT has propagation duties of fishery resource by fishery law. NG has aim of Nishikawa town promotion. FY has aim of promotion of prefectural freshwater fishery. These stakeholders are classified to have consequential legitimacy. The reasons of stakeholders classified into influence legitimacy are as follows. BO has responsibility to represent local profits. OG has support from some anglers out of town and is representative of their interest. LA has support from anglers such as members of TF and is regarded as representative of their interest. TF is a nationwide organization with many anglers' support. The reasons of stakeholders classified into personal legitimacy are as follows. VA is a group of personal legitimacy who voluntary works to support the section. RT is a researcher working to enhance river ecosystem, local economy, and voluntarily support the section. BS, YS, and PY are individually acting to improve their local river environment. The researcher failed to classify PO because the researcher was not able to interview them.

In addition to the legitimacy in Table 2, some stakeholders apparently have two or more legitimacies. For example, although CT has consequential legitimacy, CT specially support the section by frequent personal communications with BS and be considered to have personal legitimacy. In such case, main legitimacy is decided by relationship between what the stakeholder did and what legitimacy the stakeholder had. If CT has consequential legitimacy, CT could enact C&R in the fishery. However, if CT has personal legitimacy, CT couldn't enact C&R fishery by himself.

Dahl (1957) defined power as an attribute that a stakeholder can force a certain action to other stakeholder. In this research, the researcher assumed power from relationship in process of policy decision. Because the stakeholder with power can make policy decision, the stakeholder can indirectly force to exclude other stakeholders from the decision. In this case power is assumed to be able to inhibit opinions of others.

Branch chief of FFC (branch chief BS, hereafter) played a central role to set up C&R section who managed private lodging house in the district and acceded the chief since 1996. Branch chief BS once insisted introduction of sports fishing area to mayor in 1991 which allows anglers to keep only two trouts. It was because BS worried about decrease of trout population by overharvesting and deterioration of river environment by erosion control work. Branch chief BS had also insisted to reform revetment to gabions. But his insistence never actualized. However, BS was appreciated by local people for his will to viscously insist his opinion and nominated as a branch chief in spite of youngest member of FFC in the district (41 years old) among about 60 members.

'Lyrical Anglers (about 80 members. Sub name "Yamagata prefecture river conference")' (club LA, hereafter) who plays game fishing mainly in Yamagata prefecture requested Nishikawa town to set flyfishing only section in the study site in February, 1996. Mr NG, who is an officer of sightseeing section in Nishikawa town (town NG, hereafter), set meeting between club LA and branch chief BS, and they decided to have Gassan sports fishing festival (after mentioned) in the July. Branch chief BS did not agree the proposal of club LA to set flyfishing only section but club LA ordinarily support C&R of native fish and worried about over harvesting of trout and over construction of erosion control work. Those insistences were common among them.

After the setup of C&R section in 1997, members of club LA visited the section regardless of weekdays or weekends until 2000 and promote and monitor C&R regulation at the field. Poaching was sensibly prevented at the first few years by the members and they played an important role to promote the section. Although present voluntary activity of monitoring was covered by other anglers, club LA is concerned as a member of Oisawa C&R promotion conference which was established in 2000.

The regulation of C&R is not yet approbated from the fishery section of Yamagata prefecture. However, it is recognized at representative meeting of Mogamidaini FFC. For Mogamidaini FFC which consist of over 1000 members, Oisawa branch which consist of about 60 members is one of the small branches. For example, when FFC stocks trout, branch chief BS cannot say anything about species, places, and amount to stock. Branch chief BS can be informed when and where FFC stock trout few days before. Chief of Mogamidaini FFC (FFC chief CT, hereafter) and Branch chief BS had meeting about establishment of C&R section. FFC chief CT declared the establishment of C&R section by his responsibility when the second Gassan sports fishing festival was held. After the festival, FFC chief CT publicized the establishment to members as ex post facto approval. FFC chief CT was a ruling politician whose ancestries worked for chairmans and vice chairmans of municipal assembly and who was vice chairman of the assembly until he retired.

Gassan sports fishing festival was first held in July, 1996 by mainly arrangement of club LA. The purpose of the festival was to promote C&R of native trout among anglers. In the festival size contest of catch-and-released trout by self-report was held. There were about 150 participants in the 2 days festival mainly from urban areas. FFC chief CT and commissioners of FFC were convinced that there existed many anglers who enjoyed C&R of trout. This festival has been taken over to branch chief BS and town NG from club LA since 2000 and continued to be held 7th festival in 2002 though the name and contents were changed. This festival has contributed to promote C&R of native trout.

A former officer of fishery division of Yamagata prefecture YS planned a 3 year program to subsidize initial investment of trout stock to the section by prefectural budget from 1997. YS had implemented monitoring every early morning for the years before going office. YS also established a volunteer organization in cooperation with local anglers to monitor the section. YS moved to a prefectural experimental station from prefectural office in 2000 but have continued to monitor the section with volunteer anglers. Present fishery division (FY, hereafter) is busy for other projects such as eradication of foreign species or vaccine study of cold water disease for sweet fish. FY does not have special project to support the section at present.

NG (town NG, hereafter), who is a officer of the sightseeing division of Nishikawa town, had been planning optimal utilization of local rivers before the section was setup in 1997. Town NG felt out branch chief BS about a proposal from club LA. Town NG has considered trout fishing is lucrative for local industry, noted the plan, and tried to support to set the section.

Trout forum (club TF, hereafter) is a nationwide organization for anglers in Japan. Club TF proposes projects to improve river environment especially for trout. The activity includes proposals of software project such as introduction of C&R or creel limit and proposals of hardware project such as installation of fishway or arrangement of spawning bed. At a trout fishing forum sponsored by Yamagata prefecture in 1997, club TF proposed setup of C&R section to branch chief BS and that was a trigger of the setup. However, club TF started to suspect that the section was utilized only for sightseeing promotion and the section was utilized to collect anglers without improvement of river environment. As a result, club TF criticized related stakeholders such as branch chief BS, fishery division YS, and there is no communication between them now. However, some members of club TF have interested in the project in which now remaking Sabo dam to slit Sabo dam is under construction. There is a possibility to re-support the section by club TF in the future, referring mainly to the view of executive secretary of TF as he told me. The negative impression to the section by club TF has been shared with some members of club LA and club LA stopped the organizational support of the section since 2001 although club LA is one of the members of C&R promotion conference. Some members of club LA have individually continued to support the section.

In the process of promotion of C&R, Mass medium (Media YY, hereafter) gave large influence to local people. In 1996, Media YY such as Yamagata newspaper noticed the approach of C&R and covered the news. Yamagata newspaper favorably reports the section with large color photo over four columns every year. Local broadcasting station YTS have also favorably reported the section in local news. There is a relationship between branch chief BS and Media YY that branch chief BS accommodates media YY to guide mountain trail to carry broadcast machinery to TV tower on the top of the Asahi Mountains. It seems to be able to say that C&R of domestic trout, which is different from C&R of exotic fish, has been accepted to prefectural people through Media YY.

Board of trade in Oisawa district (Board BO, hereafter) is one of the member of C&R promotion conference with town NG, club LA, FFC chief CT, conference ES, department SO, branch chief BS, although some members of Board BO oppose the C&R regulation. The reason is after-mentioned. There is no independent activity of Board BO because Board BO merely complies with decisions taken by branch chief BS. Therefore, Board BO is assumed to have satellite or chameleon behavior (Dahl 1957). Board BO was statistically classified into high power (Table 2), but considered not to have high power by this behavior.

Executive secretary of C&R promotion conference (Conference ES, hereafter) is a childhood friend of branch chief BS. Conference ES is inevitable stakeholder to adjust opinions between branch chief BS and other stakeholders. Sometimes exchanges of opinion between opposite stakeholders were passed through conference ES.

A part of local residents in Oisawa has opposed the C&R regulation (anti OG, hereafter). The reason is economical disadvantage and lost opportunity of casting net. In this district only few local people go fishing in the section, some of customer anglers ceased to stay in their accustomed local private lodging houses after the set of C&R and especially one private lodging house take negative economical effect for the regulation. Though anglers who visit this section has increased since the setup of the regulation (Table 4), master of the private lodging house has recommended his guests to keep trout and new anglers intentionally avoid staying in the private lodging house. District chief is also a member of anti OG. Oisawa district won the emperor prize of agriculture–forestry–fishery festival in November 2001, awarded for the most impressive local development activity in the year. And one of the reasons was setup of C&R regulation. After winning the prize, district chief went to Imperial Palace to accept the award. Recently, remark of the chief is beginning to change from the complete opposition to part approval that ‘our district has to continue the C&R regulation but fishing net use for local people to keep trout should be admitted,’ from SA interview. Other stakeholders criticize this remark, as it is expedient.

Many volunteer anglers have been becoming big power to support the C&R section (anglers VA, hereafter). Expenses of notification signboard on the riverside and of free color map to show access points were sponsored by anglers VA. Also, management of the section consist of many uncountable volunteer activity by anglers VA such as setting of the signboard, designing of the map, monitor activity in the section, management of Gassan sports fishing festival in which some anglers came from Tokyo by over 5 h drive on voluntary base.

Poachers (poachers PO, hereafter) are ubiquitous. Poachers PO sometimes conceal trout in their breast pocket or in the pouch to keep trout and do not have creel. Or, some of them use casting net and keep trout in a short time. There is also a rumor that some of them use lamplight at midnight with casting net. Although activities of them are decreasing by surveillance, poaching is becoming elusive. There is obviously some places with few trouts. It is sure that poaching is performed. By effort of surveillance, some of the poachers PO were reported to local police, recorded their car numbers, or publicized name in a local HP. These actions have become a deterrent. Although numbers of poachers PO are gradually decreasing, scale of poaching cannot comprehend.

As a researcher, RT (author) consider that C&R does not only means the trout is released after catch but that means that the released trout will spawn in autumn and the life is bind to next generation. Moreover, for the binding, rich river environment is required so that the next generation grows up healthfully. RT has continued to talk about necessity for remaking present Sabo dam and concrete revetment to more effective facility for river environment. The stance does not change in future.

Now, C&R regulation is being steadily acknowledged and the project is spreading to reconstruct river structure such as slit Sabo dam in order to restore river ecosystem. For the implementation, negotiation to improve river hardware is positively promoted with MLIT (Ministry of Land, Infrastructure and Transport) (department SO, hereafter).

Project to restore river continuity

From the winter of 2001, remaking of Sabo dam to slit Sabo dam started to be implemented at second dam of Oisawa Stream which is a tributary of the section (Photo 1). Department SO has implemented the reconstruction. Before the reconstruction, officers of department SO visited branch chief BS to inform it because anglers claim for turbidity of stream water to him when it happens.

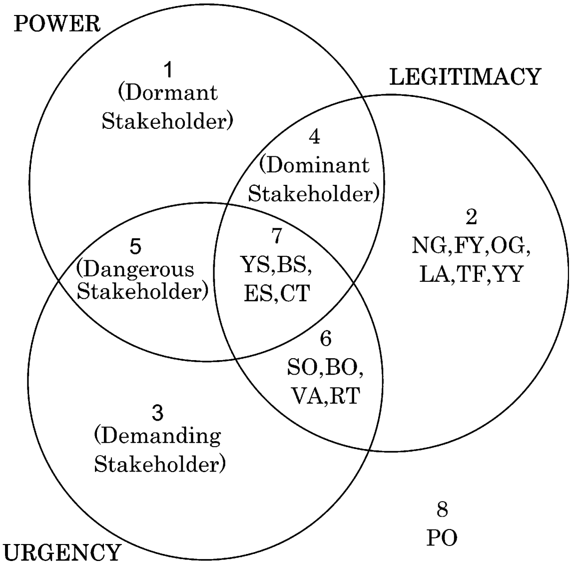

Figure 3. Stakeholder typology in this study (present).

Photo 1. Oisawa stream 2nd dam in 2002. Slit incision implemented by one-half.

It is not legally obliged that officer of department SO has to contact local FFC when he implement erosion control work to local river. There is no regulation to connect FFC and MLIT. However, branch chief BS have ordinarily close relationship with officers of MLIT because branch chief BS is a sole driver who can operate extra huge snowplow car for the highway R112 in winter and so on. Implementation of slit Sabo dam was not assured from the plan of department SO but from frequent requests of branch chief BS, department SO agreed this time to accept his request to restore river continuity.

They established a plan to implement slit Sabo dam to totally five dams which are located in Oisawa Stream, Neko Stream and Mitsuke Stream which are tributaries of Sagae River. The plan will be implemented gradually.

Photo 1 shows that slit was implemented only to the half of the height of dam. In the plan, 1st phase of reconstruction was performed until half of the height. Second phase of reconstruction is performed untill the surface of the water. By this reconstruction, bulk of sediment flew downstream by snowmelt of April and rainy season of July in 2002. Water of Oisawa Stream is used as living water. Serious muddiness to the water happened by the sediment in 2002 and officers of MLIT explained this reason in the district and apologized. This muddiness is temporal and after the flushing there are many expected advantages such that the exposed bed rock is covered by gravels from upstream, an upper pond of the dam disappear and clear water is supplied, anadromous fishes can run to the tributaries to spawn and so on. So, most of the local residents understand the plan and expect to experience the effect.

Other request which the local resident asked to MLIT are installation of fishway at inlet of Sagae dam and reconstruction of concrete revetment to gabions or something other to cover the grey construct. In this district, there is a good relationship between local people and MLIT. Branch chief BS has interest and few knowledge of the close to nature river construction method. Although there will probably be restrictions of budget, river continuity will be regained gradually without sacrificing flood control in the future.

Figure 3 shows current stakeholder typology of this study. This figure was created on the basis of power, legitimacy and urgency of Table 2. About power, only ‘High’ power stakeholders in Table 2 of branch chief BS, fishery division YS, FFC chief CT, and conference ES were considered to have substantial decisive power and other stakeholders were considered as they does not have power.

In Figure 3, discretionary stakeholder (2), dependent stakeholder (6), and definitive stakeholder (7) are recognized. Discretionary stakeholder (2) have legitimacy to carry out the project but does not have power, so the stakeholder does not directly concerned with the project. And since the stakeholder does not have urgency, motive to implement the project and request to the project will be sometimes weak. Dependent stakeholder (6) has legitimacy and urgency to the project, but does not have power. So, he cannot directly decide the direction of the project. There is a possibility that his opinion is not reflected to the project although he has his own opinion. Definitive Stakeholder (7) is a stakeholder which has power, legitimacy and urgency and literally he play the major role to implement the project. Branch chief BS, fishery division YS, and conference ES have had critical feeling that their local familiar river had been firmed by concrete structures and trout had been overharvested. Fishery division YS is now moved his office to experimental institute of fishery but he still continue to contact with prefectural officers. FFC chief CT is a chief to manage the bioenvironment in local rivers and is maintaining cooperation with BS.

Until now, Branch Chief BS, fishery division YS, and conference ES, who are definitive stakeholders, took leadership responsibility and FFC chief CT has politically supported the project. On the other hand, there is a severe problems when the future prospective is considered. Power to implement hardware project such as installation of fishway and implementation of slit Sabo dam is not given to the definitive stakeholders of branch chief BS, fishery division YS, conference ES, and FFC chief CT. Land of Sagae River is managed by MLIT and MLIT implements hardware project. Here is a notice that sometimes someone has illusion that an organization which has legitimacy does have power. For example of Japanese FFC, they have legal and traditional fishery right, continued to harvest fishery resources for several hundreds years, have legal right to be compensated when the local river is deteriorated by others. However, when there is a plan to construct dam or when FFC want to restore river continuity by slit Sabo dam installation, FFC has no right to stop/implement the hardware project. All FFC can do is to petition to MLIT to stop/implement the hardware project. In many cases, local requests is not disregarded. However, when there is a plan such as construction of huge multipurpose dam, there are many past histories to force to remove the local residents from domicile by request from downstream urban areas. For such reason, power of FFC is weak and MLIT has power to plan and implement hardware project. When the reconstruction of hardware is discussed, FFC has legitimacy to the project but FFC does not have enough power. Also branch chief BS, fishery division YS, and conference ES does not have enough power. In future hardware projects, department SO will have power and move to definitive stakeholder (7) from dependent stakeholder (6) in Figure 3. On the other hand, branch chief BS, fishery division YS, conference PY, and FFC chief CT may be displaced to dependent stakeholders (6) from definitive stakeholders (7).

The process of the project was spontaneously carried out by local people in which branch chief BS played a central role. In the present, we are having nationwide consensus to restore river ecosystem and a Promotion Act for Nature Restoration was enacted in December, 2002. That means that Japanese government finally made a route of investment project for restoring lost environment. On the other hand, local people in Oisawa had implemented the

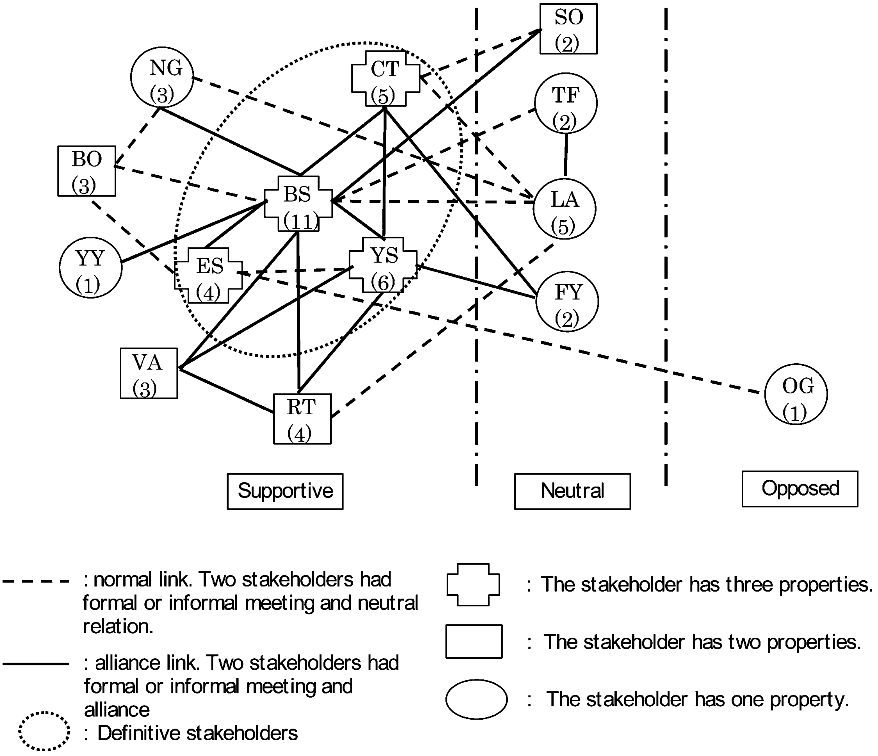

Figure 4. Network structure (sociogram) of the river restoration project (present). Cruciate boxes indicate definitive stakeholders which have all three properties of Power, Legitimacy and Urgency. Rectangles indicate stakeholders who have two properties. Circles indicate stakeholders who have one property. Parentheses under each stakeholder indicate number of links.

project since years ago by tenacious petition and voluntary works with weak political and economical governmental support.

Discussion

This article demonstrates the process of the 8 years' river restoration project which was directed and implemented by definitive stakeholders and their supporters. That was not an activity by administration or governmental organization but an activity mainly conducted by local stakeholders. Branch chief BS who has personal legitimacy played a central role. Suchman (1995) described that although there is an opinion that individual roles of charisma having personal legitimacy is insufficient because the project will be lack of externality and exteriority, but when the present policy must be changed fundamentally, the charisma frequently play substantial role. That is why he raised the charismatic character as one of the legitimacies. The researcher concluded from this research that a project lead by charismatic individual stakeholder has possibility of bias in the character of the project but when radical change of policy is better for present status, it is effective to have such stakeholder in a project. However, even if definitive stakeholder with certain legitimacy has power, the stakeholder cannot exert sufficient power when an event out of his demarcation happens. When the problem can be solved by few stakeholders, stakeholder with power and personal legitimacy will be able to play a central role such as the case of this research. However, in many cases, the problem will happen as a result of complicated interests, and many stakeholders of various kinds of legitimacies will be involved in the issue.

In Figure 4, the researcher showed relationships between various stakeholders by network structure. Cruciate boxes indicate definitive stakeholders

Table 4. Sales data of Mogamidaini FFC.

	Mogamidaini FFC	
	Yearly ticket	Daily ticket
1988	988	1247
1989	1196	1302
1990	1153	1157
1991	1387	1181
1992	1674	1354
1993	1622	1102
1994	1625	976
1995	1960	1515
1996	1818	1904
1997	1728	2358
1998	1373	5633
1999	1091	4684
2000	1001	4166
2001	857	4644

enclosed by large dot line circle. Definitive stakeholders have all three properties of power, legitimacy, and urgency. The stakeholder can implement the project because he has power, is appropriate as an entrepreneur because he has legitimacy, and is sufficiently motivated because he has urgency. Therefore, when a project is implemented, the stakeholder is considered to be a central stakeholder.

The bars in the Figure 4 indicate that the pairwise stakeholders had certain communication. The communication indicates the stakeholders had formal or informal meeting. Informal meeting means that the problem related to the section was discussed and solved when the stakeholders accidentally met in other meeting or the stakeholder dropped in on other stakeholders by other business. There were two kinds of bar. One was normal link (dot line) and the other was alliance link. Alliance link existed between two stakeholders who cooperated together for the project. Normal link existed between two stakeholders who did not have cooperation or same viewpoint. Relation of opposite stakeholders existed between anti OG and branch chief BS but meeting was indirectly held through conference ES and link did not exist between them.

Definitive stakeholders had more links than other stakeholders and had at least four or more links in Figure 4. Maximum was 11 links of branch chief BS. On the other hand, other stakeholders had relatively few links of four or less except club LA and relatively few talks between them. Club LA was an important stakeholder in the early stage of the project by supporting the setup and oversight of the section. The number of link reflected these activities. Club LA now stand on the neutral position, but, as it quietly observe the project, if future project meet its policy, it is ready to be concerned the project as an organization.

An opinion of dependent stakeholder (6) and discretionary stakeholder (2) who has legitimacy but has not power may be reflected if they have certain communication with definitive stakeholders (7) which implement the project. For that reason, it is important for definitive stakeholders to have many links but that does not mean that definitive stakeholders should have over four links. That means that definitive stakeholder should not peremptorily implement the project by his power, but should have substantial links with stakeholders with legitimacy, or urgency but weak power, and should implement the project by dialogues. In this research, definitive stakeholders had relatively many links among other stakeholders and it is proved that the project has been promoted continuously by coordination among local residents for 8 years. If definitive stakeholders have extremely few links among other stakeholders and implements the project in such relationship, the project will be insufficiently completed and has incomplete value for local people in the long run, or the worst scenario is that the project will arise conflict and be postponed even if the definitive stakeholder has enough budgets. Although it is few, there are links between stakeholders of supportive, neutral, and opposed (Figure 4). This is important to reflect various opinions to the project and it is necessary for implementation of certain projects to pay attention to the opinions of stakeholders with various positions and attributes.

Dormant stakeholder (1), demanding stakeholder (3), dominant stakeholder (4), and dangerous stakeholder (5) did not exist in this research (Figure 4). Although dormant stakeholder (1) has power to the project and can decide to implement it, but he does not have legitimacy. That means he is inappropriate to implement the project. Dormant stakeholder does not also have urgency and viability to the project may be weak. Demanding stakeholder (3) does not have power to project and cannot use his influence. He also does not have legitimacy and he is inappropriate as an entrepreneur of the project. On the other hand, he has urgency to the project. This attribute may generate a situation that the stakeholder interferes in the project. Dominant stakeholder (4) is rather appropriate entrepreneur for the project because he has power to implement the project and legitimacy for the project. However, it is considered that he never quickly intends to implement the project because he does not have urgency. Dangerous stakeholder (5) is, in most cases, inappropriate entrepreneur. He has power and urgency but does not have legitimacy for the project. If dangerous stakeholder become a decision maker and implement the project, the project will be misled sometimes.

Except poachers PO, which the researcher was not able to contact, every stakeholder possessed legitimacy. Stakeholder who does not have legitimacy does not have administration authority, people to support his insistence or their own cultural background. So the stakeholder does not literally have legitimacy. In this research, every stakeholder had his own legitimacy and that means that each stakeholder has reasonable insistence and definitive stakeholders had better to pay attention to them in implementing the project. On the other hand, a classification of legitimacy by Suchman (1995) easily pick up many stakeholders even if the insistence is luxury, or profitable only for few egoists. For example, stakeholder with personal legitimacy could be easily supported by people who have same moral. In the range of socially accepted norm, stakeholders with various morals easily have their legitimacies. When someone wants to implement a project, he has to handle a complicated situation, at which he pays a very close attention to every stakeholder. When an alternative decision is asked to definitive stakeholders, such as this example that they take in C&R regulation in their district to exclude any harvest, it is actually impossible to focus on both supportive and opposed stakeholders. In the district, zoning of the area was operated in which local residents can keep trout out of the C&R section. However, if opposed stakeholder has legitimacy and completely opposed the setup in the section, decision maker will face critical point of decision making.

In our democratic society, even if such cases happen, definitive stakeholder should try to listen to every stakeholder, list up interests, and collect the greatest consensus, or should try to implement the project by consideration especially for social weak. Actually, the project may be decided by diplomacy among stakeholders, but the case that the stakeholder does not pay attention to minority should be avoided. Legitimacy of Suchman (1995) is a classification which centers on every possible legitimacy and tries not to forget to pick up even single stakeholder. That's why the classification is too general. On the other hand, this classification may causes confusion when decision maker wants to implement a project. Strategy to manage the stakeholder will depends on the importance of the stakeholder to the focal organization (in this study, definitive stakeholders) relative to other stakeholders (Jawahar and Mclaughlin 2001). In my opinion, if the problem to solve is the matter of 'Sollen,' such as the situation is adverse to ethic or the solution should be morally such, stakeholder with moral legitimacy should be paid more attention than stakeholder with pragmatic legitimacy who wants economical or social benefit from the project. If the problem is to choose alternative among policies within morally accepted range, the decision may be chosen on the basis of free trading or Pareto optimality. Kujala (2001) proposed framework for company to analyze moral issues in stakeholder relations. In the framework, moral issues such as pollution and extinction of species is considered. Future investigation regarding this issue is needed.

Stakeholder analysis was recently conducted by United Nations for pacification in conflicting area. However, because of the lack of progress, it seems that the method is still not established. In this research, Stakeholder characteristic was demonstrated in Table 2 to illustrate power, legitimacy, urgency and position of each stakeholder. Also action and policy of each stakeholder was listed as involvement in the issue. This is a fundamental work for stakeholder analysis. Snowball technique was useful to accurately collect relational data and network structure. Then, by drawing stakeholder typology in Figure 3, characteristic of each stakeholder was illustrated. By utilization of stakeholder typology, comprehensive understanding of each stakeholder can be possible and decision maker can extract characteristic and concerning points of each stakeholder to mediate problem. This process is effective to conduct stakeholder analysis. Furthermore, by inspecting relationship between stakeholders in network structure (Figure 4), decision maker will be able to consider viability of the project or continuity of the project. Although it needs a lot of time to make use of this method, hopefully in the long run, this method will be valid to solve the problem as clearly demonstrated and also solutions can be proposed.

Although hardware reform is planned in the section in the future, as mentioned before, department SO has legal right to implement hardware project and it is considered that department SO will become to have power for future project. If future project is considered by the present status, because department SO has few links among stakeholders shown in Figure 4, it is hard to say that the project will have consensus among various stakeholders on the basis of dialogue.

Branch chief BS is a person trusted from many groups related to nature, such as Nishikawa town Alpine club, local wild bird association, local hunting association, and many anglers in local area and out of the area. Branch chief BS is a local notability who managed the national park for generations and succeeded in conservation of the historical national park forest. That is why it is appropriate for department SO to come to visit and consult with him when department SO implements a project. However, it is spontaneous activity by present chief of department SO. As long as there does not exist institutional guarantee which prescribe to have official talks among various stakeholders, this project will be as a special case which does not serve on other domestic or foreign local areas.

Management of river consists of two conceptual parts; both software management and hardware management. Software management includes legislative aspect such as fishery regulation. Hardware management includes appropriate installation of river structure for erosion control and human utility. Partial or temporal treatment for river restoration such as the increase of trout population by C&R without healthy environment does not mean anything because spawning and reproduction stage is inevitable for sustainable healthy trout population. Local residents and many anglers want to restore river environment of several decades ago with riparian forest and plenty of trout without too much concrete revetment and erosion control dam. On the other hand, department SO has constructed robust disaster protection facilities by straightening the meander to flow down debris flows as quickly as possible, developed arable or livable land by narrowing river channel, and empoldered riverside. To continue the project by recognition of various opinions among stakeholders, department SO, which will have substantial power, needs to have more links among various stakeholders. Other stakeholders need to participate in the discussion of the project to decide the future appearance of the local public goods. Although now various stakeholders are involved in the project, most important thing is that not only various stakeholders involved in the project but also there are various links between definitive stakeholders and other stakeholders with legitimacies. By that, public works implemented by authority will obtain public support and projects which many people truly need will be continuously carried out.

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References

Brenner S.N. 1993. The stakeholder theory of the firm and organizational decision making: some propositions and a model. In: Pasquero J. and Collins D. (eds), Proceedings of the Fourth annual Meeting of the International Association for Business and Society. San Diego pp. 205–210.

Brenner S.N. 1995. Stakeholder theory of the firm: its consistency with current management techniques. In: Näsi J. (ed.), Understanding Stakeholder Thinking. LSR-Julkaisut Oy, Helsinki, pp. 75–96.

Brugha R. and Varvasovszky Z. 2000. Stakeholder analysis: a review. Health Policy Plann. 15(3): 239–246.

Chevalier J. 2001. Stakeholder Analysis and Natural Resource Management [On line], Available at http://www.arleton.ca/~jchevali/STAKE2.html.

Dahl R.A. 1957. The concept of power. Behavioral Sci. 2: 201–215.

Dick B. 1997. Stakeholder analysis [On line], Available at http://www.scu.edu.au/scholls/gcm/ar/arp/stake.html.

Freeman R.E. 1984. Strategic Management: A Stakeholder Approach. Pitman, Boston.

Freeman R.E. 1994. The politics of stakeholder theory: some future directions. Bus. Ethics Quart. 4: 409–421.

Freeman R.E. and Reed D.L. 1983. Stockholders and stakeholders: a new perspective on corporate governance. Calif. Manage. Rev. 25(3): 88–106.

Harrison C. and Burgess J. 2000. Valuing nature in context: the contribution of common-good approaches. Biodivers. Conserv. 9: 1115–1130.

Hatai I. 1999. Fertile sea by caring mind. Forest Sci. 26: 32–35, (in Japanese).

Jawahar I.M. and Mclaughlin G.L. 2001. Toward a descriptive stakeholder theory: an organizational life cycle approach. Acad. Manage. Rev. 26(3): 397–414.

Kujala J. 2001. Analysing moral issues in stakeholder relations. Bus. Ethics Eur. Rev. 10(3): 233–247.

Mitchell R.K., Agle B.R. and Wood D.J. 1997. Toward a theory of stakeholder identification and salience: defining the principle of who and what really counts. Acad. Manage. Rev. 22(4): 853–886.

Ravnborg H.M. and Buerrero M.P. 1997. Stakeholder analysis in natural resource management. ILEIA Newslett. 13(1): 12–15.

Reimchen T. 2001. Salmon nutrients, nitrogen isotopes and coastal forests. Ecoforestry 16(3): 13–16.

Savage G.G., Nix T.H., Whitehead C.J. and Blair J.D. 1991. Strategies for assessing and managing organizational stakeholders. Acad. Manage. Exec. 5: 61–75.

Scott J. 1991. Social Network Analysis: A Handbook. Sage, Thousand Oaks, CA.

Suchman M.C. 1995. Managing legitimacy: strategic and institutional approaches. Acad. Manage. Rev. 20: 571–610.

Starik M. 1994. Essay by Mark Starik, pp. 89–95 of the Toronto conference: reflections on stakeholder theory. Bus. Soc. 33: 82–131.

Ministry of Public Management, Home Affairs, Posts Telecommunications. 2002. Population distribution by prefecture, sex and ages (in Japanese).

Tanaka T. 1998. Fish community in stream. In: Ezaki Y. and Tanaka T. (eds), Mizubekankyono Hozen (convervation on riparian zone). Asakura Shoten, Tokyo, pp.177–194, (in Japanese).

Varvasovszky Z. and Brugha R. 2000. How to do (or not to do)… a stakeholder analysis. Health Policy Plann. 15: 338–345.

Wasserman S. and Faust K. 1994. Social Network Analysis: Methods and Applications. Cambridge University Press, New York.

Yaginuma T. 1993. Propagate fish resource by planting tree. Ienohikari Association, 254 pp, (in Japanese).

Yoshii A., Okamura T., Funaki A. and Yanai S. 2000. Fundamental issue for the management of riparian zone and riparian forest, management of riparian zone. In: Japan Society of Erosion Control Engineering (ed.), pp. 64–102, Kokonshoin (in Japanese).

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Resolving the conflicts between biodiversity conservation and socioeconomic development in China: fuzzy clustering approach

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Abstract. Resolving the conflicts between biodiversity conservation and socioeconomic development is a global pursuit for the long-run prospects of the human species. Based on Wenchuan County, a typical county in southwestern China, a group of 20 indicators quantifying regional biodiversity and socioeconomic development was established to classify and evaluate the county area spatially. A fuzzy c-means clustering (FCM) algorithm was used as the classification method. Three indices including BD, DL and DR characterizing the value of biodiversity, the level and rate of socioeconomic development of the delineated regions were formulated. The results indicated that Wenchuan County was optimally classified into 4 types of regions (region I to IV). The area percentages of the regions vary widely from 4.3 to 65.7%. The sequences of the regions on biodiversity, socioeconomic development level, and socioeconomic development rate were, respectively, IV > II > III > I, I > III > II > IV and III > I > II > IV. The spatial strategy on coordinating biodiversity conservation and regional development is to develop mainly from the east(I, II, III) and to conserve mainly in the west(IV). Eco-industry, such as eco-tourism and eco-agriculture, need to be emphasized in the process of regional development. The quantitative methods used here may have a wide applicability.

Introduction

Biodiversity loss is the most irreversible environmental crisis threatening the long-run prospects for the human species (Gowdy and McDaniel 1995). However, it is without doubt that biodiversity conservation needs substantial input of resources such as land, human power and financial supports. These resources are also indispensable for regional socioeconomic development. In this sense, biodiversity or nature conservation and regional socioeconomic development are closely related to each other on the basis of a common resource pool.

The inextricable linkage between biodiversity and development is treated as important trade-offs in developing countries. Consequently, policies to conserve biodiversity must take into account national development objectives and vice versa (Seely et al. 2003). For ecological and economic reasons it is more cost effective to conserve habitats rather than species (Simberloff 1998), and hence biodiversity conservation becomes a land use issue. Since in developing countries, land is the most important productive asset, the opportunity costs of conservation are forgone development, while the benefits from conservation are distant and largely external to the host country (Panayotou 1994). Therefore, biodiversity conservation and regional development often come into conflicts especially in the developing world. Because of the common existence of the vicious poverty-ecological degradation spiral, policy makers in developing countries are forced to identify creative ways of conserving biodiversity while supporting development and eradicating poverty. Integrating conservation and development, in particular at the local level, is one of the key challenges (Chape 2001).

Understanding the way regional landscapes operate, evolve, and change is a key area of research for ecosystem science (Costanza et al. 2002). It is also essential to support the spatial based ecosystem management approach. Ecoregional planning is a useful spatial based tool in biodiversity conservation (e.g., Beck and Odaya 2001; Jepson and Whittaker 2002; Younge and Fowkes 2003). However, the socioeconomic and cultural constraints and conflicts behind the conservation efforts, believed to be important, tend to be neglected.

Conservation agencies should prepare sustainable development plans for areas regarded as worthy of conservation and incorporate the biological merits, social impacts and sustainable economic potential of selected areas (Osborne 1995). A regionalization approach can be used to devise this kind of plans effectively. Regionalization issues have been addressed in China since the 1950s, mainly based on experience, which is open to a high degree of subjectivity. To investigate regionalization problems quantitatively, multivariate techniques such as principal component analysis and statistical cluster analysis have been adopted (Xu et al. 2001). They are based on the traditional crisp set theory. Crisp sets correspond to two-valued logic: yes or no, on or off, black or white, 0 or 1 (Bezdek 1994). Traditional automatic clustering treats the parameters as “crisp”; the delineation as “hard”; and the results as static (Liu and Samal 2002). To complex systems, especially those with much imprecise and vague information, these techniques may seem a little bit rigid (Lü et al. 2003). Many concepts in ecology are imprecise because ecosystems are large, loosely organized objects. Fuzzy-set theory provides a mathematical approach that is able to cope with imprecision (Equihua 1990). Therefore, a fuzzy c-means clustering approach will be employed in the regionalization process of the present study.

China is an important developing country with megadiversity. It has a booming economy, and embraces varied habitats and striking species diversity with its large territory. Perhaps half of China’s species are found nowhere else; these include many archaic and distinctive evolutionary lines, like giant pandas and ginkgoes (Liu et al. 2003). Therefore, the successful protection of China’s unique habitats and species will contribute greatly to the global conservation efforts. This generally necessitates a favorable balance between conservation and development. It is rational to search for this kind of balance in the landscapes at the county level, which is the basic local administrative unit and the key bottom-up implementation unit of biodiversity conservation and regional development. China has about 2200 counties (Feng 2000) covering over 93% of the territory with a population of 73.3% of the total population of the country (http://www.china-county.org). We selected Wenchuan County as a case study site because it lies in the upper reaches of the Yangtze River, a biodiversity rich as well as a less developed area in China. And at the same time, Wolong Biosphere Reserve, the largest nature reserve for giant pandas, lies in western Wenchuan County. Therefore, the conflicts between conservation and development are typical and need appropriate resolution.

The main objectives of this research are to: (a) establish an indicator system characterizing the regional attributes of biodiversity and socioeconomic development; (b) formulate computing methods for regional biodiversity and socioeconomic development; (c) give a spatial based suggestions for resolving the conflicts between conservation and development at the county level.

Methods

Study area

Wenchuan County is located in Sichuan Province, Southwestern China (102°5′46″ to 103°4′37″ E, 30°4′37″ to 31°4′10″ N) with an area of about 4085 square kilometers. The county is situated in the transition zone from Chengdu plain to Qinghai-Tibet plateau and characterized by high mountains and deep valleys. It maintains varied ecosystem types and a rich biodiversity. Wolong Biosphere Reservelies in the southwestern part of the county. It covers about half of the land surface in the county.

There are 14 township areas in Wenchuan County (Figure 1), of which Wolong Township and Gengda Township, the main part of Wolong Biosphere Reserve, form the Wolong Special Administrative Region for Nature Conservation (WSARNC). In the study, WSARNC was treated as one processing unit. The total population of the county was about 111,000 in 2001. Farmers were the majority with a population of 72,000. Tibetan and Qiang are the two main minority ethnic groups accounting for about 45.2% of the total population of the county. The major land use types are built-up area (residential area and roads), farmland (for grain, vegetable, and fruit production), forestland, and grassland (Table 1).

The indicators

Biodiversity and its conservation vary across spatial scales and organizations (Norton and Ulanowicz 1992; Poian et al. 2000). At the landscape level, biodi-

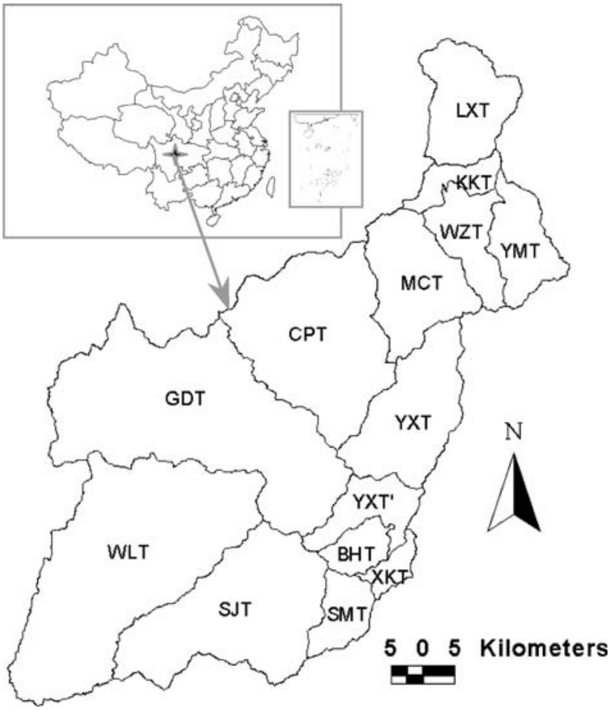

Figure 1. The location and township areas of Wenchuan County. WZT = Wei-Zhou Township; XKT = Xuan-Kou Township; MCT = Mian-Chi Township; LXT = Long-Xi Township; KKT = Ke-Ku Township; YMT = Yan-Men Township; YXT = Yin-Xing Township; YXT' = Ying-Xiu Township; SMT = Shui-Mo Township; BHT = Bai-Hua Township; CPT = Cao-Po Township; SJT = San-Jiang Township.

versity can be depicted as the richness, complexity and variability of ecosystems and habitats. Regional socioeconomic development depends on factors such as population, labor force, and economic production. A system of indicators reflecting both the regional biodiversity and socioeconomic development was formulated subject to the availability of the data source for the fuzzy comprehensive regionalization (Table 2).

Five indicators characterize the landscape level biodiversity. HR is the number of habitat/ecosystem types in a given land unit (township area or WSARNC); LFR is measured in perimeter density of a given land unit ($\mathrm{LFR} = \sum_{i=1}^{n} Pi / \sum_{i=1}^{n} A_i\, P_i$. and A_i are the perimeter and area of the ith polygon inhabited in the land unit; n is the total number of polygons); HD is measured as the Shannon–Weinner index of a given region ($\mathrm{HD} = -\sum_{i=1}^{n} P_i \cdot 1\mathrm{g}\, P_i$. P_i is the area percentage of a certain land use/land cover type in the region; n is the total number of different land use/land cover types); FC and VC are, respectively, the area percentage of forest covered and all

Table 1. The area percentage of the main land use types in Wenchuan county (%).

Region[a]	WC	WZT	YMT	KKT	LXT	MCT	CPT	YXT	YXT′	WSA	BHT	XKT	SMT	SJT
Built-up	0.30	2.12	0.37	0.54	0.10	0.51	0.04	0.44	1.52	0.11	1.46	2.33	0.63	0.04
Farmland	2.97	10.48	6.85	7.39	3.85	4.50	1.43	0.90	5.33	0.33	18.21	23.04	22.55	2.11
Forestland	63.34	57.86	69.65	58.08	66.51	67.17	71.93	90.42	83.3	45.95	68.24	66.36	67.69	87.93
Grassland	28.02	23.58	18.34	31.72	28.87	20.85	24.35	6.63	6.76	45.09	7.91	2.48	4.25	7.45
Total	94.63	94.04	95.21	97.73	99.33	93.03	97.75	98.39	96.91	91.48	95.82	94.21	95.12	97.53

[a] WC = Wenchuan County; WZT = Wei-Zhou Township; YMT = Yan-Men Township; KKT = Ke-Ku Township; LXT = Long-Xi Township; MCT = Mian-Chi Township; CPT = Cao-Po Township; YXT = Yin-Xing Township; YXT’ = Ying-Xiu Township; WSA = Wolong Special Administrative Region for Nature Conservation; BHT = Bai-Hua Township; XKT = Xuan-Kou Township; SMT = Shui-Mo Township; SJT = San-Jiang Township.

Table 2. The indicators for county level comprehensive regionalization.

Regional attributes	Indicators
Biodiversity	Habitat richness (HR); Landscape fragmentation (LFR); Habitat diversity (HD); Forest coverage (FC); Vegetation coverage (VC).
Socioeconomic development	Development level: Population (P); Population density (PD) = population/area (person/km^2); Labor force Percentage (LP) = (Labor force/population)×100%; Density of labor force on farmland (LF) = Labor force/farmland (person/ha); ratio of minority population (PE) = (population of minority ethnic group/total population)×100%; Farmland (FL) = area of farmland (ha); Farmland per capita (FLP) = area of farmland/total population (ha); foodstuff per capita (FP)(Kg); Rural income (RI)(10^{4}RMB); Net income per capita (NIP)(RMB).
	Development rate: The multi-annual average change rates of population (PR), farmland (FLR), labor force (LR), rural income (RIR), and net income per capita (NIPR). The indicators under this category can be calculated via $R_{\text{indicator}} = \sqrt[n]{x_{\text{indicator}(n)}/x_{\text{indicator}(0)}} - 1$. $R_{\text{indicator}}$ is the multi-annual average change rate of certain indicator mentioned above. $x_{\text{indicator}(n)}$ and $x_{\text{indicator}(0)}$ are the values of certain indicator at the end of year n and year 0, respectively.

vegetation covered land in a given region (FC $=$ Area$_{\text{forest}}$/Area$_{\text{region}}$ and VC $=$ Area$_{\text{vegetation}}$/Area$_{\text{region}}$). Numerically, FC is smaller than VC. Ecologically, FC and VC may surrogate the potential habitat integrity of large animals like giant pandas (*Ailuropoda melanoleuca*) and all the living orgnisms, respectively. The values of these biodiversity indicators were obtained from GIS based pattern analysis of the digital maps of land use, vegetation cover and forest form. These maps were digitized from paper maps collected from governmental agencies in charge of land and forest resources. The paper maps were made in 1997 at the scale of 1:100,000. The digitized maps were vector based and stored in an ArcView GIS environment. Therefore, the above landscape level biodiversity indicators were calculated based on the perimeter and area of the polygons derived from ArcView GIS.

There are 15 indicators in 2 categories characterizing the socioeconomic development of a given region. The definitions of the indicators are listed in Table 2. These indicators were quantified based on the statistical yearbooks of Wenchuan County (years of 1983, 1993, 1995, 2000 and 2001). The indicators of socioeconomic development level represent the state of socioeconomic development in the pertinent regionalization unit. However, the indicators of socioeconomic development rate can denote the potential or capacity for socioeconomic development of the corresponding regionalization unit.

Fuzzy c-means clustering

The fuzzy c-means (FCM) algorithm (Bezdek 1981) has successfully been applied to a wide variety of clustering problems (Hathaway et al. 2000). It is based on minimization of the following objective function, with respective to U, a fuzzy c-partition of the data set, and to V, a set of K prototypes:

$$F_m(U, V) = \sum_{j=1}^{n} \sum_{i=1}^{c} u_{ij}^m d_{ij}^2, \quad m \geq 1 \tag{1}$$

where $X = \{x_1, x_2, \ldots, x_n\}$ is a matrix in p-dimensional space, n is the number of samples; m, a real number, is a fuzzification parameter; c is the number of clusters; $u_{ij}(>0)$ is the degree of membership of x_j in cluster i, $\sum_{i=1}^{c} u_{ij} = 1, \sum_{j=1}^{n} u_{ij} > 0$; x_j is the jth of the p-dimensional measured data, v_i is the p-dimensional center of cluster i, and $d_{ij} = \| x_j - v_i \| = \sqrt{\sum_{k=1}^{p} (v_{ik} - x_{jk})^2}$ is the distance between sample x_j and clustering center v_i. $U = \{u_{ij}\}$ is a matrix of $c \times n$. $V = [v_1, v_2, \ldots, v_c]$ is a matrix of $p \times c$.

FCM attempts to simultaneously produce a description of the fuzzy cluster substructure of X along with exemplars (or prototypes) for each of the clusters via an iterative minimization of (1) with the update of u_{ij} and v_i by:

$$u_{ij} = \left[\sum_{k=1}^{c} \left(d_{ij}/d_{kj} \right)^{2/(m-1)} \right]^{-1} \tag{2}$$

and

$$v_i = \left(\sum_{j=1}^{n} u_{ij}^m \right)^{-1} \sum_{j=1}^{n} u_{ij}^m x_j \tag{3}$$

Based on the above, the FCM algorithm can be described as follows (Wang et al. 2004): (1) Choose an integer c and a threshold value ε. Let $m = 2$. Initialize the fuzzy partition matrix with proper random numbers. (2) Compute v_i according to Equation (3). (3) Compute all d_{ij} and then u_{ij} (Equation 2). u is updated subsequently. (4) Compute the objective function F. If it converges or the difference between two adjacent computed values of objective function F is less than the given threshold ε then stop. Otherwise go to step (2).

The regionalization units are WSARNC and the other 12 township areas in Wenchuan County. Each of these units has 20 measured attributes (indicators) on regional biodiversity and socioeconomic development. Therefore, in the present case: $p = 20$, $n = 13$. The 13 regionalization units can be partitioned to 2–12 regions (*i.e.* $2 \leq c \leq 12, c \in N$) using the above FCM algorithm. Therefore, let $c = 2, 3, \ldots, 12$, we perform the FCM separately. The optimal number of regions (c^*) partitioned is determined under the following constraints: (1) let r denote the number of regionalization units in partitioned region i, then $r > 1$; (2) $c^* = \max(c)$. In the initialization process, the original attribute matrix $X = (x_{ij})_{n \times p}$ was normalized as $R = (r_{ij})_{n \times p}$ in order to improve the convergence speed and performance of FCM ($r_{ij} = [\max(x_{i\cdot}) - \min(x_{i\cdot})]^{-1}[x_{ij} - \min(x_{i\cdot})]$ when $x_{i\cdot}$ has a positive contribution to indicator i, otherwise, $r_{ij} = [\max(x_{i\cdot}) - \min(x_{i\cdot})]^{-1}[\max(x_{i\cdot}) - x_{ij}]$). $x_{i\cdot}$ represents the i th row of elements in X.

The quantification of regional biodiversity and socioeconomic development

The biodiversity and socioeconomic development of the various regions delineated through the FCM process need to be quantified in order to support the decision making on conflict resolution between conservation and development at the county level. Therefore, three indices are formulated as follows:

$$\mathrm{BD}_i = \frac{1}{n}\sum_{j=1}^{m}\sum_{k=1}^{n}\alpha \times r_{jk} \tag{4}$$

$$\mathrm{DL}_i = \frac{1}{n}\sum_{j=1}^{m}\sum_{k=1}^{n}(1-\beta_i) \times r_{jk} \tag{5}$$

$$\mathrm{DR}_i = \frac{1}{n}\sum_{j=1}^{m}\sum_{k=1}^{n} r_{jk} \tag{6}$$

where BD_i is the biodiversity value of cluster (region) i; DL_i and DR_i are the development level and development rate of cluster (region) i; higher values of the BD_i , DL_i and DR_i signify better conditions of region i on biodiversity and socioeconomic development; $i \leq c*$, $i \in N$, and n is the number of regionalization units included in cluster (region) i; m represents the number of indicators on biodiversity (Equation 4), development level (Equation 5) and development rate (Equation 6), respectively; r_{jk} denotes the normalized values ($r_{ij} = a_{ij}/\mathrm{Opt}(a_{\cdot j})$; Opt(), a function of optimization, is max() when $a_{ij} \geq 0$, otherwise, Opt() is min(); a_{ij}, calculated according to Table 2, is the original value of the corresponding attributes of the regionalization units on biodiversity (Equation 4), development level (Equation 5) and development rate (Equation 6), respectively; $a_{\cdot \mathrm{j}}$ is the jth column of matrix $(a_{ij})_{13\times 20}$); $\alpha = 1$ when r_{jk} positively contributes to BD_i, otherwise, $\alpha = -1$; β_i = the area of cluster (region) i/ the area of the whole county. For the purpose of simple representation, we use r_{jk} in Equations (4–6). However, the $r_{jk}s$ are totally different because of the different original input data (a_{ij}). The $(1-\beta_i)$ component of Equation (5) is a weight representing that the smaller geographical area for a certain economic production, the higher the development level of the area.

Results

The optimal partition of Wenchuan County

The 13 regionalization units of Wenchuan County were optimally partitioned into 4 regions (Table 3). Each of them was composed of 2–5 regionalization units (mostly township areas excluding WSARNC). Area percentage of the 4 regions varied widely. The coverage of human dominated landscapes, population density, and the density of gross rural income had similar change trend among the 4 regions (I > III > II > IV) which was opposite to that of the area percentages. The regions were spatially cohesive except for region I (Figure 2). From the key attributes of the four partitioned regions, it is evident that region I harbors the highest levels of human disturbance and economic production with the smallest land area, followed by region III and region II. On the contrary, region IV is the largest in land area with the lowest level of human disturbance and economic production. Spatially, human disturbance and economic productivity concentrate in the east part of Wenchuan County (including regions I, II, and III) with totally a smaller percentage area.

The comprehensive value on biodiversity and socioeconomic development

The 4 regions were different from each other on their integrative attributes of biodiversity and socioeconomic development (Figure 3). Regional biodiversity and socioeconomic development level showed significant negative correlation ($r = -0.9967$, $p = 0.003$). The rank of regions in the order of biodiversity significance was IV > II > III > I. On the contrary, the sequence of the regions

Table 3. The result of comprehensive regionalization using FCM algorithm.

Region	I	II	III	IV
Composing units [a]	WZT, XKT	MCT,LXT, KKT, YMT, YXT	YXT', SMT, BHT	WSARNC, CPT, SJT
Area percentage (%)	4.3	23.5	6.5	65.7
Coverage of human dominated landscapes (%)	15.7	4.3	15.5	1.0
Population density (person/km^2)	86	25	75	4
Density of gross rural income (× 10^4RMB/km^2)	35.2	4.5	22.9	1.3

[a] See Table 1.

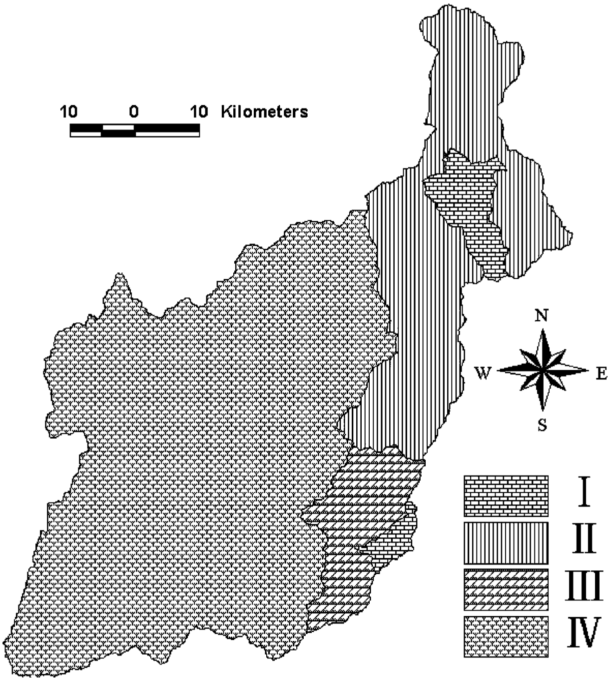

Figure 2. The partitioned regions in Wenchuan County.

on the level of socioeconomic development was I > III > II > IV. Region I and region III had similar composition patterns of biodiversity, and the level and rate of socioeconomic development. The sequence of the regions on the rate of socioeconomic development was III > I > II > IV.

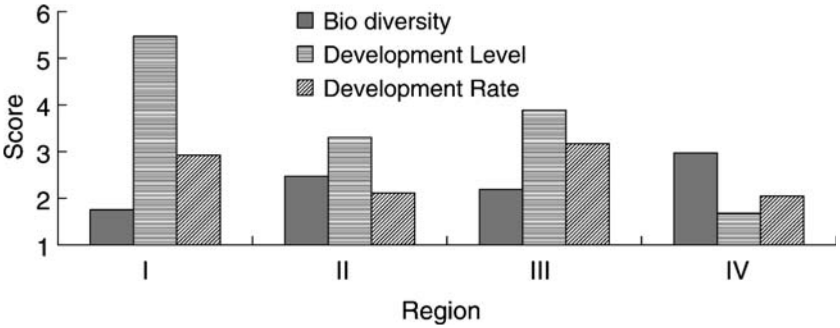

Figure 3. The quantitative attributes on regional biodiversity and socioeconomic development.

Discussion

FCM as a powerful tool for regionalization

Clustering is one of the most common approaches in resolving regionalization problems. The FCM algorithm used in this research is a kind of unsupervised clustering technique. Comparing with hard c-means (HCM) clustering algorithm, FCM improves partition performance and reveals the classification of data more correctly (Fan et al. 2003). This approach is repeatable and generalizable to any number of parameters. Given the same set of input data, this approach yields uniform partitions (Liu and Samal 2002). In this case study, FCM algorithm has been successfully used in partitioning the landscapes at the county level based on some attributes of landscape level biodiversity and regional socioeconomic development. The resulting four regions are distinctive on the extent of human disturbance, economic vitality, and biodiversity significance (Table 3 and Figure 3).

The methods for the quantification of regional biodiversity and socioeconomic development

Indicators of biodiversity are strongly biased towards species and away from the ecosystem as a whole (Pykh 2002). Further progress towards general indicators of biodiversity remains very difficult. Biodiversity, in nature, is a hierarchical and scale dependent concept. Hence the measure of biodiversity should be formulated at different spatial scales and organization levels. The species based indicators are strongly subject to sampling effects and have some pitfalls (Gotelli and Colwell 2001). As surrogates, some landscape level metrics have been used in biodiversity related research (Dramstad et al. 2001; Jeanneret et al. 2003; Carlson et al. 2004; Hietala-Koivu et al. 2004). Landscape diversity indices were found to correlate positively with species richness whereas landscape fragmentation indices affected the group of the threatened species (Honnay et al. 2003). Percentage cover of certain land use types might serve as useful indicators for species richness at the landscape scale (Dauber et al. 2003; Fairbanks 2004). Through the calculation of BD, this paper attempted to quantify the regional biodiversity at the landscape level on the basis of the landscape pattern indicators. The resulted BD values can represent the real world differentiation of biodiversity among the regions in Wenchuan County. For example, region IV is the highest on BD value which correspond to the ground truth of the highest level of habitat and species diversity in this region. In Wolong Biosphere Reserve, the main part and core area of region IV, there are approximately eight vegetation types along the elevation gradient between 1200 and 6250 m (Fu et al. 2004). According to a preliminary inventory, there are about 450 vertebrate species, 1700 entomic species, and 4000 plant species in this reserve (Wolong Nature

Reserve Administration Bureau 1998). Biodiversity of this rich can be found nowhere else in the other three regions of Wenchuan county. This qualified BD as a potential quantitative indicator of regional biodiversity at the landscape level, especially useful for conservation and development planning when species based data are unavailable. However, the wide usability of this indicator needs further verification.

The increasing interest, and the actual necessity, for adequate means to evaluate how sustainable human activities are, has led to efforts to define indicators of sustainability (Soberon et al. 2000). Many indices such as UNDP's human development index (HDI) have been formulated to quantify regional development from different perspectives. These indices can provide decision and policy makers with valuable information. However, as a prerequisite, the specific information required for good decision-making and effective resource management has to be sought out from the proliferating information and information sources (Walmsley 2002). DL and DR designed in this paper are indices quantifying, respectively, the status and potential of regional socioeconomic development. They can facilitate the monitoring, assessment and comparison of the socioeconomic development of different type of regions at the county level. They have a wide practicability because the original data used in calculating them are readily available in each county of China. Therefore, they can help to improve the decision-making and implementing process of the county level socioeconomic development.

The implications of comprehensive regionalization and quantification for conflict resolution

Human pressures and regional development needs often lead to conflicts in biodiversity conservation. Therefore, balancing the interrelated and ultimately interdependent economic development, biological conservation, and human culture is one of the most vexing problems in natural resource management (Hanley 1993). In the past, most researches have been focused on small-scale conflicts driven by economic necessity and lack of alternatives for local populations within and adjacent to protected areas (Rao et al. 2002). However, with proper tools, a comprehensive ecological regionalization approach can be used to classify environmental units into homogeneous zones, and to provide strategies and countermeasures that are needed to balance nature conservation and socioeconomic development at larger spatial scales. Based on the results of this research, spatial based macroscopic strategies can be proposed.

The designation of conservation or economic development areas in a geographic region is ultimately a multi-attribute and multi-stakeholder social decision-making process. Benefits and costs of various kinds should be considered in this process (Faith and Walker 1996; Ando et al. 1998) to make more sound decisions. Our results suggest that conserving region IV delivers maximum biodiversity benefits at lowest *in-situ* economic costs. Analogously, economically developing region I delivers maximum economic benefits at lowest biodiversity costs. In this sense, the cost-effective ranking orders of conservation and economic development allocation of the regions in Wenchuan county are IV > II > III > I and I > III > II > IV, respectively. However, the number of regions devoted to coservation or development in practice will depend on the choice of the decision makers involved. At the same time, conservation and development should be balanced and integrated as far as possible in each specific region for the existence of permanent human communities.

The comprehensive ecological regionalization process discussed in this paper was the result of using FCM algorithm based on relevant socioeconomic data and landscape level biodiversity indicators. The indicators used for the regionalization process were largely data driven that gave a primary consideration on data availability, which is especially important in conducting research projects in the developing world. Ecological and socioeconomic systems are both linked hierarchically across scales in space and time (Wu and Loucks 1995). There are three closely related spatial scales including regionalization units, regions, and the whole county in this paper. The FCM clustering is an effective bottom–up scaling tool from regionalization units to regions that can facilitate the top–down policy implementation process concerning conservation and development at the county level. The four regions resulted from the clustering process give a macroscopical spatial configuration for the integration of conservation and development. Of course, the rank orders of the 13 regionalization units can also be determined after calculating their values on BD, DL, and DR. However, the ranking should be restricted to their respective regions. Therefore, the policy fomulation and implementation proceses are also structured hierarchically to be cost-effective and efficient in resolving the conflicts between conservation and development spatially. The quantitative methods used here are scale independent and may have wide applications in China and elsewhere and at larger spatial scales beyond counties. Other than the population model based multi-criteria decision analysis (Drechsler 2004) for the decision support on conflict resolution among different conservation goals at the species level, the methods used in this research may offer an alternative holistic spatially explicit approach in resolving the conflicts between nature conservation and regional socioeconomic development at the landscape level subject to the constraints of information scarcity.

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References

Ando A., Camm J., Polasky S. and Solow A. 1998. Species distributions, land values, and efficient conservation. Science 279: 2126–2128.

Beck M.W. and Odaya M. 2001. Ecoregional planning in marine environments: identifying priority sites for conservation in the northern Gulf of Mexico. Aquat. Conserv.: Mar. Freshwater Ecosyst. 11: 235–242.

Bezdek J.C. 1981. Pattern Recognition with Fuzzy Objective Function Algorithms. Plenum, New York.

Bezdek J. 1994. Fuzzy models-what are they, and why? In: Marks R.J. (ed.), Fuzzy Logic Technology and Applications, IEEE Technology Update Series. Tecnichnacal Activities Board, Piscataway, NJ, pp. 3–7.

Chape S. 2001. An overview of integrated approaches to conservation and community development in the Lao People's Democratic Republic. Parks 11: 24–32.

Carlson B., Wang D., Capen D. and Thompson E. 2004. An evaluation of GIS-derived landscape diversity units to guide landscape-level mapping of natural communities. J. Nat. Conserv. 12(1): 15–23.

Costanza R., Voinov A., Boumans R., Maxwell T., Villa F., Wainger L. and Voinov H. 2002. Integrated ecological economic modeling of the Patuxent River watershed, Maryland. Ecol. Monogr. 72: 203–231.

Dauber J., Hirsch M., Simmering D., Waldhardt R., Otte A. and Wolters V. 2003. Landscape structure as an indicator of biodiversity: matrix effects on species richness. Agric. Ecosyst. Environ. 98: 321–329.

Dramstad W.E., Fry G., Fjellstad W.J., Skar B., Helliksen W., Sollund M.-L.B., Tveit M.S., Geelmuyden A.K. and Framstad E. 2001. Integrating landscape-based values: Norwegian monitoring of agricultural landscapes. Landscape Urban Plan 57: 257–268.

Drechsler M. 2004. Model-based conservation decision aiding in the presence of goal conflicts and uncertainty. Biodivers. Conserv. 13: 141–164.

Equihua M. 1990. Fuzzy clustering of ecological data. J. Ecol. 78: 519–534.

Fairbanks D.H.K. 2004. Regional land-use impacts affecting avian richness patterns in Southern Africa–insights from historical avian atlas data. Agric. Ecosyst. Environ. 101: 269–288.

Faith D.P. and Walker P.A. 1996. Integrating conservation and development: effective trade-offs between biodiversity and cost in the selection of protected areas. Biodivers. Coserv. 5: 431–446.

Fan J.-L., Zhen W.-Z. and Xie W.-X. 2003. Suppressed fuzzy c-means clustering algorithm. Pattern Recogn. Lett. 24: 1607–1612.

Feng Y. 2000. The research about a quantitative evaluation method of sustainable development level and ability in mountain counties. Chinese J. Econ. Geogr. 20: 16–19 (in Chinese with English abstract).

Fu B.J., Wang K.L., Lu Y.H., Liu S.L., Ma K.M., Chen L.D. and Liu G.H. 2004. Entangling the complexity of protected area management: the case of Wolong Biosphere Reserve, southwestern China. Environ. Manage. 33(6): 788–798.

Gotelli N.J. and Colwell R.K. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecol. Lett. 4: 379–391.

Gowdy J.M. and McDaniel C.N. 1995. One world, one experiment: addressing the biodiversity-economics conflict. Ecol. Econ. 15: 181–192.

Hanley T.A. 1993. Balancing economic development, biological conservation, and human culture: The Sitka black-tailed deer Odocoileus hemionus sitkensis as an ecological indicator. Biol. Conserv. 66: 61–67.

Hathaway R.J., Bezdek J.C. and Hu Y. 2000. Generalized fuzzy c-means clustering strategies using Lp norm distances. IEEE Trans. Fuzzy Syst. 8: 576–582.

Hietala-Koivu R., Lankoski J. and Tarmi S. 2004. Loss of biodiversity and its social cost in an agricultural landscape. Agric. Ecosyst. Environ. 103: 75–83.

Honnay O., Piessens K., Van Landuyt W., Hermy M. and Gulinck H. 2003. Satellite based land use and landscape complexity indices as predictors for regional plant species diversity. Landscape Urban Plan. 63: 241–250.

Jeanneret P., Schuepbach B. and Luka H. 2003. Quantifying the impact of landscape and habitat features on biodiversity in cultivated landscapes. Agric. Ecosyst. Environ. 98: 311–320.

Jepson P. and Whittaker R.J. 2002. Ecoregions in Context: a Critique with Special Reference to Indonesia. Conserv. Biol. 16: 42–57.

Liu J., Ouyang Z., Pimm S.L., Raven P.H., Wang X., Miao H. and Han N. 2003. Protecting China's biodiversity. Science 300: 1240–1241.

Liu M. and Samal A. 2002. A fuzzy clustering approach to delineate agroecozones. Ecol. Model. 149: 215–228.

Lü Y., Chen L., Fu B. and Liu S. 2003. A framework for evaluating the effectiveness of protected areas: the case of Wolong Biosphere Reserve. Landscape Urban Plan. 63: 213–223.

Osborne P.L. 1995. Biological and cultural diversity in Papua New Guinea: conservation, conflicts, constraints and compromise. Ambio 24: 231–237.

Panayotou T. 1994. Conservation of biodiversity and economic development: The concept of transferable development rights. Environ. Resour. Econ. 4: 91–110.

Poiani K.A., Richter B.D., Anderson M.G. and Richter H.E. 2000. Biodiversity conservation at multiple scales: Functional sites, landscapes, and networks. BioScience 50: 133–146.

Pykh Y.A. 2002. Lyapunov functions as a measure of biodiversity: theoretical background. Ecol. Indicators 2: 123–133.

Rao M., Rabinowitz A. and Khaing S.T. 2002. Status review of the protected-area system in Myanmar, with recommendations for conservation planning. Conserv. Biol. 16: 360–368.

Simberloff D. 1998. Flagships, umbrellas, and keystones: is single-species management passé in the landscape era? Biol. Conserv. 83: 247–257.

Seely M.K., Zeidler J., Henschel J.R. and Barnard P. 2003. Creative problem solving in support of biodiversity conservation. J. Arid Environ. 54: 155–164.

Soberon J., Rodriguez P. and Vazquez-Dominguez E. 2000. Implications of the hierarchical Structure of Biodiversity for the development of ecological indicators of sustainable use. Ambio 29: 136–142.

Walmsley J.J. 2002. Framework for measuring sustainable development in catchment systems. Environ. Manage. 29: 195–206.

Wang X., Wang Y. and Wang L. 2004. Improving fuzzy c-means clustering based on feature-weight learning. Pattern Recogn. Lett. 25: 1123–1132.

Wolong Nature Reserve Administration Bureau 1998. The Master Plan of Wolong Nature Reserve. WNRAB, Wolong, pp. 87.

Wu J. and Loucks O.L. 1995. From balance-of-nature to hierarchical patch dynamics: a paradigm shift in ecology. Q. Rev. Biol. 70: 439–466.

Xu H., Liu D. and Wu H. 2001. Environmental regionalization for the management of township and village enterprises in China. J. Environ. Manage. 63: 203–210.

Younge A. and Fowkes S. 2003. The Cape Action Plan for the environment: overview of an ecoregional planning process. Biol. Conserv. 112: 15–28.

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The importance of stakeholder engagement in invasive species management: a cross-jurisdictional perspective in Ireland

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Abstract. The management of invasive non-native species is a frequent cause of conflict in the field of biodiversity conservation because perceptions of their costs and benefits differ among stakeholder groups. A lack of cohesion between scientific researchers, the commercial sector and policy makers lies at the root of a widespread failure to develop and implement sustainable management practices for invasive species. The crisis of this situation is intensified by drivers stemming from international conventions and directives to address invasive species issues. There are further direct conflicts between legislative instruments promoting biodiversity conservation on the one hand while liberalizing trade at the national, European and global level on the other. The island of Ireland provides graphic illustration of the importance of cross-jurisdictional approaches to biological invasions. Using primarily Irish examples in this review, we emphasize the importance of approaching risk assessment, risk reduction and control or eradication policies from a cost-efficient, highly flexible perspective, incorporating linkages between environmental, economic and social objectives. The need for consolidated policies between Northern Ireland and the Republic of Ireland is particularly acute, though few model cross-border mechanisms for such consolidation are available. The importance of engaging affected stakeholders through positive interactions is discussed with regard to reducing the currently fragmented nature of invasive species management between the two jurisdictions.

Introduction

As an ambition, the conservation of biological diversity often suffers from a lack of cohesion between scientific researchers and policy makers, inhibiting the development and application of sustainable management practices within the environment (Pullin and Knight 2001; Sutherland et al. 2004). This problem is particularly marked in situations where economic and social conflict arises. For example, the deliberate or accidental introduction of non-native species brings a diverse array of costs and benefits that may accrue to different sectors of society (Callaghan 2003). Benefits are largely unequivocal and wide-ranging; non-native species may include new crop or pasture species, new aquaculture opportunities, ornamental plants and fish and novel biological control agents for economic pests (Bullock et al. 1996). However, the overall value of benefits is frequently overstated; a particularly good example is the history of exotic pasture introductions in northern Australia, which resulted in less than 1% of intentional introductions evaluated as useful without causing weed problems (Lonsdale 1994). Costs are evaluated differently according to stakeholder positions, but include damage to existing economic interests, harm to native species and habitats, and the, often substantial, costs associated with preventing introductions and spread of harmful species, monitoring existing populations and conducting control or eradication programmes (Simberloff 2003). Thus a major issue is the cross-sectoral impact; an introduced ornamental is of benefit to one group of stakeholders whereas a different group pays the associated cost.

On a global scale, the most severe impacts of non-native species on native biodiversity have occurred on remote islands, where the native flora and fauna are less diverse, more isolated and particularly susceptible to invasion (Drake et al. 1989). As a consequence of this inherent lack of native diversity, island people have frequently sought to increase the economic value of their biotic resources through trade and importation of non-native plant and animal stock. Globalization and growth in the volume of trade, transport and tourism have undermined natural barriers to spread, enhancing opportunities for accidental or deliberate introduction of non-native species (IUCN 2000). The resulting severe threats to native species and ecosystems worldwide (Vitousek et al. 1996; Williamson 1996; Perrings et al. 2000; Pimentel et al. 2000), have prompted international legislation addressing invasive species issues: principally the Convention on Biological Diversity (CBD), the Bonn Convention on the conservation of migratory species, the World Conservation Union (IUCN) guidelines for the prevention of biodiversity loss caused by invasive alien species, and a host of others with implications for this issue, including the Bern Convention and the Habitats Directive within Europe. Assuming current patterns in international trade continue, forecasts indicate future trade-related invasion rates for insects, plant pathogens and molluscs in the United States will increase, with subsequent economic impacts (Levine and d'Antonio 2003).

In this paper, we address international obligations pertaining to invasive species issues from an Irish perspective. The island of Ireland is an excellent example of the need for joint coordinated national responses to achieve effective management of invasive, non-native species between the two jurisdictions. We focus upon recommendations for risk assessment, future risk reduction and practical control of invasive species, and make minor reference to the impacts of invasive species on native biodiversity, as this has been addressed succinctly elsewhere (Manchester and Bullock 2000). It is widely acknowledged that preventing introductions is generally far more cost effective and environmentally desirable than measures taken following the establishment of an invasive, non-native species (Williamson 1989); therefore prevention should be given priority (DEFRA 2003). However, prevention measures will sometimes fail and if an invasive non-native species has already been introduced then further measures will be necessary. A key issue to contend with is justification of resource allocation between preventive measures and actions in mitigation of existing problems, with stakeholders expressing polarized viewpoints depending on how they are differently affected. Attitudes regarding appropriate allocation of government funding differ between stakeholder groups, such as the general public and the operational professionals (e.g. agriculture, forestry, fisheries, landscape or planning professionals), resulting in stakeholder competition to influence the actions of policy makers, civil servants and ministers.

Using primarily Irish examples we illustrate that integration of representatives from key trade, commerce and industrial sectors is vital to achieve longer term sustainable management in relation to invasive species issues, principally through the design of strategies that encourage cooperative participation, arising from advantageous returns to individual stakeholders. Key actions are developed to combat specific management weaknesses identified within the Irish system and prioritize focus areas for future research. We seek to emphasize pro-active risk reduction strategies and discuss the initiation of specific policies within the two jurisdictions.

Irish priorities

O'Connor et al. (2003) maintain that the most influential conservation priority-setting approaches emphasize biodiversity and threats to it when deciding where to focus investment. However, the current social and political framework influences the uptake and delivery of conservation actions; the need for cross-border policies is particularly pressing in multi-jurisdictional land masses, such as the island of Ireland; and additionally in the Americas, where a highly developed infrastructure connects an extremely diverse array of ecosystems and political communities to each other and the rest of the globe to a degree that exceeds that found in many equivalent land masses (CEC 2002). Many island economies also generate a high proportion of their revenue from tourism (Dalmazzone 2000). For example, it is vital to the Irish economy that features which are perceived as unique to; or characteristic of the Irish landscape are retained, as it is these features which enhance Ireland's appeal as a tourist destination. The terrestrial and freshwater fauna of Ireland is relatively impoverished in comparison with Britain and mainland Europe, reflecting Ireland's isolation by sea since the last glaciation (Costello 1993). The absence of particular groups (Simberloff 1995) and the lack of coevolutionary history with invaders (Diamond and Case 1986) may influence the susceptibility of Ireland to invasive species (Minchin 2000). The generalization that islands are more invasible due to a lower diversity of species is still controversial. The most comprehensive analysis to date; based on a global dataset of the number of exotic and native plant species on island and mainland sites found that although islands were more invaded than mainland sites this was not due to low species richness, as islands in the dataset were no less rich in native species than mainland sites (Lonsdale 1999).

The majority of species introductions to islands originate through patterns of trade flow; therefore many Irish introductions have originated from Great Britain, due to their close proximity and frequent trade interactions. However, Great Britain is also an island; thus historically a filtering effect has been in operation, Ireland constituting the final land mass in a fragmented chain. These factors have resulted in Ireland hosting a number of unique native species, for example, the endemic Irish pollan, *Coregonus autumnalis*, and species that are rare elsewhere in western Europe, such as the otter, *Lutra lutra*.

A variety of habitats within Northern Ireland and the Republic of Ireland are designated for protection at national or European level, principally under the European Habitats Directive. A number of these habitats are under current threat from invasive non-native species: Lough Erne is a Special Area of Conservation (SAC) in County Fermanagh (Northern Ireland) and is threatened by the zebra mussel, *Dreissena polymorpha*, (Minchin et al. 2003); while degradation of natural broadleaf woodland due to invasion by *Rhododendron ponticum* threatens notable features of Killarney and Glenveagh National parks in the west of Ireland (Cross 1981, 1982). Mudflats and salt marshes surrounding Strangford Lough, a designated SAC in Northern Ireland, and an important intertidal feeding ground for migrating bird communities, are threatened with degradation resulting from invasive spread of the common cordgrass, *Spartina anglica* (McCorrey et al. 2003).

Threats to conservation of native species are identified as a result of negative biotic interactions with potential invaders; or the introduction of species of non-local provenance, while threats to industry are perceived in terms of damage to infrastructure, accelerating costs of protection or restoration and diminishing profit margins. In Ireland one of the most seriously affected sectors to suffer from the importation of different genetic strains of a species is the glasshouse industry. The introduction of strains of previously established insect species which are resistant to an array of insecticides is an increasing concern. An example is the cotton-melon aphid, *Aphis gossypii*, which, until recent years, was a rarely encountered pest of certain glasshouse crops. However, recently a strain has been occurring in Ireland on chrysanthemums and cucumbers that is resistant to all the usual organophosphate, carbamate and synthetic pyrethroid aphicides and is susceptible only to nicotine spray (Dunne 2003).

In addition there are a number of non-native species present in Great Britain which pose an immediate threat to biodiversity and economic activities if introduced into Ireland. Examples include non-native crayfish species, such as North American signal crayfish, *Pacifastacus leniusculus*, which hosts the crayfish plague, observed to decimate native crayfish and freshwater fish populations in Great Britain (Holdich and Rodgers 1997). The Chinese mitten crab, *Eriocheir sinensis*, is a potentially threatening invasive present in Great

Britain which causes erosion to soft sediment banks and consequently concern in terms of flood defence (Clark et al. 1998). *Eriocheir sinensis* is a mobile estuarine invertebrate, native to coastal rivers and estuaries of central Asia, which lives predominantly in freshwater as an adult but migrates seawards to breed. Chinese mitten crab has spread via ballast water and/or intentional introduction to Continental Europe (Herborg et al. 2003), and the potential for larvae of this species to invade Irish coastal estuaries is high. Muntjac deer, *Muntiacus reevesi* represent a dual threat to both biodiversity and commercial industry; environmental impact assessments conducted in commercial plantations of eastern England indicate the potential for exploitation competition with native deer in the event of food scarcity (Hemami et al. 2004). Muntjac deer also suppress natural forest regeneration through predation of the available seed source and inhibit coppice re-growth (Putman and Moore 1998). The impact on woodland structure has been recorded as relatively minor in comparison to other species of deer, but could potentially increase rapidly at higher population densities (Putman and Moore 1998).

Uncertainty in risk assessment contributes to stakeholder conflict

As the range of invasive alien species continues to grow, scientists and managers are forced to predict and manage only the most serious problems. This requires the adoption of a management framework that can encompass ecosystem change and, in some cases, pragmatic acceptance of invasive species as part of ecosystem dynamics (Simberloff 2003). Such a management system must allow change within a range of predefined limits of acceptability, identified by bioeconomic tools such as 'aesthetic injury levels' (Raupp et al. 1988), whilst also effectively highlighting areas where these limits are broken and action is required. A suitable framework requires the flexibility to incorporate new research and thinking in a manner that is proactive in approach.

The ability to distinguish between invaders likely to have a major impact on native biodiversity and those having only a minor impact is essential. Unfortunately, the context-dependent nature of biological invasions creates difficulties in predicting potential impacts of potentially invasive species (Williamson 1996). One approach, endorsed by Ricciardi and Atkinson (2004), is to consider a potential invader's taxonomic relationships to members of the recipient community. Ricciardi and Atkinson (2004) conducted a meta-analysis to compare the taxonomic distinctiveness of high and low impact invaders in a variety of aquatic systems. High impact invaders, defined as those that displace native species, were more likely to belong to genera not already present in the system (Ricciardi and Atkinson 2004). However, this is not always the case; *Gammarus pulex*, an invasive aquatic amphipod has displaced the native *Gammarus duebeni celticus* in Irish freshwater systems through competitive and predatory mechanisms (Dick et al. 1995), with major effects on the composition and function of freshwater communities (MacNeil et al. 1999; Kelly et al.

2003). Additionally, grey squirrel (*Sciurus carolinensis*) has spread widely in Ireland, precipitating the steep decline of the native, congeneric red squirrel, *Sciurus vulgaris*, (Hayden and Harrington 2000).

Factors contributing to variation in success of invasive species have received much recent attention (Blackburn and Duncan 2001; Kolar and Lodge 2001; Cassey 2002; Shea and Chesson 2002; Sol et al. 2002; Duncan et al. 2003; Bellingham et al. 2004; Forsyth et al. 2004; Olden and Poff 2004). In the past it has frequently been stated that an invasion has a higher probability of success if the climate of the region being invaded is similar to that of the invasive species native range (Brown 1989). However, exceptions to this rule are common (Williamson 1996; Mack 1996). For example, *Rhododendron ponticum* is native to the Black Sea coast, Lebanon and the Iberian peninsula (Cross 1975) but has successfully invaded Ireland where annual precipitation levels are higher. It is accepted that disturbed habitats such as urban wasteland, arable fields and riverbanks are generally more readily invaded by non-natives (Smallwood 1994). Conversely, undisturbed natural and semi-natural communities tend to contain few, if any, recently introduced non-native species (Manchester and Bullock 2000).

A diversity of processes influences the likelihood of success at each stage of the invasion process. Clarification of the relative importance of these processes has stemmed from quantitative comparisons of the attributes of successful and unsuccessful species invasions (reviewed in Kolar and Lodge 2001; Duncan et al. 2003). However, there remains controversy over such comparative studies, largely due to a lack of clarity regarding the particular stage of the invasion process under scrutiny (Mack et al. 2000). For example, Bellingham et al. (2004) expanded an earlier study examining the importance of relative growth rate (RGR) in contributing to invasiveness of *Pinus* species, conducted by Grotkopp et al. (2002). The original study concluded that those *Pinus* species that were most invasive had higher seedling RGR, and that this trait best distinguished invasive pines from those that are non-invasive on at least two continents (Grotkopp et al. 2002). The study of Bellingham et al. (2004) concludes that neither seedling RGR nor survival is strongly associated with invasiveness, but acknowledges that the two studies differ in their design in choice of sampling the species pool, and therefore the subsequent measurement of the influence of species attributes on 'invasiveness'. The original study examined a variety of *Pinus* species that had been introduced but not naturalized (i.e. established self-sustaining populations in the wild), whereas the subsequent study includes only those that form self-sustaining wild populations, and thus examines the impact of species attributes on subsequent survival and spread. Therefore both studies contribute to explaining success at different stages of the invasion process (Bellingham et al. 2004). Measuring the success of species invasions from the converse perspective of biotic resistance within native communities acknowledges that interactions between different sources of biotic resistance, and between biotic and abiotic factors, also has the potential to inhibit invasions more strongly at different stages of the invasion process (Levine et al. 2004).

The lack of precision in forecasting which invasive species will establish and spread; the speed with which they will do so, and the resulting impacts on the environment and economy is a cause of conflict between different stakeholder groups. This is particularly evident in the Irish salmon farming industry; entrepreneurs seek to increase profits through importation of new genetic strains. However, farm salmon escapees pose a threat to industries seeking to brand their salmon product as wild and/or organic. Such conflicts are prominent in decisions regarding how to allocate financial resources to risk assessment. For example, the import of non-native plant species through internet purchases made by the general public is difficult to monitor and control. Whilst phytosanitary legislation does exist (reviewed in Schrader and Unger 2003); fines for criminal offences are very low in comparison to the potentially huge costs of damage and restoration and do not always constitute an effective deterrent (DEFRA 2003). In this scenario it could be said that the behaviour of different stakeholder groups leads to specific management strategies, in that sectors of the public are inadvertently promoting the necessity of a strategy of financial investment in mitigation of invasive species problems as they arise.

The lack of an established basis for risk assessments under the current climatic regime further restricts our ability to make longer term predictions about invasions in the light of potential climate change. Predictions of broad climatic trends for Ireland include increases in temperature and precipitation (Kiely 1999; Holden et al. 2003). One example of a recent establishment of an invasive species believed to be attributable to climate change is that of the Lily beetle, *Lilioceris lilii*, a garden pest first discovered in Belfast, Northern Ireland in 2002 (Anderson and Bell 2002). This species is native to Eurasia and became established in the British Isles during the 19th century (Cox 2001). Despite being erratically resident in southern Britain for many years, the appearance of *L. lilii* in Northern Ireland is by far its most northerly and westerly site, a significant step in range expansion believed to have been facilitated by recent climate change (Anderson and Bell 2002). Currently, the representation of invasive invertebrate species in Northern Ireland differs between taxa; alien species comprise a high proportion of the total fauna within the flatworms, and, to a lesser extent, within groups such as slugs, snails, isopods and millipedes. If current climatic trends continue initial consequences may be increases in the flux of hygrophilous fauna such as non-native slugs, snails, millipedes and flatworms, with a reduced influx of diurnal thermophilic organisms such as dragonflies, bees and butterflies (Grainger 1992; R. Anderson, pers. comm). Economic consequences to the agricultural community may potentially arise as a result of these changes. A prominent example is the increased abundance of invasive New Zealand flatworm, *Arthurdendyus triangulatus*, a significant predator of native earthworm populations (Moore et al. 1998; Boag and Yeates 2001). Reduction in earthworm abundance has the potential to create long-term damage to soil quality: such as increased surface litter accumulation, reduced surface drainage, widespread increase in surface compaction and increased soil acidity. In this situation risk assessment is hampered by poor ability to accurately predict future patterns of abundance.

Scoping the needs of a monitoring program

A key step in the management of biological invasions is to gain an understanding of the frequency with which a species is introduced into a specific area, the size of each introduction and the subsequent pattern of spread across the landscape (Moody and Mack 1988; Rouget and Richardson 2003), all of which emphasize the need for regular surveillance and/or monitoring. Surveillance can broadly be termed the act of undertaking repeated surveys and monitoring as surveying against a standard to determine subsequent changes (DEFRA 2003). Monitoring for pest management indicates whether a particular management strategy is effective or in need of alteration and forms the basis of adaptive management, enabling managers to learn about the system through monitoring responses to management actions (Shea 1998). One of the more common monitoring practices is recording the abundance of pest species. However, this strategy ignores spatial and temporal variation in environmental conditions and fluctuations in the densities of other species, all of which may impact upon population density of the pest. Additionally, a non-linear relationship may exist between pest abundance and ecosystem damage, possibly indicating the existence of stable states that can provide a level of resilience to change (Suding et al. 2004).

Defining the purpose of a monitoring program is often the most critical phase of the process. Scoping a monitoring task should define which clients/users require the monitoring program, what their purpose/needs for monitoring are, at what resolution of measurement and reporting scales the monitoring is required and over what time-frame the information is needed (Smyth and James 2004). If an inadequate balance is struck among the agreed purposes, sampling scheme, data collection and analytical steps, there is a high probability that little or no helpful data analysis or interpretation will be undertaken, despite the investment of substantial resources in data collection by the clients/users (Wallace et al. 2004; Watson and Novelly 2004).

Concerns regarding the effectiveness of monitoring programs include the limitations of extrapolating across spatial and temporal scales, particularly with respect to recent invasions when the need for evidence-based advice is urgent, the prevalence of anecdotal evidence, inconsistency in documentation and metrics used; dominance of single-trophic level studies and the emphasis on theoretical outcomes rather than mechanisms of control or mitigation (DEFRA 2003). In Ireland a number of unique habitats exist, such as turloughs, non-permanent water bodies which may be sufficiently dry in summer to be used as pasture yet several meters underwater during winter. Such temporal transience of some characteristic elements of biodiversity means that monitoring must be designed to reflect seasonality of associated taxa.

To be efficient a monitoring scheme must incorporate a number of different elements, including: (1) recording of all invasive/native species across taxa; (2) proactive recording of key invasive species of concern; (3) changes in numbers and distribution of invasive/native species over time and analysis within and among taxa; (4) changes in phenology of invasive/native species; and (5) maintenance of lists of species which have not yet been recorded in the location designated for protection but are known to have been accorded pest status elsewhere in regions of similar climatic regime.

Developing a culture of awareness among stakeholders

Increasing the awareness of the public can result in enhanced monitoring and surveillance within the general environment, contributing to a reduction in the number of invasive alien species entering a country and the successful completion of control programs. In common with other countries, the approach to developing a response to invasive species issues within Ireland is currently rather regulatory and retrospective, based upon restrictive measures rather than encouraging an ethos of custodial care in the national psyche. Many European countries still lag behind the custodial mindset prevalent within countries such as New Zealand, which have evolved a heightened sense of responsibility regarding native fauna due to decimation during early stages of human colonization (King 1984). Ireland also has the distinct disadvantage of possessing a car-based, ferry-driven tourist economy, placing a high burden of responsibility on both the local public and incoming tourists to safeguard against the arrival of invasive species. In addition, Ireland acts as a global magnet for sport fishing, a thriving industry which encourages the importation of new species of game and bait organisms which may be discarded alive, such as *Gammarus pulex* (Dick et al. 1995).

In addition, successful monitoring is restricted by a lack of trained taxonomists. The decline in taxonomy and the number of taxonomists within the professional community has been widely publicized (Daly 1995; Godfray 2002; House of Lords 2002; Gropp 2003; Wheeler 2004) but trends in the activities of amateur taxonomists were unclear until recently. Amateurs contribute many valuable species records; therefore lack of knowledge regarding amateur trends may have a disproportionate impact on the information available for conservation planning and represents an under-appreciated threat to developing policies on invasive species (Hopkins and Freckleton 2002). A study evaluating the changing role of both amateur and professional taxonomists was conducted by Hopkins and Freckleton (2002). Contributions by British-based authors to Entomologist's Monthly Magazine were reviewed over the past century; results showed that both amateur and professional taxonomy have undergone a long and persistent decline since the 1950s, in terms of both the number of contributors and the number of papers contributed. This emphasizes the need for promoting taxonomic education within school curricula and higher education centres. Conflicts in efficient use of professional time also arise due to the low numbers of taxonomists. Currently, key personnel tend to be inundated with identification queries from the general public, particularly during summer months when people spend an increasing proportion of time outdoors and also during the breeding seasons of conspicuous and attractive insects. A useful innovation would be to consolidate information so that the public is provided with clearly defined access routes to knowledgeable personnel whose focus is concentrated on invasive species within a group of taxa. This would necessarily require a broad advertising campaign targeted at the general public and possibly the maintenance of a web-based invasive species site.

Improving monitoring and surveillance programs through reduction of stakeholder conflict

A number of barriers inhibit the successful conduction of effective monitoring and surveillance in Ireland. A large proportion of land within Northern Ireland and the Republic of Ireland is privately owned and the difficulties of efficient monitoring on privately owned parcels of land may result in a bias towards a restricted set of ecological communities (Hilty and Merenlender 2003). At a landscape scale such unrepresentative sampling for monitoring schemes may lead to erroneous conclusions because public and private lands may differ in biodiversity and productivity. Landowners may be reluctant to allow research to be conducted on their land because of concerns regarding liability and property damage. Alternatively researchers can be discouraged from including private land in surveys due to concerns regarding transfer of property, alterations in site usage part way through a study and perceived limitations to research design or ability to publish and disseminate results (Hilty and Merenlender 2003). Selective monitoring regimes can therefore lead to lacunae in geographic information relating to species distribution and abundance.

A large proportion of privately owned land in Ireland is farmland. One possibility to enhance the incentive for cooperation among rural stakeholders (farmers) is through reward-based motivation. The inclusion of measures for the monitoring, prevention, eradication or control of invasive species could feasibly be incorporated into Agri-Environment schemes. These schemes compensate farmers financially for any loss of income associated with measures that aim to benefit the environment or biodiversity (see Kleijn and Sutherland 2003, for a review of European Agri-Environment schemes). In the Republic of Ireland the Irish Rural Environmental Protection Scheme (REPS) consists of one scheme with 11 compulsory measures and a further 6 ‘supplementary measures’. The basic scheme is comprehensive and addresses biodiversity and environmental protection, training courses and keeping of farm and environmental records. The success of the REPS scheme has been attributed to its universal geographic availability, voluntary nature, comprehensiveness, tailoring to individual farm limited payments (which controls the extent to which larger farms can benefit from the scheme) and financial training incentives (Emerson and Gillmor 1999). Inclusion of an additional REPS measure aimed at preventing the infiltration and spread of invasive alien species would have the additional benefit of utilizing existing legislation.

In Northern Ireland the Department of Agriculture launched the Countryside Management Scheme in 1999. This scheme has a tiered approach, Tiers 2 and 3 adopt measures that exceed the baseline management approach and are aimed at habitats or features where specific management prescriptions must be instigated. Implementation of the Single Payment Scheme (SPS) under the Common Agricultural Policy (CAP) reform (Council Regulation 1782/2003) is effective from 1st January 2005 and requires member states to achieve cross-compliance standards (which largely originate from existing EU Directives and Regulations) in order to qualify for subsidies under the SPS. Implementation of cross-compliance is currently under consideration in Northern Ireland (DARD 2004). Future schemes will enable participants to receive a subsidy for active maintenance and environmental enhancement, both complimenting and building upon cross-compliance conditions, and could potentially include measures aimed at reducing abundance and spread of invasive alien species as they mature.

Tailoring environmental schemes to commercial enterprises

Perrings et al. (2002) consider that the market prices of potentially invasive species seldom reflect the costs they may impose on society because the harm inflicted by invasive species is typically external to the market. Tax, price, and incomes policies have all increased the susceptibility of agroecosystems to invasion. For example, subsidies designed to promote the export of cash crops have reduced plant genetic diversity and encouraged the use of farm inputs, such as pesticides and fertilizers, in a manner that has made agroecosystems vulnerable to invasion (Perrings et al. 2002). Future intensification, such as the use of genetically-modified, herbicide-tolerant crops, is likely to create further detrimental impacts on biodiversity (Watkinson et al. 2000).

The quest for profit leads to the establishment of new commercial enterprises which frequently advocate the importation of new species, for example the Irish aquaculture industry introduced the Japanese cold water abalone, *Haliotis discus hannai*, to Ireland in 1986 (Watson and Stokes 2004). Codes of practice designed to regulate commercial enterprises importing new species are frequently developed but their efficiency is subject to the performance of private individuals. Perrings et al. (2002) advocate a structure of incentives and discentives to induce behaviour in support of the public good. An Irish example is, the Environmental Code of Practice for Irish Aquaculture Companies and Traders (ECOPACT), launched in the Republic of Ireland in 2003 by the Minister of State at the Department of Communications, Marine and Natural Resources on behalf of *Bord Iascaigh Mhara* (the Irish Sea Fisheries Board). The principle aim of ECOPACT is to promote the widespread introduction of independently certified environmental management schemes into the Irish aquaculture industry, conducted to a standard beyond compliance with legal requirements. Given the preponderance of small finfish and shellfish farms in Ireland, participants are advantaged in a reduction of the administrative burden associated with the larger European schemes, whilst still gaining recognition of commitment to environmental sustainability and thus enhancing the attractiveness of their product on the European market. In relation to invasive species an aquaculture participant would be required to maintain detailed stock records in order to accurately quantify the potential scale of a problem should an escape incident occur, notify appropriate legislative departments and initiate recapture attempts. However, effective monitoring and enforcement is vital to the survival of such schemes, indicating that the alternative option of imposing an environmental tax on importers may provide a more potent threat.

Legislative and trade-related conflicts

A conflict faced by many European Governments is the ability to restrict or impose regulatory tax regimes on imports without violating trade agreements. However, a European case exists where national conservation law has legitimately overruled trade regulations and reference is made to this example to highlight the need for establishment of principles concerning intra-EC trade and biodiversity conservation.

In 1993 the Danish Minister for Agriculture and Fisheries issued Decision No. 528, which prohibited the keeping of nectar-gathering bees on the island of Læsø, other than those of the subspecies *Apis mellifera mellifera*. Any existing swarms of other bees had to be destroyed, removed, or the queen replaced with an inseminated queen of the specific species. The aim was to conserve the population of Brown Bee subspecies from hybridization with other bee species. Criminal proceedings were initiated by the Danish Government against a resident of Læsø for continuing to keep a swarm of another bee species after Decision No. 528 came into force. The defendant argued that the Decision constituted a measure having effect equivalent to a quantitative restriction on imports contrary to Article 30 of the Treaty of Rome and further contended that the Læsø brown bee was not unique to the island and threatened with extinction, so that Article 36 could not be used to justify the restriction. Article 36 allows for measures which would otherwise be prohibited under Article 30 if they can be justified on the grounds of 'protection of health and life of animals'. The public prosecutor argued that the effects of the Decision were entirely internal to Denmark and thus Article 30 did not apply. The national court referred the case to the European Court of Justice for a ruling.

The effect of the Decision on trade of each sub-species of bee was analysed separately and concluded to discriminate in favour of the Danish (and in particular Læsø) production of the Brown Bee relative to non-Danish Brown Bee and thus did fall under the scope of Article 30. However, the opinion of the Court's Advocate was that a legitimate aim of Article 36 would be protection below the subspecies level (for example subgroups within a subspecies) and the population in question need not be in immediate danger of eradication. Therefore Decision No. 528 was justified by reference to Article 36 and the CBD (Judgement of the Court 03-12-1998).

This lack of integration between national and European law needs to be effectively resolved to prevent alienation of stakeholders and the growth of a culture which fails to respect legislation pertaining to invasive species issues.

Control of invasive species: decision-making under uncertainty

The unpredictable nature of species introductions means that fully quantitative and economic assessments can rarely be prepared. The quantifications which are usually attempted are calculations of the area endangered by a non-native species and costs to individual enterprises whose gross margin budgets can be readily obtained (DEFRA 2003). Technical forecasting of risk regarding invasive species is still at an early developmental stage and confidence limits about estimates of likelihood that a species will become a pest are large, increasing the probability of making a highly costly false hypothesis of no negative effect (Simberloff and Alexander 1998). Uncertainty is inherent in ecological systems and this can be countered by developing effective management options that adjust for different levels of risk and uncertainty. The use of mathematical models is fundamental to this procedure. However, modelling can only play an effective role in this process if there is close interaction between modellers and policy makers regarding the specific question and outcome to be addressed, for example elucidating the quantitative effects of a specific management option on a species of concern.

Some of the more successful management tools have been applied using an economically based system of cost, risk and benefit measures applied in a location-specific manner (Sharov and Liebhold 1998; Higgins et al. 2000; Turpie 2004). Location-specific indicators of 'damage' may be structured to represent economic concepts of capacity to produce a service, differential value of services at different locations, scarcity and replaceability of services and risk of service flow disruptions (Wainger and Price 2004). The use of geographical information systems (GIS) allows these factors to be quantified at multiple scales. For example, different potential benefits from a treatment may come into play over the extent of a national park, catchment basin or county.

A large proportion of management relating to invasive species is steeped in a 'search-and-destroy' mentality (Gosling and Baker 1989). In the case of rapid action against a species which is detected early, a large amount of information on population biology is not necessarily essential to eliminate the problem. Simberloff (2003) states that due to the rapid population growth and high dispersal abilities of invasive species they are one target at which it is better to 'shoot first and ask questions later'. However, this approach leads to uncertainty whether the successful eradication of the species could be attributed to good luck rather than an effective management strategy (Simberloff 2003). For example, severe drought or a prolonged period of below average temperature may actually have had a greater detrimental effect upon the population than the control strategy did. Therefore application of the same control procedure during a second invasion may not produce the desired effect.

Stakeholder contribution to successful control schemes

Once an informed decision regarding control has been taken a variety of different techniques may be utilized to control or eradicate species, including: physical and mechanical means, such as trapping and shooting, chemical methods (poisoning) and biological methods, such as use of immuno-contraceptives or the directed use of pathological agents, for example the use of the *Myxoma* virus to achieve biocontrol of European rabbit, *Oryctolagus cuniculus*, in Australia, Great Britain and Ireland (Fenner and Ratcliffe 1965). Whatever the strategy used its long-term success is critically dependent on support from different areas, including financial support, staff commitment and the support of the public. For example, differences in property ownership can inhibit actions relating to the control of invasive species; Perrings et al. (2002) consider that land held in common property requires collective action against invasive species, whereas open-access land militates against any significant action at all. Studies evaluating the public's support or willingness to pay for differing control options regarding management of introduced pests are rare. However, a survey conducted by Jetter and Paine (2004), which quantifies the comparative public value of differing control options for an urban forest pest through evaluation of consumer preferences, indicated that it may be possible to generate social and financial support from urban residents for classical biological control options.

An Irish example of a successful control campaign to eradicate muskrat (*Ondatra zibethica*) is described which emphasizes the importance of ecological knowledge in enabling estimation of the effort required, the costs involved and the probability of successful eradication, all of which justified ongoing financial commitment from the Irish government of the time. Muskrats are rodents native to North America that were intentionally introduced to Great Britain for fur farming in the 1920s. Muskrats are generalist herbivores which damage native plants and crops (Warwick 1940). Additionally, these rodents cause damage to drainage systems by burrowing. Muskrats were was first imported into Ireland in 1929 into County Tipperary in the south of the Republic (Fairley 2001). Escaped animals spread quickly and grew in number unnoticed for a time due to their elusive behaviour and nocturnal habits (Fairley 2001). The Department of Agriculture became increasingly concerned regarding the potential for river bank erosion. In 1931 the *Foot and Mouth Disease (Importation of Rodents and Insectivora) Order* prevented the further import of muskrats, after a slight delay resulting from uncertainty as to whether muskrats could actually transmit the disease (Fairley 2001). This Act was followed by the *Destructive Imported Animals Bill*, in February 1933 and the *Destructive Imported Animals Act (Northern Ireland)*, March 1933 which dealt primarily with muskrats. Finally, the *MuskRats Act* (1933) in the Republic of Ireland initiated an intensive trapping programme which ran from September, 1933 until April, 1935 when the muskrat was believed to have been eradicated. The success of the scheme was partly attributable to the commendably short interval between the discovery of the establishment in the wild and the initiation of a destruction programme (Fairley 2001). The muskrat was a known pest in Europe (Sheail 1988); therefore, as in the British case (Gosling and Baker 1989), information was available in order to assess the effort required, the costs involved and the probability of success; all of which were essential in sustaining government support and funding to promote effective coordination of control programs between the two countries.

In the above example the impact of the muskrat was perceived as entirely economically detrimental. However, inter-sectoral conflict can arise when a deliberately introduced species has both positive and negative impacts. In south Australia the proposed biological control of Paterson's curse (*Echium plantagineum*), a deliberately introduced weed species, was opposed by stakeholders in the honey trade. Paterson's curse produces alkaloids which affect liver function in grazing animals (Seaman et al. 1989) but which also produce honey with a pale colour preferred by exporters to the Japanese market. An independent inquiry into the merits of both the positive and negative impacts of biological control of this weed recommended release of insects to control growth and development of Paterson's curse on the basis of economic costs ($30 million annually) and benefits ($2 million annually) to Australia (IAC 1985).

Cross-border complications regarding responses to new invasions

Additional barriers to rapid action regarding control arise when invasive species permeate national borders. It is difficult to predict how a cross-border invasion should be addressed, both in terms of legislative procedures and financial responsibility for ecosystem restoration. The design of standard protocols to combat the complications resulting from a cross-border scenario would be beneficial in the majority of cases.

In the island of Ireland a number of protected sites span the jurisdictional border between the north and the south (Table 1). For example, Lough Melvin (County Fermanagh, Northern Ireland and County Leitrim, Republic of

Table 1. SACs in Northern Ireland which adjoin SACs in the Republic of Ireland (Source: http://www.jncc.gov.uk/page-1522.

UK cSAC		Republic of Ireland cSAC	
Site code	Site name	Site code	Site name
UK0016603	Cuilcagh Mountain	IE0000584	Cuilkcagh-Anieran Uplands
UK0030047	Lough Melvin	IE0000428	Lough Melvin
UK0016621	Magheraveely Marl Lakes	IE0001786	Kilrooskey Lough Cluster
UK0016607	Pettigo Plateau	IE0001992	Tamur Bog
UK0016607	Pettigo Plateau	IE0002164	Lough Golagh & Breesy Hill

Ireland) is an important resource for tourism due to the high level of recreational fishing. The infiltration of an invasive alien species resulting in a detrimental impact on the fishing industry would be of serious economic concern to both countries. Such a scenario is illustrated by the sequence of events depicted in Figure 1.

In this hypothetical situation a member of the public is brought into contact with an 'unusual species', which we shall consider to be North American signal crayfish, *Pacifastacus leniusculus*, (a host to crayfish plague, *Aphanomyces astaci*), discovered in Dawson's Lough (lat. 54°12′07″ N long. 07°14′35″ W), in the north of the Republic close to the border. This individual may then take one of several options, they may choose not to act or they may dispatch the item to a local conservation office, a local fisheries officer, or a museum in Dublin. The choice of destination will influence the length of time to arrive at a positive identification of the species. Once the species has been identified the relevant statutory nature conservation body (SNCB) may be informed of a potential threat. Authorization to conduct survey sampling of Dawson's Lough would reveal the presence of North American signal crayfish at low abundance. The threat to the site south of the border could be perceived as low, as this area is not a designated Special Area of Conservation (SAC) under the European Habitats Directive. However, it must be remembered that signal crayfish are highly mobile and can move considerable distances over land (Alderman and Wickins 1996). North of the border lies Lough Erne, the whole of which is an SAC, and Magheraveely Marl Loughs, a second SAC for which native freshwater crayfish are specifically a designated feature. Therefore a differential exists in the prioritization of the threat between the north and south.

No formal mechanism exists for transfer of information and cross-border communication in this matter, yet it is probable that nature conservation staff would personally inform their contemporaries in the relevant statutory conservation body in the north. Senior level authorization will be required to commence surveying of sites north of the border in order to determine the extent of the local threat. Access to private land may be restricted by landowners and trained personnel may be scarce. Species-specific information may also be lacking, increasing the difficulty in ascertaining the degree of threat and possibility of eradication. Nonetheless, it is probable that attempts will be

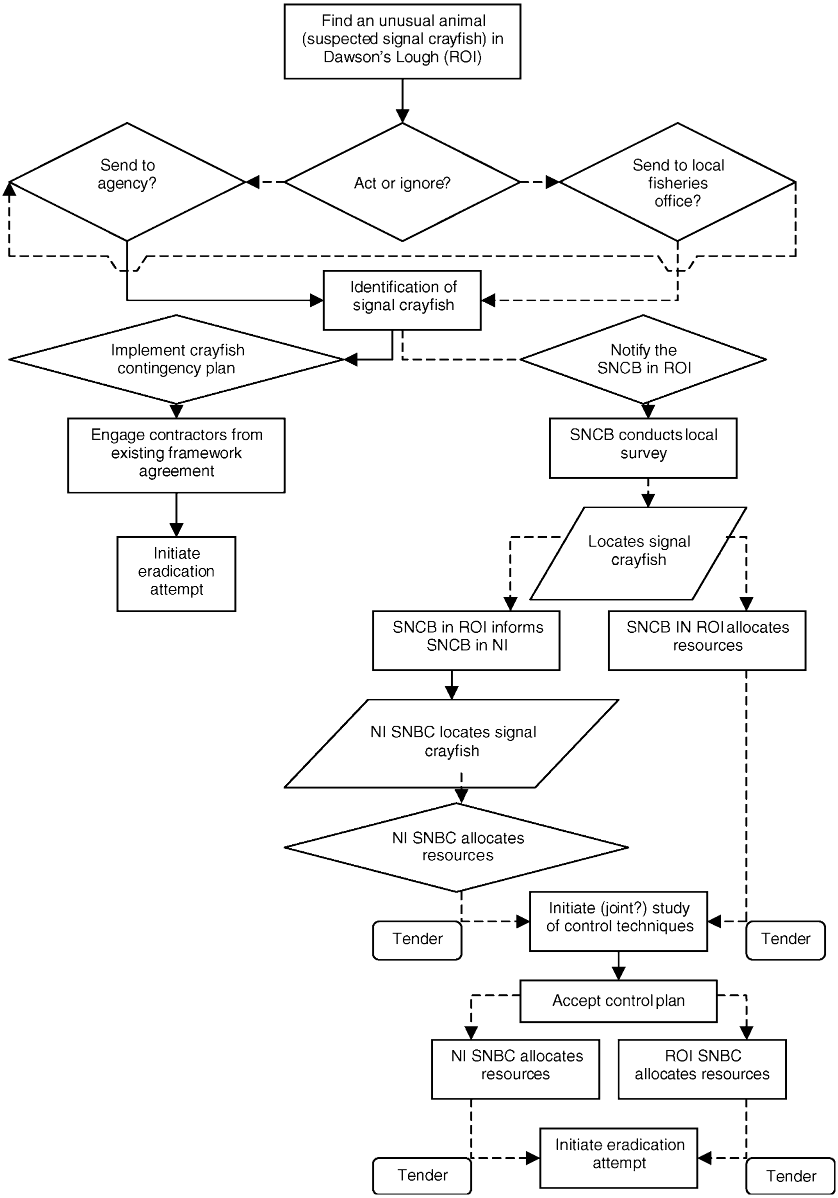

Figure 1. Hypothetical scenario of decisions and processes affecting the cross-border response to finding a potential new invasive species near the border. Dotted lines indicate risk prone stages. The key factor is the development of a contingency plan, comprising the detailed processes and decisions, led by a cross-border body in advance of the discovery of the invasive. Thus the potential delays occur before the invasion occurs. As delays arise from a *post-hoc* response the chances of success rapidly diminish. SNCB = statutory nature conservation body, ROI = Republic of Ireland, NI = Northern Ireland.

made to evaluate the extent of the distribution and the probability of success of control or eradication methods. Coordination of any eradication policy between north and south will be essential due to the connectivity of this ecosystem. Either the northern or the southern conservation body may lack the scope or manpower to act on this matter and may advertise a contract to tender, leading to initial feasibility studies and eventually eradication attempts, evaluation and post-evaluation, regarding the quality of control and success of ecosystem restoration. The time scale of this process is delayed by the lack of pre-defined pathways, resulting in the initiation of an eradication policy some years after discovery, by which time the crayfish will have reproduced and increased their numbers.

The alternative scenario considers the beneficial role of a cross-border invasive species body. In this situation the unusual species is dispatched direct to this body, where identification takes place and a specific contingency plan is set in motion. In this case an eradication campaign could be initiated in 3 months or less, based on existing framework agreements with contractors working to an established plan. This rapid response would considerably reduce the possibility of the crayfish completing its reproductive cycle before eradication, increasing ease of eradication and reducing cost.

Discussion

The Irish examples presented here emphasize the importance of approaching management of invasive species from a cost-efficient, highly flexible perspective, acknowledging the linkages which exist between environmental, economic and social objectives. Integration between scientists, conservation managers and policy makers is essential to generate plans for sustainable protection of native biodiversity and effective prioritization of both research and policy developments. Perceptions of cost and benefit in relation to invasive species issues are often polarized, underlining the importance of effective communication among stakeholders. Engaging the commercial and industrial sector, both through coercive methods: such as establishment of the ‘polluter pays’ principle which enables courts to impose fines bearing some relation to the cost of reparation, and through more positive interactions such as legal underpinning of policies that define and allocate duty of care, enables achievement of a more sustainable outcome through co-operative compliance. Imposing a ‘polluter pays’ penalty may not be feasible in the majority of cases due to difficulty in allocating responsibility. Therefore realistic consideration of the financial resources inhibiting commercial compliance is essential to generate respected custodial schemes to which industry will subscribe. The general lack of enforcement powers also needs to be addressed, in particular with regard to access rights to private land for monitoring or control purposes. This is essential in order to reduce the fragmentary nature of invasive species management across geographic areas.

Harmonizing domestic, European and international law in the context of trade, biological conservation and invasive species policy is a global necessity. This process is likely to be a difficult undertaking but it is fundamental in order to retain international respect and compliance with invasive species legislation. In Ireland the implementation of a biosecurity strategy that cuts across the two jurisdictions is a priority. Structuring of cross-border constitutional arrangements in relation to risk reduction and control policies is possible to achieve through establishment of a cross-border forum, consisting of policy makers from the relevant departments, scientists from statutory agencies, research institutions, NGOs and independent authorities. Representatives from the industrial, trade and commercial sectors are a priority in order to effectively achieve long-term commitment to risk reduction and control programs. It is also advisable to foster linkages with public health departments for guidance in the formulation of contingency plans, both as models for biodiversity problems and in the event of an invasive species becoming a public health hazard.

The dissemination of information to the public and encouragement of adaptive alterations to behavioural and consumer patterns has the potential to provide a degree of protection against invasive species. Geographic differences in market pressure and population density result in differing accessibility levels to markets, a factor which enhances the potential for degradation of landscapes by invasive species. Promoting moves towards increased consumption of local produce may be beneficial in reducing the impact of invasive species through a reduction in imports, although the outcome is not straightforward. Stephens et al. (2003) emphasize that discriminating between products on the basis of provenance rather than price is a luxury many consumers cannot afford, and advise promoting the competitiveness of local produce by taxing long-distance transport of goods in a manner which accounts for damage caused to the environment, human health and national infrastructure. The potential contribution of local community actions in reducing invasive species impacts should be investigated further, such as the feasibility of generating financial support for control programs from the general public.

Cost-based risk assessments are vital in contributing to the success of control programs. Accurate forecasting using environmental tools to evaluate aesthetic and economic injury enables justification of financial resources towards mitigation of existing problems. In relation to risk forecasting it is evident that scientific research should be focused on narrowing the uncertainty associated with the factors contributing to the success and speed of a potential invasion, including potential negative impacts. Models incorporating ecological processes will enable more accurate simulations of the probable events following a species introduction and the potential consequences, both for biodiversity and for public and private finances.

Effective management of invasive species requires focus on both adaptive and mitigative interactions between the different stakeholders involved, from a local to a global scale. At an international level the degree of protection implemented by one country has implications for the risks faced by others and protection will be constrained by the resources available to the poorest countries in a 'weakest link' scenario (Sandler 1997; Perrings et al. 2002). This concept also applies at the national and regional level. Only by continual and constructive engagement of stakeholders at all stages of the process and at a range of temporal scales can key requirements be addressed. Risk assessment, monitoring, forecasting and responding to new invasions, management of established invasive species, refinement of legislative drivers, and the urgency of enhancing community awareness should all be addressed with the critical aim of achieving stakeholder cooperation for the sustainable conservation of biodiversity, both within the island of Ireland and at an international level.

References

Anderson R. and Bell A.C. 2002. A first record of the Lily Beetle *Liliocerus lilii* (Scopoli) in Ireland. Coleopterist 11: 90.

Alderman D.J. and Wickins J.F. 1996. Crayfish CULTURE, Laboratory Leaflet No. 76. CEFAS Lowestoft, MAFF, UK.

Bellingham P.J., Duncan R.P., Lee W.G. and Buxton R.P. 2004. Seedling growth rate and survival do not predict invasiveness in naturalized woody plants in New Zealand. Oikos 106: 308–316.

Blackburn T.M. and Duncan R.P. 2001. Determinants of establishment success in introduced birds. Nature 414: 195–197.

Boag B. and Yeates G.W. 2001. The potential impact of the New Zealand flatworm, a predator of earthworms, in western Europe. Ecol. Appl. 11: 1276–1286.

Bullock J.M., Hodder K.H., Manchester S.J. and Stevenson M.J. 1996. Review of Information, Policy and Legislation on Species Translocations. JNCC Report No. 261. Joint Nature Conservation Committee, Peterborough, UK.

Brown J.H. 1989. Patterns, modes and extents of invasions by vertebrates. In: Drake J.A., Mooney H.A., di Castri F., Groves R.H., Kruger F.G., Rejamek M. and Williamson M. (eds), Biological Invasions: A Global Perspective. John Wiley & Sons, Chichester, UK, pp. 85–110.

Callaghan D. 2003. Alien species research requirements for delivery of the UK Biodiversity Action Plan – Discussion Paper. Just Ecology, URL: www.justecology.co.uk.

Cassey P. 2002. Life history and ecology influences establishment success of introduced birds. Biol. J. Linn. Soc. 76: 465–480.

Clark P.F., Rainbow P.S., Robbins R.S., Smith B., Yeomans W.E., Thomas M. and Dobson G. 1998. The alien Chinese mitten crab, *Eriocheir sinesis* (Crustacea: Decapoda: Brachyura), in the Thames catchment. J. Marine Biol. Assoc. UK. 78: 1215–1221.

Commission for Environmental Co-operation (CEC) 2002. The North American Mosaic: A State of the Environment Report. Montréal, Canada.

Costello M.J. 1993. Biogeography of alien amphipods occurring in Ireland, and interactions with native species. Crustaceana 65: 287–299.

Cox M.L. 2001. The status of the Lily Beetle *Lilioceris lilii* (Scopoli, 1763) in Britain (Chrysomelidae: Criocerinae). Coleopterist 10: 5–20.

Cross R.J. 1975. Biological flora of the British Isles *Rhododendron ponticum*. J. Ecol. 63: 345–365.

Cross J.R. 1981. The establishment of *Rhododendron ponticum* in the Killarney oakwoods, SW Ireland. J. Ecol. 69: 807–824.

Cross J.R. 1982. The invasion and impact of *Rhododendron ponticum* in native Irish vegetation. J. Life Sci. Roy. Dublin Soc. 3: 209–220.

Dalmazzone S. 2000. Economic factors affecting the vulnerability to biological invasions. In: Perrings C., Williamson M. and Dalmazzone S. (eds), The Economics of Biological Invasions. Edward Elgar Publishing, Cheltenham, UK, pp. 17–30.

Daly H.V. 1995. Endangered species: doctoral students in systematic entomology. Am. Entomol. 41: 55–59.

Department for Environment, Food and Rural Affairs (DEFRA), 2003. Review of Non-native Species Policy. Report of the Working Group. DEFRA publications, London, UK.

Department of Agriculture and Rural Development, Northern Ireland (DARD), 2004. Cap Reform. Cross-Compliance Consultation Paper. http://www.dardni.gov.uk/file/con0409b.doc.

Diamond J. and Case T.J. 1986. Overview: introductions, extinctions, exterminations and invasions. In: Diamond J. and Case T.J. (eds), Community Ecology. Harper & Row, New York, USA, pp. 65–79.

Dick J.T.A., Elwood R.W. and Montgomery W.I. 1995. The behavioural basis of a species-replacement – differential aggression and predation between the introduced *Gammarus-pulex* and the native *Gammarus duebeni celticus* (Amphipoda). Behav. Ecol. Sociobiol. 37: 393–398.

Drake J.A., Mooney H.A., di Castri F., Groves R.H., Kruger F.G., Rejmánek M. and Williamson M. (eds) 1989. Biological Invasions: A Global Perspective. John Wiley & Sons, Chichester, UK.

Duncan R.P., Blackburn T.M. and Sol D. 2003. The ecology of bird introductions. Annu. Rev. Ecol. Syst. 34: 71–98.

Dunne R. 2003. Some recent insect and mite introductions to Ireland. In: Moriarty C. and Murray D. (eds), Biological Invaders: The Impact of Exotic Species. Royal Irish Academy, Dublin, Ireland, pp. 115–118.

Emerson H.J. and Gillmor D.A. 1999. The Rural Environment Protection Scheme of the Republic of Ireland. Land Use Policy 16: 235–245.

Fairley J. 2001. A Basket of Weasels (Published privately). Belfast, Northern Ireland.

Fenner F. and Ratcliffe F.N. 1965. Myxomatosis. Cambridge University Press, Cambridge, UK.

Forsyth D.M., Duncan R.P., Bomford M. and Moore G. 2004. Climatic suitability, life-history traits, introduction effort and the establishment and spread of introduced mammals in Australia. Conserv. Biol. 18: 557–569.

Godfray H.C.J. 2002. Challenges for taxonomy. The discipline will have to reinvent itself if it is to survive and flourish. Nature 417: 17–19.

Gosling L.M. and Baker S.J. 1989. The eradication of the muskrats and coypus from Britain. Bot. J. Linn. Soc. 38: 39–51.

Grainger J.N.R. 1992. The probable effects of climate change on invertebrate growth and reproduction with particular reference to Ireland. Invertebr. Reprod. Dev. 22: 239–244.

Gropp R.E. 2003. Are university natural science collections going extinct? Bioscience 5: 550.

Grotkopp E., Rejmanek M. and Rost T.L. 2002. Towards a causal explanation of plant invasiveness: seedling growth and life-history strategies of 29 Pine (Pinus) species. Am. Nat. 159: 396–419.

Hayden T. and Harrington R. 2000. Exploring Irish Mammals. Townhouse, Dublin, Ireland.

Hemami M.R., Watkinson A.R. and Dolman P.M. 2004. Habitat selection by sympatric muntjac (*Muntiacus reevesi*) and roe deer (*Capreolus capreolus*) in a lowland commercial pine forest. For. Ecol. Manage. 194: 49–60.

Herborg L.M., Rushton S.P., Clare A.S. and Bentley M.G. 2003. Spread of the Chinese mitten crab (*Eriocheir sinensis* H. Milne Edwards) in Continental Europe: analysis of a historical data set. Hydrobiologia 503: 21–28.

Higgins S.I., Richardson D.M. and Cowling R.M. 2000. Using a dynamic landscape model for planning the management of alien plant invasions. Ecol. Appl. 10: 1833–1848.

Hilty J. and Merenlender A.M. 2003. Studying biodiversity on private lands. Conserv. Biol. 17: 132–137.

Holden N.M., Bereton A.J., Fealy R. and Sweeney J. 2003. Possible changes in Irish climate and its impact on barley and potatoe yields. Agric. For. Meterol. 116: 181–196.

Holdich D.M. and Rodgers W.D. 1997. The white-clawed crayfish *Austropotamobius pallipes* in Great Britain and Ireland with particular reference to its conservation in Great Britain. Bull. Francais Peche Pisicult. 347: 597–616.

House of Lords. 2002. What on Earth? The Threat to the Science Underpinning Conservation. Select Committee on Science and Technology, third report, HL Paper 118(i), London, Stationary Office, UK.

Hopkins G.W. and Freckleton R.P. 2002. Declines in the number of amateur and professional taxonomists: implications for conservation. Anim. Conserv. 5: 245–249.

IAC (Industries Assistance Commission) 1985. Biological Control of *Echium* Species (Including Patersons Curse/Salvation Jane). Industries Assistance Commission Report No. 371. Australian Government Publishing Service, Canberra, Australia.

IUCN (World Conservation Union) 2000. Guidelines for the Prevention of Biodiversity Loss Caused by Alien Invasive Species. IUCN, Gland, Switzerland.

Jetter K. and Paine T.D. 2004. Consumer preferences and willingness to pay for biological control in the urban landscape. Biol. Control 30: 312–322.

Judgement of the Court 03-12-1998. Anklagemyndighed v. Ditlev Bluhme. http://www.eel.nl/cases/HvJEG/697j0067.htm

Kelly D.W., Dick J.T.A., Montgomery W.I. and MacNeil C. 2003. Differences in composition of macroinvertebrate communities with invasive and native *Gammarus* spp.(Crustacea: Amphipoda). Freshwater Biol. 48: 306–315.

Kiely G. 1999. Climate change in Ireland from precipitation and streamflow observations. Adv. Water Resour. 23: 141–151.

King C.M. 1984. Immigrant Killers. Introduced Predators and the Conservation of Birds in New Zealand. Oxford University Press, Auckland, New Zealand.

Kleijn D. and Sutherland W.J. 2003. How effective are European agri-environment schemes in conserving and promoting biodiversity? J. Appl. Ecol. 40: 947–969.

Kolar C.S. and Lodge D.M.. 2001. Progress in invasion biology: predicting invaders. Trends Ecol. Evol. 16: 199–204.

Levine J.M. and d'Antonio C.M. 2003. Forecasting biological invasions with increasing international trade. Conserv. Biol. 17: 322–326.

Levine J.M., Adler P.B. and Yelenik S.G. 2004. A meta-analysis of biotic resistance to exotic plant invasions. Ecol. Lett. 7: 975–989.

Lonsdale W.M. 1994. Inviting trouble – introduced pasture species in northern Australia. Aust. J. Ecol. 19: 345–354.

Lonsdale W.M. 1999. Global patterns of plant invasions and the concept of invasibility. Ecology 80: 1522–1536.

Mack R.N. 1996. Predicting the identity and fate of plant invaders: emergent and emerging approaches. Biol. Conserv. 78: 107–121.

Mack R.N., Simberloff D., Lonsdale W.M., Evans H., Clout M. and Bazzaz F.A. 2000. Biotic invasions: causes, epidemiology, global consequences and control. Ecol. Appl. 10: 689–710.

MacNeil C., Elwood R.W. and Dick J.T.A. 1999. Predator–prey interactions between brown trout *Salmo trutta* and native and introduced amphipods; their implications for fish diets. Ecography 22: 686–696.

Manchester S.J. and Bullock J.M. 2000. The impacts of non-native species on UK biodiversity and the effectiveness of control. J. Appl. Ecol. 37: 845–864.

McCorrey M., Curtis T.G.F. and Otte M.L. 2003. *Spartina* in Ireland. In Otte M.L. (ed.), Wetlands of Ireland, Distribution, Ecology, Uses and Economic Value. University College Press, Dublin, Ireland, pp. 44–50.

Minchin D. 2000. Modes of introduction of exotic animals into Irish waters. In: Rushton B.S. (ed.), Biodiversity: The Irish Dimension. Royal Irish Academy, Dublin Ireland, pp. 147–155.

Minchin D., Maguire C.M. and Rossell R. 2003. The zebra mussel (*Dreissena polymorha.* Pallas) invades Ireland: human mediated vectors and the potential for rapid international dispersal. Biol. Environ. 103B: 23–30.

Moody M.E. and Mack R.N. 1988. Controlling the spread of plant invasions – the importance of nascent foci. J. Appl. Ecol. 25: 1009–1021.

Moore J.P., Dynes C. and Murchie A.K. 1998. The status and public perception of the New Zealand flatworm, *Artioposthia triangulata* (Dendy) in Northern Ireland. Pedobiologia 2: 563–571.

O'Connor C., Marvier M. and Kareiva P. 2003. Biological vs. social, economic and political priority-setting in conservation. Ecol. Lett. 6: 706–711.

Olden J.D. and Poff N.L. 2004. Clarifying biotic homogenization. Trends Ecol. Evol. 19: 283–284.

Perrings C., Williamson M. and Dalmazzone S. (eds) 2000. The Economics of Biological Invasions. Edward Elgar, Cheltenham, UK.

Perrings C., Williamson M., Barbier E.B., Delfino D., Dalmazzone S., Shogren J., Simmons P. and Watkinson A.R. 2002. Biological invasion risks and the public good: an economic perspective. Conserv. Ecol. 6: 1.

Pimentel D., Lach L., Zuniga R. and Morrison D. 2000. Environmental and economic costs of non-indigenous species in the United States. Bioscience 50: 53–65.

Pullin A.S. and Knight T.M. 2001. Effectiveness in conservation practice: pointers from medicine and public health. Conserv. Biol. 15: 50–54.

Putman R.J. and Moore N.P. 1998. Impact of deer in lowland Britain on agriculture, forestry and conservation habitats. Mammal Rev. 28: 141–163.

Raupp M.J., Davidson J.A., Koehler C.J., Sador C.S. and Reichelderfer K. 1988. Decision-making consideration for aesthetic damage caused by pests. Bull. Ecol. Soc. Am. 34: 27–32.

Ricciardi A. and Atkinson S.K. 2004. Distinctiveness magnifies the impact of biological invaders in aquatic ecosystems. Ecol. Lett. 7: 781–784.

Rouget M. and Richardson D.M. 2003. Inferring process from pattern in plant invasions: a semimechanistic model incorporating propagule pressure and environmental factors. Am. Nat. 162: 713–724.

Sandler T. 1997. Global Challenges. Cambridge University Press, Cambridge, UK.

Schrader G. and Unger J.G. 2003. Plant quarantine as a measure against invasive alien species: the framework of the International Plant Protection Convention and the plant health regulations in the European Union. Biol. Invas. 5: 357–364.

Seaman J.T., Turvey W.S., Ottaway J.S., Dixon R.J. and Gilmour A.R. 1989. Investigations into the toxicity of *Echium plantagineum* in sheep. Part 1. Field grazing experiments. Aust. Veter. J. 66: 279–285.

Sharov A.A. and Liebhold A.M. 1998. Bioeconomics of managing the spread of exotic pest species with barrier zones. Ecol. Appl. 8: 833–845.

Shea K. 1998. Management of populations in conservation, harvesting and control. Trends Ecol. Evol. 13: 371–375.

Shea K. and Chesson P. 2002. Community ecology theory as a framework for biological invasions. Trends Ecol. Evol. 17: 170–176.

Sheail J. 1988. The extermination of the muskrat (*Ondatra zibethicus*) in inter-war Britain. Arch. Nat. Hist. 15: 155–170.

Simberloff D. 1995. Why do introduced species appear to devastate islands more than mainland areas? Pacific Sci. 49: 87–97.

Simberloff D. and Alexander M. 1998. Assessing risks to ecological systems from biological introductions (excluding genetically modified organisms). In: Calow P. (ed.), Handbook of Environmental Risk Assessment and Management. Blackwell, Oxford, UK.

Simberloff D. 2003. How much information on population biology is needed to manage introduced species? Conserv. Biol. 17: 83–92.

Smallwood K.S. 1994. Site invisibility by exotic birds and mammals. Biol. Conserv. 69: 251–259.

Smyth A.K. and James C.D. 2004. Characteristics of Australia's rangelands and key design features for monitoring biodiversity. Aust. Ecol. 29: 3–15.

Sol D., Timmermans S. and Lefebvre L. 2002. Behavioural flexibility and invasion success in birds. Anim. Behav. 63: 495–502.

Stephens P.A., Jules N.P. and Sutherland W.J. 2003. Agriculture, transport policy and landscape heterogeneity. Trends Ecol. Evol. 18: 555–556.

Suding K.N., Gross K.L. and Houseman G.R. 2004. Alternative stable states and positive feedbacks in restoration ecology. Trends Ecol. Evol. 19: 46–53.

Sutherland W.J., Pullin A.S., Dolman P.M. and Knight T.M. 2004. The need for evidence-based conservation. Trends Ecol. Evol. 19: 305–308.

Turpie J. 2004. The role of resource economics in the control of invasive alien plants in South Africa. S. Afr. J. Sci. 100: 87–93.

Vitousek P.M., d'Antonio C.M., Loope L.L. and Westbrooks R. 1996. Biological invasions as global environmental change. Am. Sci. 84: 468–478.

Wainger L.A. and Price E.W. 2004. Evaluating quality of life, economic vulnerabilities, and drivers of ecosystem change. Environ. Monitor. Assess. 94: 69–84.

Wallace J.F., Caccetta P.A. and Kiiveri T. 2004. Recent developments in analysis of spatial and temporal data for landscape qualities and monitoring. Aust. Ecol. 29: 100–107.

Warwick T. 1940. A contribution to the ecology of the musk-rat (*Ondatra zibethica*) in the British Isles. Proc. Zool. Soc. London, Ser. A 110: 165–201.

Watkinson A.R., Freckleton R.P., Robinson R.A. and Sutherland W.J. 2000. Predictions of biodiversity response to genetically modified herbicide-tolerant crops. Science 289: 1554–1557.

Watson I. and Novelly P. 2004. Making the biodiversity monitoring system sustainable: design issues for large-scale monitoring systems. Aust. Ecol. 29: 16–30.

Watson L. and Stokes A. 2004. Seahorses to Seaurchins. The Next Big Splash in Irish Aquaculture. Technical Report. Bord Iascaigh Mara Aquaculture Development Division, Irish Sea Fisheries Board, Ireland.

Wheeler Q.D. 2004. Taxonomic triage and the poverty of taxonomy. Phil. Trans. Roy. Soc. 359: 571–583.

Williamson M. 1989. Mathematical models of invasion. In: Drake J.A., Mooney H.A., di Castri F., Groves R.H., Kruger F.J., Rejmánek M. and Williamson M. (eds), Biological Invasions: A Global Perspective. John Wiley & Sons, Chichester, UK, pp. 329–350.

Williamson M. 1996. Biological Invasions. Chapman and Hall, London, UK.

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