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Dung beetle and terrestrial mammal diversity in forests, indigenous agroforestry systems and plantain monocultures in Talamanca, Costa Rica

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Abstract. In order to explore the importance of indigenous agroforestry systems for biodiversity conservation, we compared the abundance, species richness and diversity of dung beetles and terrestrial mammals across a gradient of different land use types from agricultural monocultures (plantains) to agroforestry systems (cocoa and banana) and forests in the BriBri and Cabécar indigenous reserves in Talamanca, Costa Rica. A total of 132,460 dung beetles of 52 species and 913 tracks of 27 terrestrial mammal species were registered. Dung beetle species richness and diversity were greatest in the forests, intermediate in the agroforestry systems and lowest in the plantain monocultures, while dung beetle abundance was greatest in the plantain monocultures. The number of mammal tracks per plot was significantly higher in forests than in plantain monocultures, whereas mammal species richness was higher in forests than in either cocoa agroforestry systems or plantain monocultures. Species composition of both terrestrial mammals and dung beetles also varied across the different land use types. Our study indicates that indigenous cocoa and banana agroforestry systems maintain an intermediate level of biodiversity (which is less than that of the original forest but significantly greater than that of plantain monocultures) and provide suitable habitat for a number of forest-dependent species. Although the agroforestry systems appear to serve as favorable habitats for many terrestrial mammal species, their potential positive contribution to mammal conservation is being offset by heavy hunting pressure in the reserves. As in other agricultural landscapes, the conservation of biodiversity in Talamanca will depend not only on maintaining the existing forest patches and reducing the conversion of traditional agroforestry systems to monocultures, but also on reducing hunting pressure.

Introduction

Much of the world's biodiversity occurs within tropical forests inhabited by indigenous people (Terborgh and Peres 2002; Colchester 2004). In Central America, the remaining forest areas coincide almost exactly with areas where indigenous people live, and many of the protected areas are inhabited or exploited by indigenous peoples for agriculture, hunting or other activities (Herlihy 1997). It is estimated that roughly 75 of Central America's approximately 240 protected areas are occupied or exploited by indigenous peoples, as are the five large Biosphere Reserves of Rio Platano, La Amistad, Darien, Maya and Sierra de las Minas (Herlihy 1997). Efforts to conserve biodiversity in Central America (and other areas in the tropics) must therefore work closely with indigenous people to promote sustainable land use systems that facilitate the conservation of biodiversity while enabling local communities to meet their livelihood needs and continue traditional practices (Colchester 2004).

A central issue in these conservation efforts is understanding how current patterns of land use by indigenous people affect biodiversity conservation within protected areas or indigenous reserves and using this information to develop strategies to mitigate the negative impacts of land use. In Central America, most indigenous groups practice agriculture, whether it be traditional cropping systems (such as shifting cultivation, polycultures or agroforestry systems) or more intensified agriculture (such as the production of crops in monocultures involving the use of fertilizers, pesticides and other agrochemicals). Collectively, these activities result in the reduction and fragmentation of the forest cover and the creation of complex mosaics of small agricultural plots, pastures, fallows, secondary growth and forests, in which the diversity and composition of the plant and animal communities is often dramatically modified. In addition, indigenous people often hunt wildlife species for subsistence and commerce, placing additional pressure on wildlife communities (Redford 1992; Escamilla et al. 2000).

The net impact of indigenous agriculture on biodiversity is likely to depend on the type of agricultural systems that replace forests, the management of these systems, and the extent and pattern of land conversion, among other factors (Pimentel et al. 1992; McNeely and Scherr 2003; Clay 2004; Donald 2004). For example, the replacement of forest habitat by land use systems that retain a dense and diverse canopy of shade trees (e.g. agroforestry systems) is likely to have a less negative impact on at least some components of biodiversity than the conversion of forests to land use types such as open pastures or crop monocultures, which dramatically simplify and modify the vegetative composition and structure (Estrada et al. 1993; Greenberg et al. 1997; Estrada et al. 1998; Schroth et al. 2004b). In general, agricultural systems with a high degree of floristic and structural complexity retain a greater proportion of the original biodiversity than monocultures, as they can offer a larger variety of habitats and resources for wildlife and may help maintain landscape connectivity (Moguel and Toledo 1999; Schroth et al. 2004c). Similarly, land use types that require little or no agrochemical inputs are likely to have a less deleterious impact on the biodiversity than those that use high pesticide, fertilizer and herbicide inputs which contaminate water and adversely affect native animal populations (Pfiffner and Niggli 1996; Fueller et al. 1998). Although there is a growing literature on the biodiversity present in different agricultural systems in tropical landscapes, relatively few studies have explicitly compared the biodiversity within traditional indigenous agroforestry systems to that of more modern, intensified production systems (but see chapters in Schroth et al.

2004a), making it difficult to assess the value of indigenous agroforestry systems for biodiversity conservation.

In the BriBri and Cabécar indigenous reserves of Talamanca, Costa Rica, the indigenous groups have traditionally cultivated cocoa (*Theobroma cocoa*) and bananas (*Musa* AAA) in small plots (generally less than 2 ha) under diverse and multi-strata agroforestry systems, interspersed within the matrix of agriculture and forests in varying stages of succession (Borge and Castillo 1997). Both cocoa and bananas are grown organically beneath a shade canopy of larger trees, though the density and diversity of shade varies across farms and systems, with cocoa generally having a more floristically diverse shade canopy than bananas (Guiracocha et al. 2001). In recent years, some farmers have begun abandoning the indigenous agroforestry systems and replacing them with plantain monocultures (*Musa* ABB spp.), in response to high prices and demand for this crop. In contrast to the shaded cocoa and banana systems, plantains are grown in open areas devoid of all tree cover and require high agrochemical input to increase soil fertility and combat diseases, insects and weeds (Borge and Castillo 1997). While it is thought that this conversion of the shaded agroforestry systems to plantain monocultures (and the concurrent loss of tree cover and increase in agrochemical use) is likely to have a negative impact on biodiversity at the local habitat scale, we are not aware of any studies that have examined the impact of this land use change either in Talamanca or elsewhere.

In order to explore the relative importance of indigenous cocoa and banana agroforestry systems for biodiversity conservation and the potential negative effect of the conversion of agroforestry systems to plantain monocultures, we characterized the biodiversity present in the four main land use types present in the indigenous reserves of Talamanca, Costa Rica. These land use types represented a gradient of decreasing floristic diversity and structural complexity, from forests to agroforestry systems (shaded cocoa and shaded banana) to intensive agriculture (plantain monocultures).

Our study focused on two groups of organisms (terrestrial mammals and dung beetles) that have been widely used as indicators of forest fragmentation and habitat disturbance due to their close relationships with forest cover and vegetative complexity. Dung beetles are highly sensitive to deforestation due to the accompanying changes in local microclimatic conditions, microhabitats and resource availability, and forest clearance and fragmentation have been reported to reduce both dung beetle species richness and abundance (Klein 1989; Gill 1991; Halffter and Favila 1993; Davis and Sutton 1998; Davis et al. 2001). Terrestrial mammal communities can also be negatively affected by habitat loss, fragmentation and isolation, primarily due to the loss of resources and habitats, the reduction of landscape connectivity and edge effects, with certain species becoming locally extinct or experiencing population declines in highly modified landscapes (Chiarello 2000; Laidlaw 2000; Lopes and Ferrari 2000). In addition to the fact that both dung beetles and terrestrial mammals are good indicators of changes in vegetation structure, these groups were also chosen because they can be sampled with relatively simple methods (pitfall traps for dung beetles, transects for terrestrial mammal tracks; Halffter and Favila 1993; Conroy and Nichols 1996; Carrillo et al. 2000); this was important for our study as all data were collected by trained indigenous farmers. Another reason for the study of terrestrial mammals was that they serve as important sources of food for indigenous peoples and therefore local farmers have considerable knowledge in track identification and mammal behavior (Gaudrain and Harvey 2003); in addition large mammals are the focus on many ongoing conservation efforts in the region (Palminteri et al. 1999). Finally, we used two very distinct taxa to determine whether individual taxa show the same patterns of diversity in land uses types within the same landscape.

To our knowledge, our study provides some of the first quantitative data on dung beetle and mammal communities in the Talamancan region, and one of the first comparisons across forest, indigenous cocoa and banana agroforestry systems and plantain monocultures of these groups. By comparing biodiversity across a spectrum of different land use types and by comparing patterns of diversity across two distinct taxa, our study contributes to the scientific basis for effective conservation planning across agricultural landscapes and helps fill the urgent need for information on the relative biodiversity conservation value of alternate agricultural systems (Daily et al. 2001; Donald 2004).

Study site and methods

The study was conducted in the BriBri and Cabécar Indigenous Reserves of Talamanca, which are part of the Talamanca and Síquirres municipalities, on the Atlantic coast of Costa Rica (9°00′–9°50′ N, 82°35′–83°05′ W). The region includes both tropical humid forest and premontane wet forest life zones (Tosi 1969). The average daily temperature is 25.8 °C, and the average annual precipitation is 2370 mm with a slight dry season during the months of March to April and September to October (Herrera 1985). All the study sites were located at between 63 and 480 masl, with the majority of the plots being located at around 130 masl.

The study included sites in eight BriBri communities (Watsi, Amubri, Cachabri, Shuap, Tsuiri, La Isla, Yorkin, Sepeque) and three Cabécar communities (San Vincente, San Miguel, Sibuju) and was conducted as part of a larger project entitled ‘‘Biodiversity conservation and sustainable production in indigenous organic cocoa small farms of the Talamanca–Caribbean corridor, Costa Rica’’. The BriBri and Cabécar communities include an estimated 6900 and 1400 inhabitants and cover 47,228 and 22,729 ha, respectively (Acuña 2002; EPYPSA and INCLAM 2003b). The reserves include roughly 20,000 ha of flat, alluvial soils where most of the population is concentrated and land is dedicated to farming. Farming is also practiced in the foothills up to 500 m. The indigenous farms within the region are typically small, with a mean total size of 10 ha (Somarriba et al. 2003). The landscape is a complex agricultural matrix, consisting of small agricultural plots (rice, beans, maize and plantains), cocoa and banana agroforestry systems and pastures interspersed with forest patches at various points in succession. Roughly 41% of the total reserve consists of old secondary forests and patches of remnants forests selectively logged over the last 100 years, however forest cover within the valley area is estimated to be less than 25% (Somarriba et al. 2003).

The Talamanca region is an area of high species richness, containing more than 10,000 species of plants, 215 species of mammals, 250 species of amphibians and reptiles, and 560 bird species (Borge and Castillo 1997). The indigenous reserves serve as buffer zones to the Parque Internacional La Amistad, Reserva Biologica Hitoy Cerere, Parque Nacional Cahuita, Refugio de Vida Silvestre Gandoca Manzanillo and the Kekoldi and Tayni indigenous territories, and form part of the Talamanca- Caribbean biological corridor, which is part of the larger Mesoamerican Biological Corridor. The region area is considered of critical importance to both local and regional biodiversity conservation efforts (Olson and Dinerstein 2002).

Land uses surveyed

We characterized dung beetle and mammal diversity in four land use types: forests, cocoa agroforestry systems, banana agroforestry systems and plantain monocultures. The main characteristics of each of these land use types are shown in Table 1. The forest sites studied were generally small remnants occurring within the agricultural landscape, which had been selectively logged in the past, but still retain an intact, closed canopy (although most of the large emergent canopy trees have been removed). Most forest patches are currently harvested for palm leaves and stems for housing, vines, poles, posts and other non-timber forest products. Cocoa agroforestry systems were small plots of organic cocoa (mean of 2.1 ha) grown under a variable shade canopy of remnant forest trees, naturally regenerated species such as *Cordia alliodora* or planted species, such as *Inga* species and several fruit tree species. Banana agroforestry systems were similarly small in size (mean of 1.1 ha) and organically cultivated, and typically had lower tree species richness but slightly higher tree densities than the cocoa agroforestry systems. In contrast, the plantains were cultivated as monocultures in small plots (mean area of 2.1 ha), without any shade, and produced with pesticides and other chemicals. Commonly applied agrochemicals include insecticides (containing Chlorpyrifos), nematicides (Terbufos, Oxamyl, Ethoprophos), fungicides (Propiconizole), and herbicides (Glyphosate, Paraquat; Beth Poliodoro, personal communication).

We selected a total of 59 plots, including 8 forest fragments, 36 cocoa agroforestry systems, 7 banana agroforestry systems, and 8 plantain monocultures. The large number of cocoa sites selected reflected the project's emphasis on cocoa agroforestry systems and a simultaneous detailed study of the vegetation structure and composition in these systems (Somarriba et al.

Table 1. Main characteristics of the four land use types studied in Talamanca, Costa Rica.

	High floristic and structural diversity	→ → →		Low floristic and structural diversity
Variable	Forest patches (n = 8)	Cocoa agroforestry systems (n = 36)	Banana agroforestry systems (n = 7)	Plantain Monocultures (n = 8)
Use of agrochemicals?	N/a	No (organic production)	No (organic production)	Yes (insecticides, nematicides, fungicides and herbicides)
Presence of tree shade canopy?	Yes	Yes	Yes	No (except for the occasional isolated tree)
Number of strata present	3–4	2–4	2–3	1–2
Most abundant tree species present within system	*Iriartea deltoidea, Pentaclethra macroloba, Poulsenia armata*	*Cordia alliodora, Spondias mombin, Nephelium lappaceum, Bactris gasipaes, Inga edulis*	*Cordia alliodora*	N/a
Mean number of trees (with d dbh >10 cm) $\pm$SE per 0.1 ha	78.5 ± 7.96 a	16.92 ± 1.11 c	28.0 ± 5.13 b	1.13 ± 0.88 d
Mean tree species richness $\pm$SE per 0.1 ha plot	41.38 ± 1.98 a	6.0 ± 0.60 b	8.57 ± 2.30 b	2.06 ± 1.43 c
Mean tree height $\pm$SE (m)	13.02 ± 0.93 b	19.0 ± 0.90 a	13.34 ± 1.73 b	2.06 ± 1.43 c
Mean tree dbh $\pm$SE (cm)	19.26 ± 1.25 b	28.66 ± 1.90 a	19.84 ± 2.44 b	6.63 ± 5.01 b
Mean size $\pm$SE of the individual land use types where mammal and dung beetle diversity was evaluated (ha)	11.54 ± 4.87 a	2.13 ± 0.13 b	1.13 ± 0.14 b	2.13 ± 0.43 b

Vegetation data are based on a parallel study (Somarriba et al., in preparation) within the 59 plots surveyed for mammal and dung beetle diversity. In this study, a 20×50 m temporary plot was established in each of the 59 plots, and all trees with dbh ≥10 cm were identified and measured. Small case letters indicate significant differences between habitat types ($p < 0.05$).

data in preparation). Plots were selected on the basis of their representativity of the chosen habitat type, a minimum size of 1 ha and the willingness of the owner to participate in the study.

Dung beetle characterization

In each of the 59 plots, dung beetles were surveyed using a grid of 25 pitfall traps, with 5 traps per row and rows spaced 10 m apart. Pitfall traps within a

Table 2. Summary of sampling effort for dung beetles and terrestrial mammals in the four habitats monitored in Talamanca, Costa Rica.

Variable	Forest	Cocoa agroforestry systems	Banana agroforestry systems	Plantain monocultures	Total
Sampling effort					
Number of plots	8	36	7	8	59
Dung beetles					
Number of pitfall traps placed monthly	200	900	175	200	1475
Total number of pitfall trap-days (during 14 months)	2800	12,600	2450	2800	20,650
Total number of individuals captured	20,003	64,040	19,458	28,985	132,460
Total number of species observed	43	48	39	30	52
Mammals					
Total length of transects surveyed for terrestrial mammal tracks per month (m)	800	3600	700	800	5900
Total length of transects surveyed during 13 months (m)	10,400	46,800	9100	10,400	76,700
Total of tracks registered	218	436	235	24	913
Total number of terrestrial mammal species registered	19	23	17	6	27

row were spaced at a distance of 10 m. Each pitfall trap consisted of a plastic cup buried in the soil, with its rim at soil level, covered by a wire mesh onto which a small portion of pig dung (roughly 100 g) was positioned. Each cup was filled with soapy water to prevent dung beetles from escaping the cup after falling into it. To prevent rain from washing out the contents of the pitfall traps, they were covered with a roof consisting of a plastic plate, balanced on 3-inch nails.

All pitfall traps were positioned and baited in the morning (before 8am) and were checked 24 h later for dung beetles. Each plot was sampled once a month, during a 14-month period (April 2002 to May 2003), with a total of 1475 traps (25 traps/site $\times$ 59 sites) being positioned each month. A summary of the sampling effort per habitat is found in Table 2. All dung beetles were conserved in a bottle with alcohol for later identification by Angel Solís, a dung beetle expert at InBio (Instituto Nacional de Biodiversidad San José).

Terrestrial mammals

To sample terrestrial mammals, we used the track transect method outlined by Carrillo et al. (2000). In the center of each plot, we established a 100 m $\times$ 1 m wide transect, on which the presence of mammal tracks was recorded. The total length of transects established across the 59 sites was 5900 m. Each transect was located in a humid portion of the plot (to facilitate the registration of tracks in the soil) and was manually prepared each month by clearing weeds and raking the soil to create a soft layer on which tracks could be recorded. During the dry months, transects were also watered to ensure a moist surface on which tracks could be recorded; however despite these efforts, some transects dried up during the dry periods and did not record tracks well. Each transect was monitored once a month, with tracks being prepared in the early morning (before 8 am) and examined 24 h later for tracks. Terrestrial mammals were sampled from April 2002 to May 2003 (14 months), but the first month was considered a pilot month (in which methods were refined), so data are only presented for 13 months (May 2002 to May 2003). A summary of the sampling effort per habitat can be found in Table 2. All tracks were identified and recorded, and their widths and lengths recorded (for later verification of species identification). When animal tracks were seen crossing a trail, we counted them as a single sighting. Similarly, if an animal's tracks followed a trail, we considered them as a single observation.

The conservation status of individual mammal species (threatened, reduced populations, or not threatened) follow that used by Daily et al. (2003) who classified mammal species in three categories: those highly sensitive to forest loss (forest specialists); those moderately sensitive to forest modification (which require forest but frequently range outside forest and do not depend on specific forest habitats); and those relatively insensitive to forest loss (species that use both natural and human-created habitats and are able to maintain their abundance in agricultural landscapes). This classification was done for 25 of the 27 mammal species recorded, as no information was available for the remaining two species (*Sciurus variegatoides* and *Sylvilagus brasiliensis*).

Participation of local people in biodiversity monitoring

All data were collected by the 59 indigenous landowners (or their relatives) where the plots were located. All farmers were rigorously trained in the construction and placement of pitfall traps, the establishment and maintenance of transects for observing animal tracks, and track identification (although most indigenous farmers already were very familiar with animal tracks due to their hunting traditions), and pilot studies were conducted in the field prior to the collection of the data reported here to ensure proper application of data collection methods. Data collection was closely supervised by the principal authors (CH, JG), and between 60 and 80% of all plots were visited by the principal authors each month to ensure correct data collection, and all possible efforts were made to remove any observer bias. The participation of local people enabled data to be collected simultaneously across the 59 plots, which would otherwise have been impossible due to the remote location and difficult access of these sites. At the same time, by including local farmers in the collection process, the monthly monitoring activity provided an important forum for discussing conservation issues and the impact of land use on conservation of biodiversity.

Data analysis

For the dung beetle data, the individual monthly data were combined to obtain a total species richness and abundance for each individual plot, and the Shannon diversity index was calculated per plot (Magurran 1988). Because sampling effort of dung beetles (25 pitfall traps $\times$ 14 months) was identical across the 59 plots studied, we compared dung beetle communities across the four types of land use using the total abundance, total species richness, and Shannon diversity index per plot. Differences in these variables across the four types of land use types were explored using one-way ANOVA's (for normally distributed data; followed by Tukey comparisons) or Kruskal Wallis nonparametric analyses. All data were tested for normality prior to analyses. To explore differences in abundance of individual dung beetle species across the four habitat types, individual Kruskal Wallis nonparametric analyses were conducted for individual species. These analyses were only performed for the dung beetle species that were sufficiently abundant for differences in habitat use to be determined (i.e. 30 species with more than 100 individuals recorded).

For the terrestrial mammal data, we combined the individual monthly data to obtain the total number of tracks registered during the 13 month period and total species richness per plot. The total number of tracks per site is an indicator of animal activity, but is not necessarily a good indicator of mammal abundance (as additional data obtained through line-transect sampling or other methods would be necessary to obtain actual abundance data; Carrillo et al. 2000). Therefore, the track data should be viewed as a proxy of mammal activity in each site. Differences in the total mammal species richness per plot and the number of mammal tracks per plot were compared using one-way ANOVA's (for normally distributed data; followed by Tukey comparisons) or Kruskal Wallis nonparametric analyses. All data were tested for normality prior to analyses.

The percent similarity in community composition among the 59 plots was calculated using the Sorenson similarity index (Magurran 1988), for both mammal and dung beetles separately. To distinguish between the species composition present in the four different habitat types, a cluster analysis (using Ward method and Euclidean distances) was conducted using the information of all 59 plots and a dendrogram was produced to facilitate the visualization of patterns of similarity across habitat types. All statistical analyses were conducted in InfoStats v 1.4.(Infostat 2004)

Results

Dung beetles

A total of 132,460 dung beetles of 52 species were captured during the 13 months of sampling (Appendix 1, Table 2). The dung beetle community was dominated by three species: *Canthon meridionalis* (28% of all beetles caught), *Onthophagus acuminatus* (23%), and *Canthon aequinoctialis* (16%) which together accounted for 67% of all of the beetles captured (Appendix 1). All three of these species were caught in all of the habitats surveyed and occurred in almost all of the plots surveyed. The abundance of individual species was highly variable, ranging from 1 individual to 36,981 individuals (mean of 2547 individuals ± 990 SE per species). Twenty species were rarely collected, with less than 100 individuals of these species being collected during the entire monitoring period. Of these, nine were represented by less than 10 individuals. Similarly, there was great variation in the frequency of individual species across the 59 plots (Appendix 1).

Differences across land use types

There were significant differences in the abundance, species richness and dung beetle diversity among habitats (Figure 1). Dung beetle species richness and diversity was greater in forests than in all other habitats; and dung beetle species richness and diversity was greater in the cocoa and banana agroforestry systems than in the plantain monocultures ($F_{3,55} = 8.26$, $p = 0.0001$ for species richness, $F_{3,\ 55} = 14.57$, $p < 0.0001$ for Shannon diversity). In contrast, dung beetle abundance was greater in plantain monocultures than in forests ($F_{3,55} = 4.49$, $p = 0.00069$), primarily due to the large numbers of a single species – *Canthon meridonalis* – within this habitat.

Although the overall similarity in species composition across land use types was quite high (with Sorenson similarity indices between pairs of habitats ranging from 0.75 to 0.98), there were some important differences. Of the 52 dung beetle species, 2 occurred only in forest, 15 occurred in forests and agroforestry systems, 4 occurred only in agroforestry systems, 5 occurred in agroforestry systems and plantain monocultures and 26 occurred in all habitat types. No species were unique to the plantain monocultures. Forest dung beetle communities were most similar to cocoa agroforestry systems (Sorenson similarity index of 0.98), followed by bananas (0.87) and plantain monocultures (0.75). Dung beetle communities in banana and cocoa agroforestry systems showed a Sorenson similarity index of 0.89. A cluster analysis of land use types based on the Ward method (using Euclidean distances) clearly separated the

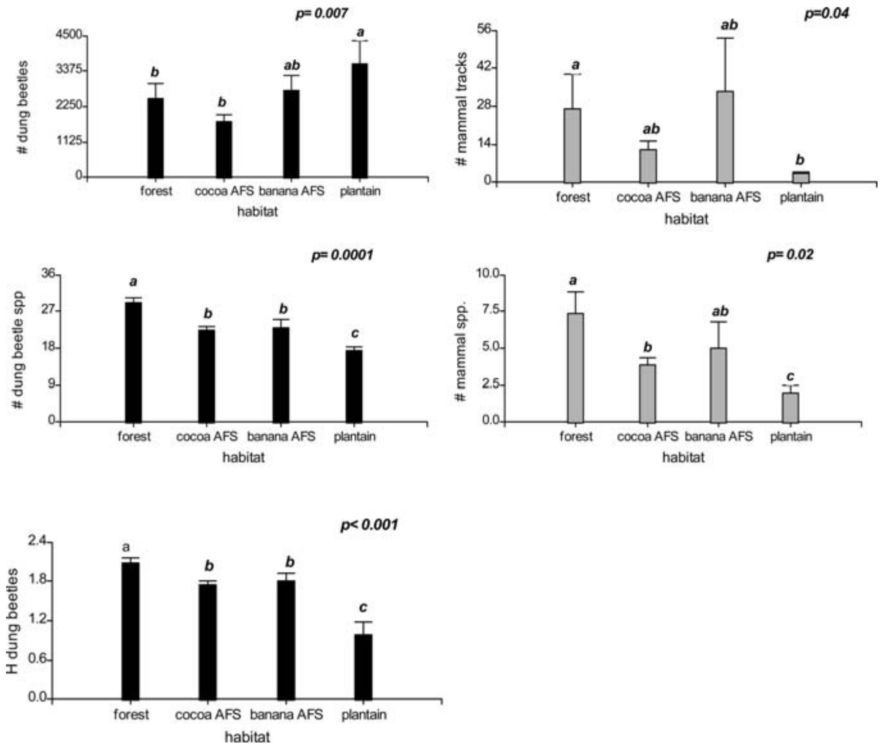

Figure 1. Abundance, species richness and diversity (Shannon) of dung beetles and terrestrial mammals in four land use types in Talamanca, Costa Rica. Data represent means and standard errors (forest $n = 8$, cocoa agroforestry systems $n = 36$, banana agroforestry systems $n = 7$, and plantain monocultures $n = 8$). Different letters indicate statistical differences across habitats based on ANOVA or Kruskal Wallis analyses.

agricultural habitats from the forest habitat; in addition, it separated the agroforestry land use types from the plantain monocultures (Figure 2a).

In all four land use types, only a handful of species accounted for the vast majority of dung beetles captured, however the dominant species present in each land use varied (Table 3). In the forest systems, two species accounted for 57.5% of all species collected, whereas in the cocoa agroforestry systems and banana agroforestry systems the top two species accounted for 50.3 and 51% respectively. In contrast, in the plantain monocultures, a single species – *Canthon meridionalis* – accounted for 78.9% of all captures. This species was also common in the cocoa and banana agroforestry systems but was present in very low numbers in the forests (representing only 0.5% of the beetles captured in forests).

A closer analysis of the species composition across the land use types showed that certain species had clear affinities to either the forest or the open agricultural habitat (plantain monocultures). Of the 32 dung beetle species with $n > 100$ individuals, 20 were more abundant in forests, seven were more

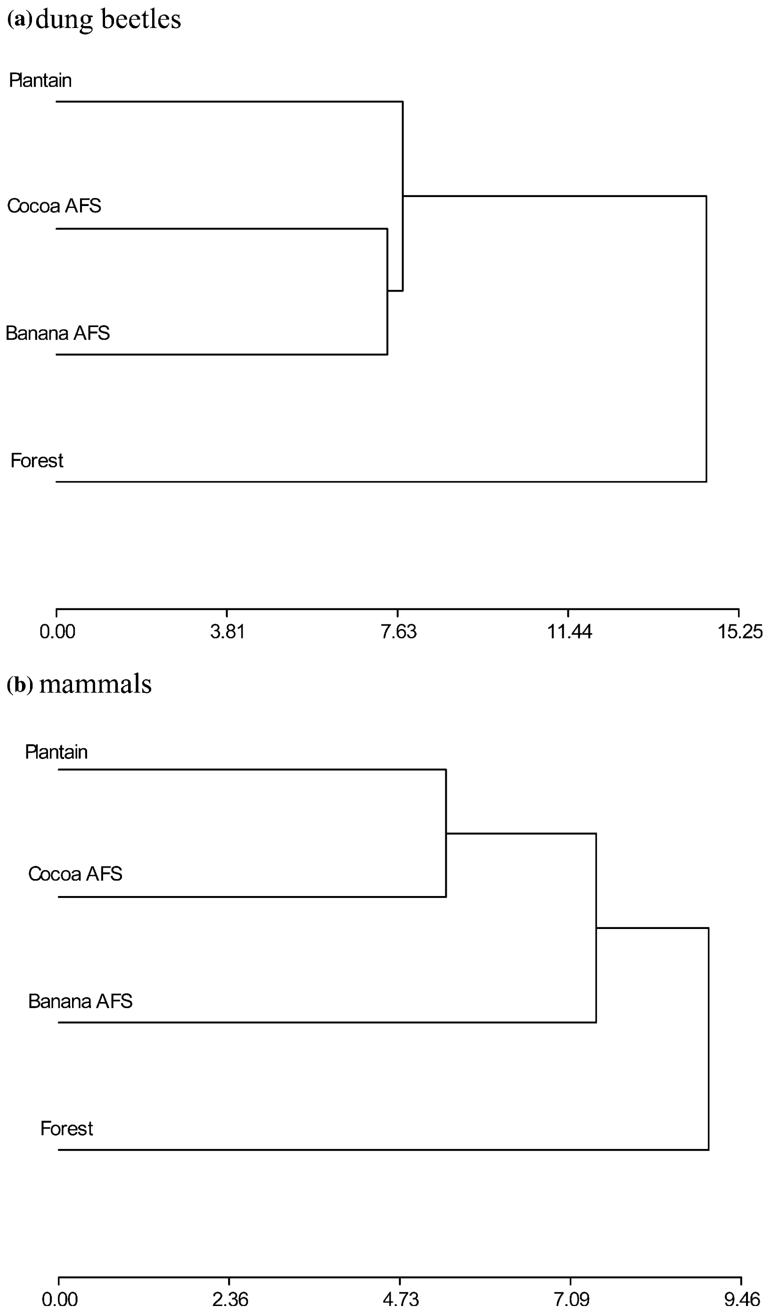

Figure 2. Cluster analysis based on Ward method and Euclidean distances of (a) dung beetle communities and (b) terrestrial mammal communities across agricultural, agroforestry and forest land use types in Talamanca, Costa Rica.

Table 3. Summary of the most abundant dung beetle species present in forest and agricultural systems in Talamanca, Costa Rica (in ranked order of abundance).

Rank	Forest (n = 20,003)		Cocoa agroforestry systems (n = 64,040)		Banana agroforestry systems (n = 19,458)		Plantain monocultures (n = 28,959)		Landscape (n = 132,460)	
	Species	%	Species	%	Species	%	Species	%	Species	%
1	*Canthon aequinoctialis*	31.7	*Onthophagus acuminatus*	29.5	*Canthon meridionalis*	31.1	*Canthon meridionalis*	78.9	*Canthon meridionalis*	27.9
2	*Onthophagus acuminatus*	25.8	*Canthon aequinoctialis*	20.8	*Onthophagus acuminatus*	19.9	*Onthophagus acuminatus*	9.3	*Onthophagus acuminatus*	23.1
3	*Dichotomius satanas*	8.0	*Canthon meridionalis*	12.5	*Canthon moniliatus*	18.4	*Dichotomius annae*	2.9	*Canthon aequinoctilis*	16.1
4	*Eurysternus plebejus*	4.5	*Canthon moniliatus*	7.9	*Canthon aequinoctialis*	7.6	*Onthophagus batesi*	2.6	*Canthon moniliatus*	6.9
5	*Eurysternus caribaeus*	3.6	*Eurysternus plebejus*	5.2	*Canthon cyanellus*	5.5	*Canthon cyanellus*	1.6	*Eurysternus mexicanus*	3.7

Data represent the % of all dung beetles caught in a given habitat.

abundant in the plantain monocultures, whereas the abundance of five species did not differ with land use type (Table 4). Among the 20 species that were most abundant in forests, it was possible to distinguish species with varying degrees of forest dependence. A total of six species can be considered the most forest dependent, as these species had high abundances only in the forest habitats (and much lower abundances in both the agroforestry systems and plantain monocultures). These species include *Canthidium haroldi*, *Copris incertus*, *Onthophagus nycotopus*, *Onthophagus stockwelli*, *Pedaridium pilosum* and *Scatimus erinnyos*. Twelve species showed a clear decrease in abundance from forested to agricultural habitats, with agroforestry systems having intermediate abundances. Finally, two species were equally abundant in forests and agroforestry systems but had present in lower numbers in plantain monocultures. The dung beetle species that were more abundant in agricultural landscapes included *Canthidium ardens*, *Canthon cyanellus*, *Canthon meridionalis*, *Canthon moniliatus*, *Dichotomius annae*, *Onthophagus batesi* and *Pseudocanthon perplexus*, and these species are likely indicators of habitat disturbance.

Terrestrial mammals

A total of 913 animal tracks of 27 species were recorded in the 59 plots (5900 m of transects), during the 13 months of monitoring (Table 2, Appendix 2). The most commonly registered tracks were those of the northern raccoon (*Procyon lotor)*, which represented 18% of all mammal tracks, the common opossum (*Didelphis marsupialis*; 15%), the nine-banded armadillo (*Dasypus novemcintus*, 15%) and the agouti (*Dasyprocta puntacta*, 12%). Of the 27 species recorded in the Talamancan landscape, 7 species were classified as being forest specialists of high conservation concern; 9 were classified as forest generalists being of moderate conservation concern, and 9 as species of low conservation concern (Appendix 2). An additional two species were not classified, as information for these species was not available in Daily et al. (2003).

There were significant differences in the mean abundance of tracks ($H = 8.21$, $p = 0.04$), and mean species richness of terrestrial mammals per plot ($H = 10.10$, $p = 0.02$) registered in the four land use types (Figure 2). The mean number of mammal tracks per plot was significantly greater in forest habitats than plantain monocultures, while agroforestry systems had intermediate values indistinguishable from either forests or plantain monocultures. Mean mammal species richness per plot was greater in forests than in either plantain monocultures or cocoa agroforestry systems, but did not differ from that found in banana agroforestry systems.

Mammal species composition also varied across habitats. Of the 27 mammal species, 2 were found only in forest habitats, 13 were found in both forest and agroforestry systems, 6 were found only in agroforestry systems, 2 were found in agroforestry and plantain habitats, and 4 were present in all four habitat types. No species were found uniquely in plantain monocultures. Forests

Table 4. Summary of dung beetle species (of those with $n > 100$ individuals) that showed significant differences in abundance across the four habitat types.

Habitat affinity	Species	n	Forest ($n = 8$)	Cocoa agroforestry systems ($n = 36$)	Banana agroforestry systems ($n = 7$)	Plantain monocultures ($n = 8$)	H (Kruskal Wallis)	p value
Species with highest degree of forest dependence (= highly abundant only in forest habitats)	*Canthidium haroldi*	131	14.25 a	0.47 b	0 b	0 b	7.56	< 0.0001
	Copris incertus	1,046	85.88 a	9.19 b	3.71 b	0.25 b	17.26	0.0003
	Onthophagus nyctopus	374	41.75 a	1.06 b	0.14 b	0.13 b	14.14	0.0002
	Onthophagus stockwelli	210	22.00 a	0.89 b	0.29 b	0.00 b	12.86	0.0008
	Pedaridium pilosum	124	5.5 a	2.03 b	0.71 b	0.25 b	11.29	0.0033
	Scatimus erinnyos	346	36.63 a	1.44 b	0.14 b	0 b	4.23	0.045
Species showing clear decline in abundance from forests to agroforestry systems to plantain monocultures	*Ateuchus candezei*	186	7.75 a	2.78 b	2.29 ab	1b	8.65	0.029
	Canthidium annagabrielae	122	5.38 a	2.19 b	0 c	0 c	20.27	< 0.0001
	Canthon aequinoctialis	21,261	791.5 a	369.67 ab	211.14 b	17.88 c	24.18	< 0.0001
	Deltochilum pseudoparile	129	2.25 a	3.06 a	0.14 ab	0 b	7.15	0.026
	Dichotomius favi	546	51.63 a	2.5 b	5.43 ab	0.63 b	13.69	0.0009
	Dichotomius satanas	2,994	199 a	38.19 b	3.71 bc	0.13 c	22.60	< 0.0001
	Eurysternus caribaeus	1,157	89.13 a	11.69 b	3.00 bc	0.25 c	20.45	< 0.0001
	Eurysternus foedus	205	11.5 a	2.69 b	2.29 bc	0.00 c	18.82	0.0002
	Onthophagus limonensis	2,614	65.38 a	50.78 a	34.43 ab	2.75 b	16.15	0.001
	Phanaeus pyrois	1,375	60.5 a	22.17 b	8.57 bc	4.13 c	18.34	0.0004
	Sulcophanaeus noctis	768	53.25 a	8.47 b	5.14 bc	0.13 c	21.4	< 0.0001
	Uroxys macrocularis	924	29.25 a	14.61 b	18.29 ab	4.5 b	10.22	0.016

Table 4. Continued.

Habitat affinity	Species	*n*	Forest ($n = 8$)	Cocoa agroforestry systems ($n = 36$)	Banana agroforestry systems ($n = 7$)	Plantain monocultures ($n = 8$)	H (Kruskal Wallis)	*p* value
Species equally abundant in forests and agroforestry systems, but less abundant in plantain monocultures	*Eurysternus plebejus*	4,627	111.63 a	93.06 a	50.00 a	4.25 b	17.70	0.0005
	Onthophagus coscineus	492	12.00 a	9.08 a	9.57 a	0.25 b	9.99	0.015
Species with higher abundances in the agricultural habitats	*Canthidium ardens*	773	0.5 b	11.31 a	21.86 a	26.13 a	9.96	0.014
	Canthon cyanellus	2,653	6.63 c	30.22 b	151.71 a	56.25 ab	19.34	0.0002
	Canthon meridionalis	36,981	13.00 c	221.78 b	865.29 a	2854.5 a	27.10	< 0.0001
	Canthon moniliatus	9,141	46.75 b	140.39 b	512.00 a	16.13 b	10.69	0.013
	Dichotomius annae	2,331	2.00 b	31.58 a	49.43 a	104.00 a	9.73	0.018
	Onthophagus batesi	4,182	5.63 b	73.08 a	105.86 a	95.63 a	17.27	0.0006
	Pseudocanthon perplexus	295	0.00 b	0.00 b	0.29 b	36.63 a	16.44	< 0.0001

Data represent means per habitat. Distinct letters in the same row indicate statistical differences across habitat types.

contained a total of 11 species that were classified as either of high or moderate conservation concern and these species accounted for 46.3% of the tracks registered. Cocoa agroforestry systems contained 13 species (33.7% of tracks) and banana agroforestry systems eight species (9.7% of tracks) of high or moderate concern. Plantain monocultures, in contrast, registered tracks of only one species of high conservation concern and no species of moderate conservation concern.

Sorenson similarity indices showed that overall similarity in mammal communities across land use types was highly variable, ranging from 0.35 to 0.91. Forests were the most similar to cocoa agroforestry systems (similarity index of 0.91), followed by banana agroforestry systems (0.73); forests and plantain monocultures had a similarity index of only 0.35. Cocoa and banana agroforestry systems had a similarity index of 0.74. A cluster analysis (using Ward method and Euclidean distances) showed a clear separation of the agricultural land use types from the forest, and further separated banana agroforestry systems from plantain monocultures and cocoa agroforestry systems (Figure 2b).

Discussion

General conservation value of the Talamancan landscape

Our study suggests that landscapes which include small-scale indigenous agroforestry systems embedded within a larger agricultural matrix can contain significant animal diversity and be important sites for biodiversity conservation. The dung beetle community found in Talamanca is very diverse (consisting of 52 spp.) and compares favorably to the species richness reported in intact Neotropical rain forests which range from 28 to 60 species (Klein 1989; Hanski and Cambefort 1991). The mammal community, in contrast, is less diverse than that recorded in intact tropical wet forests (with a total of 27 terrestrial mammals recorded, compared with between 29 and 76 species recorded in other neotropical forests; Medellin 1994) although it is likely that some additional species would be found if other complementary sampling methods were used. A disadvantage of the method used in this study is that transects inadequately register small animals and do not measure arboreal animals, so these species are likely to be missing from our surveys (Carrillo et al. 2000).

The considerable diversity within the Talamancan agricultural landscape is encouraging and illustrates the potential value of vegetatively diverse landscapes for conservation efforts. In doing so, it concurs with other recent studies that have similarly noted the potential role of neotropical agricultural landscapes to retain a rich pool of terrestrial mammals (Gallina et al. 1996; Daily et al. 2001), dung beetles (Estrada et al. 1998; Estrada and Coates-Estrada 2002), birds (Estrada et al. 1997; Estrada et al. 2000; Daily et al. 2001; Petit and

Petit 2003), bats (Estrada and Coates-Estrada 2001), and moths (Ricketts et al. 2001) – especially if these landscapes retain diverse and structurally complex vegetation – and strengthens the evidence and rationale for including agricultural landscapes in both local and regional conservation efforts.

Comparison of diversity across different land use types

There were important differences in the dung beetle and mammal biodiversity present in the agricultural, agroforestry and forest habitats, with a general pattern (across the two taxa) of high diversity in forests, intermediate to high levels in agroforestry systems and low diversity in the plantain monocultures. Differences were also evident in the species composition of dung beetle communities across the habitats, with forests being dominated by species with highest abundance in these habitats, plantain monocultures being dominated by open-habitat species and agroforestry systems having a mixture of both forest dependent and open habitat species. Cluster analyses (for both terrestrial mammals and dung beetles, separately) similarly showed a sharp division between forest and agricultural habitats, and in the case of dung beetles further separated the agricultural habitats into the shaded cocoa and banana agroforestry systems versus plantain monocultures. This pattern of decreasing diversity from forest to agroforestry systems to plantain monocultures closely follows a general gradient of diminishing vegetative diversity and increasing disturbance by human activity, and provides additional evidence that the conversion forest to other land use types modifies the animal communities present. At the same time, it suggests that the conversion to cocoa and banana agroforestry systems has a less negative impact on terrestrial mammal and dung beetle communities than conversion to plantain monocultures.

Conservation value of individual habitats

Of the four land use types studied, forest patches undoubtedly hold the greatest conservation value. Despite being small (mean of 11.5 ha) and subjected to periodic, small scale harvesting, the forest patches had the highest dung beetle diversity, registered the highest species richness per plot of both dung beetles and terrestrial mammals, registered the greater number of mammal tracks per plot and contained 11 terrestrial mammal species that are classified as either of high or moderate conservation concern including margays and ocelots (both of which are considered endangered by Costa Rican law) and two species – the collared peccary and the olingo – that were only registered in this habitat. In addition, most of the dung beetle species captured were closely associated with forests and showed higher abundances in this habitat. Together, these results suggest that forest fragments are key to retaining biodiversity within agricultural landscapes and support recent conclusions about the potentially high conservation value of small forest patches within modified landscapes (Schelhas and Greenberg 1996; Laurance and Bierregaard 1997; Daily et al. 2001; Matlock et al. 2002).

The indigenous cocoa and banana agroforestry systems were of intermediate conservation value, harboring less biodiversity than the original forest habitats, but much more than the plantain monocultures. The mean dung beetle species richness and diversity per plot in agroforestry systems were distinctly intermediate between the high forest levels and the low values in plantain monocultures, and dung beetle communities in agroforestry systems contained a mixture of both forest dependent species and species that can tolerate the open, disturbed agricultural areas, indicating that these systems represent a transition from forest to agriculture. The mean number of animal tracks within cocoa and banana agroforestry systems per plot was not significantly different from that of forests, but mean mammal species richness was less in cocoa plots than in forest plots (while banana plantations had similar mammal species richness to that of forests). The higher mean species richness of mammals in the banana agroforestry plots, relative to cocoa agroforestry plots, is likely due to the year-long availability of fruit within the banana agroforestry systems that attracts many terrestrial mammals (pers. obs.). Both agroforestry systems contained some forest-dependent species, but these accounted for a smaller proportion of the tracks registered than in forests (33.7% of tracks in cocoa and 9.8% in banana were of forest-dependent species compared to 46.3% in forests).

The relatively high diversity of both dung beetles and terrestrial mammals within the cocoa and banana agroforestry systems probably reflects their dense and diverse tree canopies (which provide fruits and other resources), their small size and proximity to forest, and their organic cultivation. Although the vegetation in cocoa and banana agroforestry systems is less dense and diverse than that of forest patches, the overall vegetative structure is quite similar to that of forests, with similar canopy heights, trees of varying diameters and several strata (Guiracocha et al. 2001). The presence of a few large remnant trees within some of the cocoa and banana agroforestry systems creates a forest-like habitat which may functionally extend forest cover across the agricultural landscape, thereby potentially enhancing the size and quality of the remaining forest cover, providing landscape connectivity for some species and potentially minimizing edge effects between forests and surrounding agroecosystems, as has been reported in other studies of biodiversity in cocoa agroforestry systems (Johns 1999; Parrish et al. 1999; Reitsma et al. 2001). However, although our study illustrates that many dung beetle and mammal species are using cocoa and banana agroforestry systems, additional data are required to determine whether or not these systems can sustain viable populations over the long term, and to what degree those organisms within the agroforestry systems still depend on adjacent forest patches.

The relatively high diversity within agroforestry systems is also possibly due to their small size and the high degree of forest cover surrounding them. It is estimated that roughly 25% of the landscape within the lower Talamancan valley is still under forest in varying degrees of succession and most of the agroforestry systems studied occur within several hundred meters of small forest patches and several kilometers from larger forest expanses (EPYPSA and INCLAM 2003a, b). This proximity to forest is likely beneficial for many organisms that visit and use agroforestry systems, but require forest for part of their life cycle (Rice and Greenberg 2000). Other studies have similarly reported that cocoa agroforestry systems close to natural forest or occurring in landscapes with high forest cover may have a greater diversity of forest birds, mammals and insects than those occurring in areas with little remaining forest (Alves 1990; Estrada et al. 1993; Estrada et al. 1994; Young 1994). The small size of the agroforestry systems (< 2 ha) and wide distribution in the landscape also means that the overall landscape scale effect of these systems is considerably less than if these systems were large and contiguous. In Mexico, Medellin and Equihua (1998) similarly found that small isolated corn fields less than 3 hectares in size and embedded in a large forest matrix had mammal communities as rich as the adjacent forests, presumably because forest cover and resources were nearby. The organic production and low management intensity of both cocoa and banana may also account for the relatively high diversity levels within the agroforestry systems. Last, in the case of dung beetles, the presence of both wild and domestic animals (mainly pigs) in the landscape appears to ensure an ample supply of dung for dung beetle communities.

In contrast to the forest and agroforestry habitats, plantain monocultures hold little, if any, value for biodiversity conservation, despite being located in an agricultural matrix with abundant forest cover. Plantain fields consistently had lower species richness and diversity than both forest and agroforestry habitats, hosting a total of only 30 dung beetle species (compared to 39–43 species in the other habitats) and registered only 6 mammal species (compared to 17–23 species in the other habitats). Although dung beetle abundance was highest in plantain monocultures (relative to the other habitats), a single species – *Canthon meridionalis* – dominated the dung beetle community accounting for > 78% of all dung beetle captured. This species is clearly favored by the conditions present within or adjacent to plantain monocultures and our results indicate that it could be considered an indicator of habitat disturbance. The low diversity of both terrestrial mammals and dung beetles within plantain monocultures probably reflects the combination of the highly modified vegetative structure and diversity, the lack of resources and habitats for forest-dependent species, the greatly modified microclimatic conditions, and the use of pesticides and other chemicals.

Mammal populations within the Talamancan indigenous reserves

In addition to highlighting differences across the four land use types, our study also provided clear evidence that mammal populations within the Talamanca indigenous reserve are very low. Despite monthly surveys of animal tracks in almost 6 km of prepared transects during 13 months of surveying, a total of only 27 species were recorded and only 913 registers obtained. In addition, few large mammal tracks were registered, even in the forest patches. Several species which should occur in the reserve (for example, white lipped peccaries, pumas and tapirs) were never registered during the 13-month study.

The low abundance and lack of large mammals in the Talamancan forests may in part reflect the effect of habitat disturbance and forest fragmentation, as has been noted in other forests subjected to habitat disturbance (Newmark 1991; Chiarello 1999; Laidlaw 2000). Large carnivores and herbivores require large, continuous areas of forest (Bodmer 1995; Laidlaw 2000), and it is possible that the agricultural matrix in lower Talamanca is too fragmented and disturbed to support these species. However, as noted earlier, the forest canopy across the agricultural matrix is fairly continuous (with the exception of the openings created for plantain monocultures), and both habitats and resources for terrestrial mammals appear plentiful. In fact, species that can feed on cocoa and banana fruits may even encounter increased food availability within the agroforestry patches, and benefit from their presence, as was found for mammal populations in abandoned polyculture agricultural plots in Mexico within a forest matrix (Medellin and Equihua 1998), but at the same time, the animals expose themselves to greater risk of being hunted.

A more likely explanation of the low mammal abundances and the lack of large animals registered is the high hunting pressure within the reserve. Although hunting is officially illegal within the reserves, both indigenous people and outsiders (who enter the reserve illegally) regularly hunt large birds and mammal for subsistence, pest control and (in the case of outsiders) sport. While it is difficult to document the intensity and frequency of hunting within the reserve (due to its illicit nature and the unwillingness of hunters to disclose capture rates), surveys indicate that indigenous people hunt and consume at least 33 animal species, mainly terrestrial mammals and large bird species, with the most commonly hunted mammal species including agoutis, pacas, rabbits, raccoons, armadillos, peccaries and squirrels (Guiracocha et al. 2001; Gaudrain and Harvey 2003), and it is common knowledge among the indigenous communities that hunting levels are unsustainable. The Talamancan landscape therefore appears to be a classic example of an 'empty forest' (Redford 1992; Robinson and Bennett 2000), having a seemingly diverse and structurally complex forest and agroforestry vegetation that has been emptied of its large mammal species by hunting.

Conservation implications

By providing basic information on dung beetle and mammal communities within the Talamancan reserves and comparing the relative impact of different land use types on these two taxa, our study serves as a useful basis for conservation planning and management within the reserves and provides a baseline against which future studies can be compared. Although there were slight differences in the terrestrial mammal and dung beetle data, the overall patterns were similar and point to similar conservation recommendations.

Three main conservation lessons arise from our work. First, efforts to conserve biodiversity within the Talamancan landscape should give highest priority to retaining and conserving all existing forest patches (irrespective of their small size) within the agricultural landscape, as these patches have the most diverse animal communities and harbor the greatest number of forest dependent species. Second, conservation organizations should recognize the important role of the indigenous cocoa and banana agroforestry systems as conservation tools in areas where forest has already been converted to agriculture, and work with indigenous communities to stop the current conversion of cocoa and banana agroforestry systems to plantain monocultures which have little, if any, conservation value. Finally, high priority must also be given to seeking ways of reducing hunting pressure within the reserve so that mammal populations can recover. If hunting is not discouraged, all efforts to conserve mammal populations through other means (e.g. forest conservation, maintenance of sufficient habitat, resources and landscape connectivity, restriction of the expansion of plantain monocultures, etc.) are likely to be unsuccessful. As in other human-dominated landscapes, the conservation of biodiversity within the agricultural landscape of Talamanca will depend not only on the presence of sufficient forest cover, habitats and resources for wildlife, but also on the careful regulation of human impact on these communities.

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Appendix 1. Total number of individuals captured in pitfall traps in four habitat types and overall in Talamanca, Costa Rica, organized by order of abundance.

Species	Forest (n = 8)	Cocoa agroforestry systems (n = 36)	Banana agroforestry systems (n = 7)	Plantain (n = 8)	Total	% of total dung beetles collected	Frequency (Number of plots of 59 total where encountered)
Canthon meridionalis	104	7,984	6,057	22,836	36,981	27.92	55
Onthophagus acuminatus	5,152	18,897	3,864	2,675	30,588	23.09	59
Canthon aequinoctialis	6,332	13,308	1,478	143	21,261	16.05	59
Canthon moniliatus	374	5,054	3,584	129	9,141	6.90	52
Eurysternus mexicanus	466	3,092	935	370	4,863	3.67	59
Eurysternus plebejus	893	3,350	350	34	4,627	3.49	57
Onthophagus batesi	45	2,631	741	765	4,182	3.16	56
Dichotomius satanas	1,592	1,375	26	1	2,994	2.26	38
Canthon cyanellus	53	1,088	1,062	450	2,653	2.00	49
Onthophagus limonensis	523	1,828	241	22	2,614	1.97	52
Dichotomius annae	16	1,137	346	832	2,331	1.76	40
Phanaeus pyrois	484	798	60	33	1,375	1.04	58
Eurysternus caribaeus	713	421	21	2	1,157	0.87	37
Copris incertus	687	331	26	2	1,046	0.79	33
Uroxys macrocularis	234	526	128	36	924	0.70	50
Canthidium ardens	4	407	153	209	773	0.58	35
Sulcophanaeus noctis	426	305	36	1	768	0.58	37
Dichotomius favi	413	90	38	5	546	0.41	26
Onthophagus coscineus	96	327	67	2	492	0.37	39
Onthophagus nyctopus	334	38	1	1	374	0.28	20
Scatimus erinnyos	293	52	1	0	346	0.26	13

Appendix 1. Continued.

Species	Forest ($n = 8$)	Cocoa agroforestry systems ($n = 36$)	Banana agroforestry systems ($n = 7$)	Plantain ($n = 8$)	Total	% of total dung beetles collected	Frequency (Number of plots of 59 total where encountered)
Pseudocanthon perplexus	0	0	2	293	295	0.22	9
Copris laeviceps	6	104	98	31	239	0.18	21
Onthophagus stockwelli	176	32	2	0	210	0.16	23
Eurysternus foedus	92	97	16	0	205	0.15	36
Ateuchus candezei	62	100	16	8	186	0.14	40
Canthidium haroldi	114	17	0	0	131	0.10	7
Deltochilum pseudoparile	18	110	1	0	129	0.10	23
Pedaridium pilosum	44	73	5	2	124	0.09	26
Canthidium annagabrielae	43	79	0	0	122	0.09	30
Canthidium aurifex	0	115	1	1	117	0.09	9
Onthophagus marginicollis	3	42	41	18	104	0.08	30
Uroxys platypyga	74	17	0	0	91	0.07	17
Uroxys microcularis	0	37	17	31	85	0.06	13
Coprophanaeus telamom	0	42	10	15	67	0.05	18
Onthophagus praecellens	13	42	0	0	55	0.04	6
Canthidium centrale	3	31	16	2	52	0.04	20
Megathoposoma candezei	40	3	0	0	43	0.03	6
Canthidium vespertinum	15	22	5	0	42	0.03	22
Coprophanaeus kohlmanni	32	8	1	0	41	0.03	13
Onthophagus tapirus	2	17	9	10	38	0.03	18
Canthon subhyalinus	18	3	0	0	21	0.02	9
Deltochilum gibbosum	10	2	0	0	12	0.01	8

Canthon silvaticus	0	3	1	0	4	0.00	4
Canthon angustatus	1	1	1	0	3	0.00	3
Onthophagus pseudodi	1	1	0	0	2	0.00	2
Ateuchus solisi	1	0	0	0	1	0.00	1
Canthidium hespenheidei	0	1	0	0	1	0.00	1
Oxysternon silenus	1	0	0	0	1	0.00	1
Pedaridium bottimeri	0	1	0	0	1	0.00	1
Phanaeus beltianus	0	0	1	0	1	0.00	1
Uroxys gorgon	0	1	0	0	1	0.00	1
Total number of dung beetles	20,003	64,040	19,458	28,959	132,460	100.00	
Total number of spp.	43	48	39	30	52		

Note differences in sampling effort across habitat types. Numbers in parentheses indicate the number of plots per habitat type.

Appendix 2. Summary of the total number of terrestrial mammal tracks reported in each habitat, during the 13 months of monitoring (in order of abundance).

Scientific name	Local name	Vulnerability class (*sensu* Daily et al. 2003)	Forests (n = 8)	Cocoa agroforestry systems (n = 36)	Banana agroforestry systems (n = 7)	Plantain monocultures (n = 8)	Total	% of total	Frequency (Number of plots of 59 total where encountered)
Procyon lotor	Northern raccoon	low	25	67	66	5	163	17.85	31
Didelphis marsupialis	Common Opossum	low	16	63	50	7	136	14.90	32
Dasypus novemcintus	Nine-banded armadillo	low	51	39	45	0	135	14.79	20
Dasyprocta punctata	Agouti	moderate	37	65	4	0	106	11.61	21
Sylvilagus brasiliensis	Forest rabbit	n/a	7	27	25	5	64	7.01	20
Agouti paca	Paca	moderate	20	32	6	0	58	6.35	17
Conepatus semistriatus	Common striped Hog-nosed skunk	low	7	21	17	3	48	5.26	17
Philander opossum	Gray four-eyed opossum	low	0	26	4	2	32	3.50	11
Sciurus variegatoides	Variegated squirrel	n/a	9	16	0	0	25	2.74	10
Leopardus pardalis	Ocelot	moderate	10	11	2	0	23	2.52	10
Sciurus granatensis	Red-tailed squirrel	low	1	13	0	0	14	1.53	5
Mazama americana	Red brocket deer	moderate	9	4	0	0	13	1.42	8
Tamandua mexicana	Collared anteater	moderate	5	6	2	0	13	1.42	6
Leopardus wiedii	Margay	high	7	3	0	0	10	1.10	3
Caluromys derbianus	Central American woolly opossum	low	0	9	1	0	10	1.10	5
Allouatta palliata	Howler monkey	high	0	9	0	0	9	0.99	1
Eira barbara	Tayra	moderate	2	4	3	0	9	0.99	6
Marmosa mexicana	Mexican mouse opossum	low	0	8	1	0	9	0.99	2

Odocoileus virginianus	White-tailed deer	high	0	4	4	0	8	0.88	4
Gallictis vittata	Greater grison	high	0	4	1	2	7	0.77	6
Nasua narica	White-nosed coati	moderate	3	3	0	0	6	0.66	5
Mustela frenata	Long-tailed weasel	low	1	0	3	0	4	0.44	2
Bassariscus gabbii	Olingo	high	3	0	0	0	3	0.33	1
Tayassu tajacu	Collared peccary	moderate	3	0	0	0	3	0.33	2
Chironectes minimus	Water opossum	high	2	1	0	0	3	0.33	3
Potos flavus	Kinkajou	moderate	0	1	0	0	1	0.11	1
Lontra longicaudis	Neotropical river otter	High	0	0	1	0	1	0.11	1
Total number of mammals			218	436	235	24	913	100.00	31
Total number of species			19	23	17	6	27		32

The total represents the total number of times the animal tracks were reported. Data are organized in terms of decreasing abundance.

References

Acuña K. 2002. Producción y comercialización de cacao en Alta Talamanca: una propuesta de periodización socio-productiva. Tesis Lic.Escuela de Antropología y Sociología, UCR San Jose Costa Rica.

Alves M.C. 1990. The role of cocoa plantations in the conservation of the Atlantic Forest of Southern Bahia, Brazil. Ms. Thesis, University of Florida, Gainesville, Florida.

Bodmer R.E. 1995. Managing Amazonian wildlife: biological correlates of game choice by detribalized hunters. Ecol. Appl. 5: 872–877.

Borge C. and Castillo R. 1997. Cultura y conservación en la Talamanca indígena. Editorial Universidad Estatal a Distancia (UNED), San José, Costa Rica, pp. 261

Carrillo E., Wong G. and Cuarón A.D. 2000. Monitoring mammal populations in Costa Rican protected areas under different hunting restrictions. Conserv. Biol. 14: 1580–1591.

Chiarello G. 1999. Effects of fragmentation of the Atlantic forest in mammals communities in South-Eastern Brazil. Biol. Conserv. 87: 71–82.

Chiarello G. 2000. Density and population size of mammals in remnants of Brazilian Atlantic Forest. Conserv. Biol. 14: 1649–1657.

Clay J. 2004. World Agriculture and Environment: A Commodity-by-Commodity Guide to Impacts and Practices. Island Press, pp. 570

Colchester M. 2004. Conservation policy and indigenous peoples. Environ. Sci. policy 7: 145–153.

Conroy M. and Nichols D. 1996. Designing a study to assess mammalian diversity. In: Wilson D., Cole R., Nichols J., Rudran R. and Foster M. (Eds.), Measuring and Monitoring Biological Diversity. Standard Methods for Mammals. Smithsonian Institution Press, United Kingdom, pp. 41–49.

Daily G.C., Ehrlich P.R. and Sanchez-Azofeifa G.A. 2001. Countryside biogeography: use of human dominated habitats by the avifauna of southern Costa Rica. Ecol. Appl. 11: 1–13.

Daily G.C., Ceballos G., Pacheco J., Suzan G. and Sanchez-Azofeifa A. 2003. Countryside biogeography of neotropical mammals: conservation opportunities in agricultural landscapes of Costa Rica. Conserv. Biol. 17: 1814–1826.

Davis A.J., Holloway J.D., Huijbregts H., Krikken J., Kirk-Spriggs A.H. and Sutton S.L. 2001. Dung beetles as indicators of change in the forests of northern Borneo. J. Appl. Ecol. 38: 593–616.

Davis A.J. and Sutton S.L. 1998. The effects of rainforest canopy loss on arboreal dung beetles in Borneo: implications for the measurement of biodiversity in derived tropical ecosystems. Diver. Distrib. 4: 167–173.

Donald P.F. 2004. Biodiversity impacts of some agricultural commodity production systems. Conserv. Biol. 18: 17–37.

EPYPSA and INCLAM 2003a. Estrategia regional de desarrollo sostenible de la cuenca binacional del Rio Sixaola. IIP/BID/Ministerio de Economía y Finanzas de Panamá. Aspectos biofísicos Vol. 1, pp. 272

EPYPSA and INCLAM 2003b. Estrategia regional de desarrollo sostenible de la cuenca binacional del Rio Sixaola. IIP/BID/Ministerio de Economía y Finanzas de Panamá. Información análisis y diagnósticos: aspectos socioeconómicos Vol. 1, pp. 292

Escamilla A., Sanvincente M., Sosa M. and Galindo Leal C. 2000. Habitat mosaic, wildlife availability and hunting in the Tropical Forest of Calakmul, México. Conserv. Biol. 14: 1592–1601.

Estrada A., Coates-Estrada R., Meritt D.Jr., Montiel S. and Curiel D. 1993. Patterns of frugivore species richness and abundance in forest islands and in agricultural habitats at Los Tuxtlas, Mexico. Vegetatio 107(108): 245–257.

Estrada A., Coates-Estrada R. and Merritt D.A. 1994. Non-flying mammals and landscape changes in the tropical rain forest region of Los Tuxtlas, Mexico. Ecography 17: 229–241.

Estrada A., Coates-Estrada R. and Merritt D.A. 1997. Anthropogenic landscape changes and avian diversity at Los Tuxtlas, Mexico. Biodiv. Conserv. 6: 19–42.

Estrada A., Coates-Estrada R., Anzures A. and Cammarano P.L. 1998. Dung and carrion beetles in tropical rain forest fragments and agricultural habitats at Los Tuxtlas, Mexico. J. Trop. Ecol. 14: 577–593.

Estrada A., Cammarano P.L. and Coates-Estrada R. 2000. Bird species richness in vegetation fences and in strips of residual rain forest vegetation at Los Tuxtlas, Mexico. Biodiv. Conserv. 9: 1399–1416.

Estrada A. and Coates-Estrada R. 2001. Bat species richness in live fences and in corridors of residual rain forest vegetation at Los Tuxtlas, Mexico. Ecography 24: 94–102.

Estrada A. and Coates-Estrada R. 2002. Dung beetles in continuous forest, forest fragments and in an agricultural mosaic habitat island at Los Tuxtlas, Mexico. Biodiv. Conserv. 11: 1903–1918.

Faria D., Laps R.R., Baumgarten J. and Cetra M. 2005. Bat and bird assemblages from forests and shade cacao plantations in two contrasting landscapes in the Atlantic Forest of southern Bahia, Brazil. Biodiv. Conserv. 15: 587–612.

Fueller R., Gregory R., Gibbons D., Marchant J., Wilson J., Ballie S. and Carter N. 1998. Population declines and range contractions among lowland farmland birds in Britain. Conserv. Biol. 12: 1425–1441.

Gallina S., Mandujano S. and Gonzalez-Romero A. 1996. Conservation of mammalian biodiversity in coffee plantations of Central Veracruz, Mexico. Agroforestry Syst. 33: 13–27.

Gaudrain C. and Harvey C.A. 2003. Caza y diversidad faunística en paisajes fragmentados del territorio indígena BriBri de Talamanca, Costa Rica. Agroforestería en las Américas 8: 46–51.

Gill B.D. 1991. Dung beetles in tropical American forests. In: Hanski I. and Cambefort Y. (eds), Dung Beetle Ecology. Princeton University Press, New Jersey, pp. 211–229.

Greenberg R., Bichier P., Cruz Angon A. and Reitsma R. 1997. Bird populations in shade and sun coffee plantations in Central Guatemala. Conserv. Biol. 11: 448–459.

Guiracochoa G., Harvey C., Somarriba E., Krauss U. and Carrillo E. 2001. Conservación de la biodiversidad en sistemas agroforestales con cacao y banano en Talamanca, Costa Rica. Agroforestería en las Américas 8: 7–11.

Halffter G. and Favila M.E. 1993. The Scarabaeinae (Insecta: Coleoptera), an animal group for analyzing, inventorying and monitoring biodiversity in tropical rain forest and modified landscapes. Biol. Int. 36: 3–17.

Hanski I. and Cambefort Y. 1991. Dung Beetle Ecology. Princeton University Press, Princenton, New Jersey.

Herlihy P.H. 1997. Central American Indian peoples and lands today. In: Coates A.G. (eds), Central America: A Natural and Cultural History. Yale University Press, New Haven, pp. 215–240.

Herrera W. 1985. Vegetación y clima de Costa Rica. EUNED, San Jose, pp. 118

InfoStat 2004. InfoStat versión1.4.. Grupo InfoStat, FCA, Universidad Nacional de Córdoba, Argentina.

Johns N.D. 1999. Conservation in Brazil's chocolate forest: the unlikely persistence of the traditional cocoa agroecosystem. Environ. Manage. 23: 31–47.

Klein B.C. 1989. Effects of forest fragmentation on dung and carrion beetle communities in central Amazonia. Ecology 70: 1715–1725.

Laidlaw R.K. 2000. Effects of habitat disturbance and protected areas on mammals of peninsular Malaysia. Conserv. Biol. 14: 1639–1648.

Laurance W. and Bierregaard R.O. 1997. Tropical Forest Remnants: Ecology, Management and Conservation of Fragmented Communities. University of Chicago Press, pp. 616

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.

Magurran A.E. 1988. Ecological Diversity and its Measurement. Princeton University Press, Princeton New Jersey, pp. 179

Matlock R.B.Jr., Rogers D., Edwards P.J. and Martin S.G. 2002. Avian communities in forests fragments and reforestation areas associated with banana plantations in Costa Rica. Agric. Ecosyst. Environ. 91: 199–215.

Medellin R.A. 1994. Mammal diversity and conservation in the Selva Lacandona, Chiapas, Mexico. Conserv. Biol. 8: 788–799.

Medellin R.A. and Equihua M. 1998. Mammal species richness and habitat use in rainforest and abandoned agricultural fields in Chiapas, Mexico. J. Appl. Ecol. 35: 13–23.

McNeely J.A. and Scherr S.J. 2003. Agriculture and wild biodiversity. In: McNeely J.A. and Scherr S.J. (eds), Ecoagriculture Strategies to Feed the World and Save Wild Biodiversity. Island Press, pp. 51–85.

Moguel P. and Toledo V.M. 1999. Biodiversity conservation in traditional coffee systems of Mexico. Conserv. Biol. 13: 11–21.

Newmark W.D. 1991. Tropical forest fragmentation and the local extinction of understory birds in the eastern Usambara Mountains, Tanzania. Conserv. Biol. 5: 67–78.

Olson D.M. and Dinerstein E. 2002. The global 200: priority ecoregions for global conservation. Annuals of the Missouri Botanical Garden 89: 199–224.

Palminteri S., Powell, G., Fernandez G. and Tovar D. 1999. Talamanca Montane-Isthmian Pacific Ecoregion-based Conservation Plan: Preliminary Reconnaissance Phase. Tropical Science Center, San Jose, Costa Rica.

Parrish J., Reitsma R. and Greenberg R. 1999. Cocoa as crop and conservation tool: lessons from the Talamanca region of Costa Rica. http://nationalzoo.si.edu/ConservationAndScience/MigratoryBirds/Research/Cocoa/parrish.cfm.

Petit D. and Petit L. 2003. Evaluating the importance of human-modified lands for neotropical bird conservation. Conserv. Biol. 17: 687–694.

Pfiffner L. and Niggli U. 1996. Effects of bio-dynamic, organic and conventional farming on ground beetles and other epigeic arthropods in winter wheat. Biol. Agric. Hortic. 12: 353–364.

Pimentel D., Stachow F., Takacs D., Brubaker H., Dumas A., Meaney J., O'Neil J., Onsi D. and Corzilius D. 1992. Conserving biological diversity in agricultural/forestry systems. Bioscience 42: 354–362.

Redford K.H. 1992. The empty forest. BioScience 42: 412–422.

Reitsma R., Parrish J.D. and McLarney W. 2001. The role of cocoa plantations in maintaining forest avian diversity in southeastern Costa Rica. Agroforestry Syst. 53: 185–193.

Rice A. and Greenberg R. 2000. Cocoa cultivation and the conservation of biological diversity. Ambio 29: 167–173.

Ricketts T.H., Daily G.C., Ehrlich P.R. and Fay J.P. 2001. Countryside biogeography of moths in a fragmented landscape: biodiversity in native and agricultural habitats. Conserv. Biol. 15: 378–388.

Robinson J.G. and Bennett E.L. 2000. Hunting for Sustainability in Tropical Forests. Columbia University Press, pp. 582

Schelhas J. and Greenberg R. 1996. Forest Patches in Tropical Landscapes. Island Press, Washington, DC, pp. 426

Schroth G., Fonseca G.A.B., Harvey C.A., Gascon C., Vasconcelos H.L. and Izac A.M.N. 2004a. Biodiversity Conservation in Tropical Landscapes – What Role for Agroforestry?. In: Schroth G., Fonseca G.A.B., Harvey C.A., Gascon C., Vasconcelos H.L. and Izac A.M.N. (eds), in Agroforestry and Biodiversity Conservation in Tropical Landscapes. Island Press, Washington, DC, pp. 1–14.

Schroth G., da Fonseca G.A.B., Harvey C.A., Gascon C., Vasoncelos H.L., Izac A.M.N., Angelsen R., Finegan B., Kaimowitz D., Krauss U., Laurance S.G.W., Laurance W.F., Nasi R., Naughton-Treves L., Niesten E., Richardson D.M., Somarriba E., Tucker N.I.J., Vincent G. and Wilkie D.S. 2004b. In: Schroth G., Fonseca G.A.B., Harvey C.A., Gascon C., Vasconcelos H.L. and Izac A.M.N. (eds), Agroforestry and Biodiversity Conservation in Tropical Landscapes. Island Press, Washington, DC, pp. 487–502.

Schroth, G., da Fonseca B.A., Harvey C.A., Gascon C., Vasoncelos H.L., Izac R.A.M.N., Angelsen R., Finegan B., Kaimowitz D., Krauss U., Laurance S.G.W., Laurance W.F., Nasi R., Naughton-Treves L., Niesten E., Richardson D.M., Somarriba E., Tucker N.I.J., Vincent G. and Wilkie D.S. 2004c. Agroforestry and biodiversity conservation in tropical landscapes. In:

Schroth G., Fonseca G.A.B., Harvey C.A., Gascon C., Vasconcelos H.L. and Izac A.M.N. (eds), In Agroforestry and Biodiversity Conservation in Tropical Landscapes. Island Press, Washington, DC, pp. 487–502.

Somarriba E., Trivelato M., Villalobos M., Suárez A., Benavides P., Morán K., Orozco L. and López A. 2003. Diagnóstico agroforestal de pequeñas fincas cacoteras orgánicas de indígenas Bri-Bri y Cabécar de Talamanca, Costa Rica. Agroforestería en las Américas 10: 24–30.

Terborgh J. and Peres C.A. 2002. The problem of people in parks. In: Terborgh J., van Schaik C., Davenport L. and Rao M. (eds), Making Parks Work: Strategies for Preserving Tropical Nature. Island Press, Washington, pp. 307–319.

Tosi J.A. 1969. Republica de Costa Rica: mapa ecológico según la clasificación de zonas de vida de L.R. Holdridge. Centro Científico Tropical, San José, Costa Rica.

Young A.M. 1994. A Chocolate Tree: A Natural History of Cocoa. Smithsonian Institution Press, Washington, DC, pp. 200