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RESEARCH ARTICLE

Linkages beyond borders: targeting spatial processes in fragmented urban landscapes

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Abstract Management of ecosystems often focuses on specific species chosen for their habitat demand, public appeal, or levels of threat. We propose a complementary framework for choosing focal species, the mobile link concept, which allows managers to focus on spatial processes and deal with multi-scale ecological dynamics. Spatial processes are important for three reasons: maintenance, re-organization, and restoration of ecological values. We illustrate the framework with a case study of the Eurasian Jay, a mobile link species of importance for the oak forest regeneration in the Stockholm National Urban Park, Sweden, and its surroundings. The case study concludes with a conceptual model for how the framework can be applied in management. The model is based on a review of published data complemented with a seed predation experiment and mapping of Jay territories to reduce the risk of applying non-urban site-specific information in an urban setting. Our case study shows that the mobile link approach has several advantages: (1) Reducing the vulnerability of ecological functions to disturbances and fluctuations in resources allocated to management, (2) Reducing management costs by maintaining natural processes, and (3) Maintaining gene flow and genetic diversity at a landscape level. We argue that management that includes mobile link organisms is an important step towards the prevention of ecosystem degradation and biodiversity loss in increasingly fragmented landscapes. Identifying and managing mobile links is a way to align management with the ecologically relevant scales in any landscape.

Keywords Ecological functions · Connectivity · Dispersal · Ecosystem management · Mobile links · Urban ecology

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Introduction

Current recommendations for biodiversity conservation highlight the need to conserve dynamic, multi-scale ecological patterns and processes that sustain the full complement of biota and their supporting natural systems (Poiani et al. 2000). However, conservation efforts have often concentrated on preserving single patches and threatened species rather than the processes underlying and upholding ecological values in heterogeneous landscapes. This article describes how important ecosystem processes can be targeted by giving attention to and managing populations of certain species. We focus on cities since urban green areas are often characterized by a high degree of isolation within a heterogeneous, highly human-modified urban landscape (e.g. Grimm et al. 2000; Pickett et al. 2001). Finding management solutions in such an environment can perhaps help us prepare for an increasingly human-dominated world. Research has revealed that the ability of urban green areas to support biodiversity and ecosystem functions over time depends on their degree of habitat connectivity and matrix permeability (Recher and Serventy 1991; Drayton and Primack 1996; Chapin et al. 1997; Harris and Reed 2002). Drayton and Primack (1996) showed that isolation caused even a large urban park to lose 25% of its plant diversity over a period of 100 years. Apart from preventing local extinctions from occurring, habitat connectivity maintains vital biological interactions, e.g. plant-pollinator and plant-seed disperser interactions (e.g. Cox et al. 1991; Steffan-Dewenter and Tscharntke 1999; Lundberg and Moberg 2003). Furthermore, within cities, management often suffers from a mismatch between administrative boundaries and ecosystem “boundaries” (spatial scales of ecological processes). Administrative boundaries frequently dictate quite different land uses and managers, and can create sharp borders across open ecosystems (Meffe et al. 2002). Fragmentation and administrative boundaries also tend to favor management of single patches or at least small and isolated units, often with little communication between managers of neighboring areas.

Biological diversity, and functional diversity in particular, is essential to maintain complex ecosystems (Chapin et al. 1997) that provide us with a number of ecosystem services, e.g. food, clean water, human health and well-being, recreational and educational values, as well as pollination and seed dispersal (Daily 1997; Chiesura 2004). All ecosystems are shaped by processes and factors acting at different spatial and temporal scales, and if the system is to be understood, these processes must be identified (Gunderson and Holling 2002). In this article we focus on spatial processes, here exemplified with seed dispersal. Spatial processes are important for three reasons: maintenance, re-organization, and restoration of ecological values.

We will describe a complementary management framework that links populations to ecosystem processes and services on a landscape level. Focus on a single or a few species has been successfully used since it is easier to unite management efforts and public interest around a single target than a more holistic and thereby often less concrete approach to ecosystem management (see e.g. Meffe et al. 2002). Over the last 15 years, several frameworks for identifying species most suitable for management efforts have been discussed, including keystone species (e.g. Simberloff 1998), indicator species, flagship species, umbrella species (e.g. Caro and O’Doherty 1999; Simberloff 1998) and focal species (Lambeck 1997). These frameworks are not exclusive and individual species may fit into more than one.

However, we suggest that an integration of ecosystem ecology and landscape ecology could produce a better understanding of landscape dynamics, especially in fragmented, heterogeneous landscapes, and therefore offer a basis for improved management. This integration is realized here through the concept of mobile link species, which have been defined by Lundberg and Moberg (2003) as organisms supporting essential ecosystem functions by connecting either two different types of patches or two similar patch types with some kind of “barrier” between them. Mobile links can be responsible for substantial nutrient relocation (e.g. Murphy 1981; Polis et al. 1997); linking systems genetically through seeds or pollen transport (Cox et al. 1991; Nabhan and Buchmann 1997); providing or supporting essential process such as grazing, pest control, or influencing the physicochemical environments (e.g. Carpenter 1986; Naiman et al. 1988). The role of mobile links is perhaps most apparent during the re-organization phase following disturbance, when they provide ecological memory by linking the disturbed site to undisturbed source areas (Nyström and Folke 2001; Elmqvist et al. 2002). It has also been shown that spatial processes, such as seed dispersal, can facilitate ecological restoration in urban areas (Robinson and Handel 1993; Robinson and Handel 2000). Hence, mobile links are an important part of the “natural insurance capital” when we face uncertain futures in constantly changing environments (Folke et al. 1996).

We illustrate this framework, and its implications, through a case study of the Eurasian Jay (*Garrulus glandarius*), a mobile link species of importance for the oak forest (mainly *Quercus robur* and some *Q. petrea*) regeneration in the Stockholm National Urban Park, Sweden, and its surroundings. Oaks are regarded as a keystone species for the maintenance of biodiversity as they host up to 1,500 other species (Hultengren et al. 1997). The oak is also central for upholding recreational values (Bråvander and Jacobson 2006). Human activities have fragmented the oak forests and left the oak population vulnerable to deleterious effects of reduced gene flows, if the linkages between areas would be cut. The oak populations in the National Urban Park is internationally significant since oak forests, mainly due to epidemic oak disease, have seriously declined over wide areas of Europe during the past two decades (Führer 1998). We conclude the case study with a simple model of how to apply the framework in management. The interaction between Jays and oaks is well documented and we base our model on information synthesized from the literature, complemented by two field studies to avoid the risk of applying potentially site-specific information from non-urban environments.

In this study we addressed the following two questions: (1) How can processes be managed through a focus on specific organisms? (2) What are the potential administrative and economical benefits of management of mobile link species in fragmented landscapes?

Case study

The case study is based on secondary data (literature review and GIS) complemented by field surveys of predation on acorns exposed on the ground and of Jay numbers and habitat preferences.

Study site

Stockholm County covers a land area of 6,500 km^2, divided into 26 municipalities, with a population of nearly 2 million people. The green areas are in many cases functionally connected but spatially and administratively fragmented. Each municipal government is in charge of its respective conservation planning and green area management, and regional strategies are usually absent. The Stockholm National Urban Park is a landscape with high natural and cultural values that covers 27 km^2. It is located adjacent to the inner city of Stockholm, Sweden (59°20′N, 18°05′E) (Fig. 1). Size and land use history makes the National Urban Park, like many other old and large parks, a suitable habitat for many species with specific habitat requirements (see Elmqvist et al. 2004). It is characterized by large areas of wooded grasslands and deciduous forests, where old oak trees are a dominant feature. Compared to the park, surrounding green areas have less oak and more coniferous forest. There are also lakes, residential areas, royal palaces and gardens,

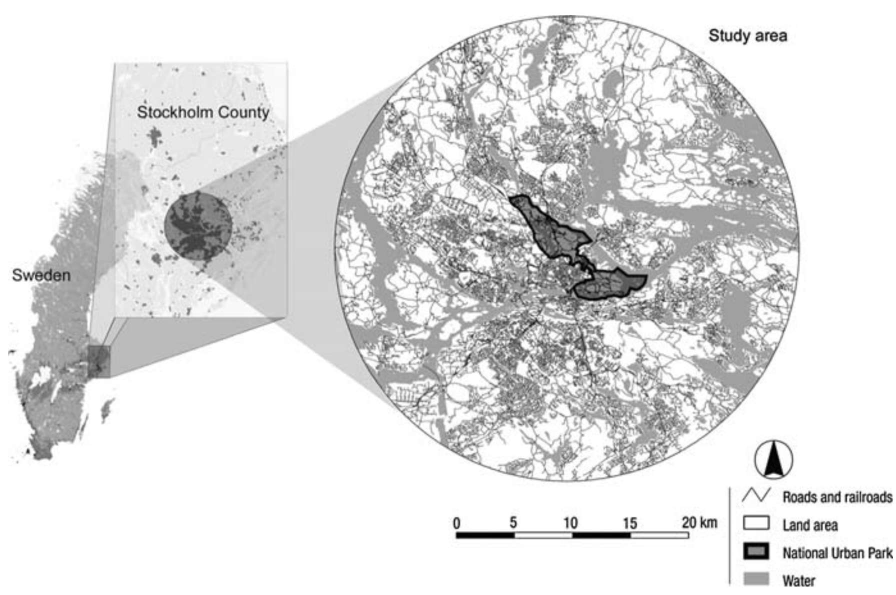

Fig. 1 Study area: The Stockholm National Urban Park and the Stockholm metropolitan area. The park area encompasses 27 km^2 and is located in the centre of the capital of Sweden

museums, a university campus, and roads within the park, which is today one of the most prominent public recreation areas in Sweden. The park is partitioned by three municipalities and shares common borders with another four. During the 1970s and 80s eight and seven percent, respectively, of the Stockholm County's green areas were lost due to urban development (The County Administrative Board of Stockholm 1996, public communications). Despite legal protection of the park in 1995, urban expansion continues to apply pressure on the park's fringe areas and numerous different building schemes within or in direct connection to the park are currently planned.

Literature review

Over the last 16,000 years, following the glacial retreat from northern North America and Europe, nut-bearing trees have undergone rapid changes in their distributions and the current dispersers of nuts (i.e. squirrels, Jays and other corvids) appear to have been responsible for these shifts (Vander Wall 2001). Although many of the acorns dispersed by Jays are moved only a short distance (Gómez 2003), the Jays are also capable of transporting acorns over long distances. According to Mosandl (pers. comm.), Jays are responsible for regeneration of oaks in a pine forest in Eastern Germany where the distance to fruit bearing oaks exceeded 200 m. Long-distance dispersal of the acorns from holm oaks (*Q. ilex*) in South East Spain was also found to depend on the Jay's pattern of movement (Gómez 2003). Thus, we assume that the same patterns also holds true in Sweden. Apart from the Jay, the yellow-necked mouse (*Apodemus flavicollis*) and wood mouse (*A. sylvaticus*) can be of importance for oak dispersal (Jensen and Nielsen 1986; Frost 1997). However, as the mice carry acorns for shorter distances only (Jensen and Nielsen 1986), their importance as mobile links is limited to a much smaller spatial scale (Ouden et al. 2005). Furthermore, the red squirrel (*Sciurus vulgaris*) is a potential disperser (Wauters and Casale 1996), but, as with the mice, the effect that squirrels can have on the dispersal of oaks is likely to be on a smaller spatial scale. Thus, mice and squirrels may play an important role for oak renewal within, and near, the oak stands in the National Urban Park, but not for dispersal among separated green areas.

The importance of long distance seed dispersal has been known for some time (e.g. Darwin 1859; Ridley 1930), but only recently has its extensive implications for population dynamics been appreciated (e.g. Cain et al. 2000; Levin et al. 2003). It has been suggested that dispersal by Jays has several qualities that enhance regeneration and successful establishment of oaks (Bossema 1979): (a) Advantageous selection of acorns. (b) Reduced predation, due to dispersal and burying. (c) Favorable placement. A single Jay can store 4,500–11,000 acorns per year, and fly up to 18 km in order to find a sufficiently abundant source of acorns (Cramp 1994; Clayton et al. 1996). Acorns are carried from the mother tree to a suitable cache-spot, often located within the bird's breeding territory (Bossema 1979). Andrén (1992) found that the density of Jays was higher in relation to forest as the size of forest fragments decreased, as long as the forest fragments were larger than 20 ha. The average number of oak seedlings originating from dispersed acorns has been estimated to be 54 per hectare (Frost 1997) and the number of oaks may range from 500 to 2,000 oaks per ha (Frost 1997; Mosandl and Kleinert 1998).

Materials and methods

Acorn removal assessment

We used 36 octagonal experimental plots with a radius of 10 m to reduce the risk of disturbances affecting whole plots. In each octagon nine piles of ten acorns per pile were placed. Three octagons were set up in each of three survey sites located in four habitat types: oak forest, coniferous forest, open grassland (more than 20 m from an edge), and edge grassland (starting less than a meter from a forest edge). The acorns were placed in sites that had rather similar landscape contexts. Acorns used in the experiment were collected from within a 9 km^2 radius around the study plots and a total of 3,240 acorns were used. The experiment started in October 2001, and the plots were monitored in December 2001 and then in February and April 2002 and the number of acorns removed recorded. The removal rates were calculated as percentages and were arcsine transformed before analysis.

Mapping of Jay territories

Four study sites of approximately 1 km^2 each were chosen among the less built-up areas of the park. Each site was visited once a week, for a 10-week period, starting in the second week of April 2002. The methodology was adapted from the standard territory mapping technique described in Svensson (1975) to include only Jays. A visit lasted for 3–4 h and was spent walking through the area. The fieldwork was carried out in the morning, between 07.00 and 12.00 h. All parts of the area were passed within 100 m, though the precise route taken through an area varied from one visit to another.

Territory delineation was made by identifying clusters of observations (from different visits), i.e. less than 200 m (see Svensson 1975). Only resident Jays were of interest and to exclude observations of non-resident Jays a potential territory needed observations from at least three different visits to be accepted as a real territory. Neighboring observation clusters (less than 200 m between) were distinguished as two separate territories if Jays were observed in both territories during the same visit, at a minimum of two different occasions. There was one exception from these general rules: if a nest or recently fledged juveniles were found in an area it was counted as part of a territory regardless of other observations. Habitat preferences were estimated in an existing ArcView-GIS database (described in Lövenhaft and Ihse 1998) by creating buffer zones with a radius of 100 m around every observation point belonging to that territory and then measuring the relative amount of different forest habitats within these zones. This is a rough estimate for comparisons with findings from other studies and will not yield the exact habitat preferences. The distribution of Jay observations between different forest habitats were tested against a hypothesized even distribution (equal to the habitat composition within the study areas) with a χ^2-analysis.

Results

Acorn predation rates

The rate of acorn removal at the December census was significantly different among habitats (ANOVA $F_{3.312} = 24.1$, $P < 0.001$) being higher in the coniferous forest habitats compared to the other habitats (Tukey, $P < 0.05$) (Fig. 2a). At the last census in February/April (after snow melt) the difference among habitats was significant (ANOVA, $F_{3.312} = 58.2$, $P < 0.001$) with removal rates close to 100% in both oak and coniferous habitats (Fig. 2b). The removal rates in open and edge grassland habitats were close to 40% and no significant difference between these two habitat types was recorded (Tukey, $P > 0.05$).

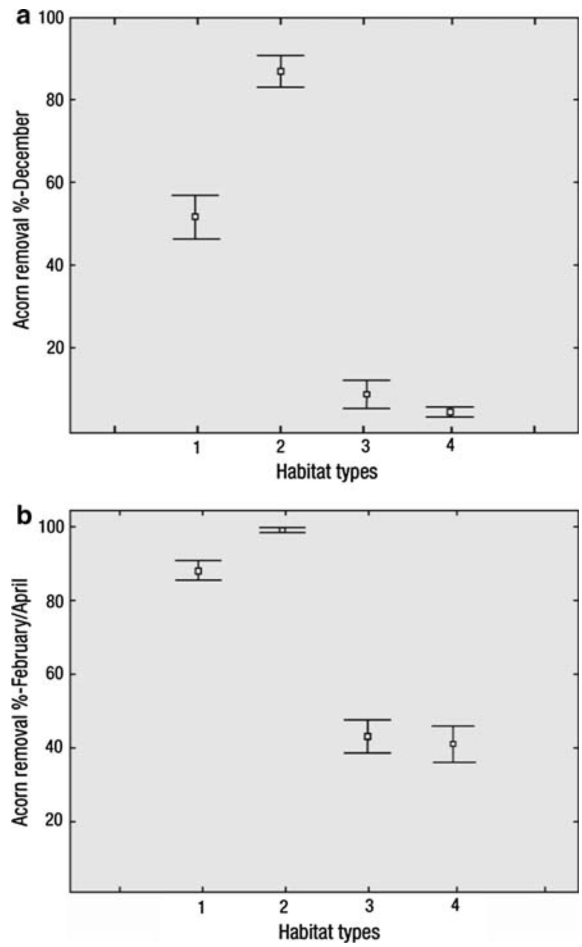

Fig. 2 Percent acorns removed in experimental plots in four different habitat types, 1: oak forest, 2: coniferous forest, 3: edge grassland, 4: open grassland. (**a**) December records, (**b**) February (April) records. Experiment started in October 2001. Mean ± SE given

Jay territories

A total of 10 territories were found. Of 88 Jay observations made, 65 belonged to territories. The observations of territorial Jays had a distribution different from a hypothesized random distribution ($\chi^2 = 25.75$, df = 6, $P < 0.001$). Two habitat types, coniferous forest and mixed forest, were used more often than expected 38.5–21.8% and 27.7–14.8%, respectively. Broad-leaved deciduous forest was used less than expected, 27.7% compared to 43.8%. The habitat use varied greatly between different territories. Based on habitat availability and average territory size the total number of birds in the National Urban Park was estimated to be 42 breeding pairs, or slightly more than five pairs per km^2 forest.

Discussion

Jay-oak interactions in the National Urban Park

Natural regeneration rates of *Quercus* spp. are often low, with a number of factors such as the quantity and quality of acorn production and heavy predation on acorns, contributing to low regeneration rates (Lof et al. 1998). According to the literature, the fragmented nature and high predation pressure on acorns in the National Urban Park of Stockholm suggests that the natural regeneration capacity of the oak dominated landscape is strongly dependent on the Jay for acorn dispersal. The lack of other effective inter-patch acorn dispersers makes the oak dominated landscape fragile. The predation experiment indicates that post-dispersal predation rates are high, particularly in forest habitats. Although removal is not necessarily tantamount to consumption, we observed enough traces of on-site consumption to indicate that most of the removals were indeed due to predation. Other studies have also found post-dispersal predation to be close to 100% on exposed acorns in pastures and deciduous forests (e.g. Frost 1997). Zipperer et al. (1997) suggest that urban landscapes have a higher abundance of seed predators than rural landscapes, influencing the distribution and persistence of plant species. In urban oak populations, animal mediated dispersal and seed caching may thus be more crucial for regeneration than in rural oak populations. The high predation rates in both oak- and coniferous forest indicate a low potential survival of passively dispersed acorns, especially if physical factors such as drought, removal, and freezing are considered. Our results also suggest an overall avoidance of open areas by seed predators.

Jays were seen in all forest habitats in the National Urban Park but preferred coniferous forest, which agrees with a detailed population study of Jays in South Central Sweden (Andrén 1990). Despite being strongly arboreal, the Jay may not count as an interior species; Andrén (1992) found that the density of Jays is actually higher in relation to forest as the size of forest fragments decreases, as long as the forest fragments are larger than 20 ha. Our results seem to support Andrén's since the number of birds per km^2 forest in the National City Park was higher than the density in boreal forests estimated by Lundberg et al. (1980). Breeding success has been shown to be positively related to the amount of coniferous forest, which can be explained by three principal factors: nest concealment, food supply, and predation on adults (Andrén 1990). Hence, in order to protect Jays, coniferous stands, particularly of spruce (*Picea abies*) areas need to be properly managed and protected. We do not claim that the Jay alone would preserve the oak forests as they are today—they are a product of the long history of human management—but the Jays will ensure the presence of new cohorts of oaks in the future landscape.

While it is of course possible that humans could take full responsibility for the regeneration of oaks in an urban landscape we suggest that the seed-dispersal ecosystem service provided by the Jay has the following advantages over artificial plantation:

(1) Oaks lack long-term seed dormancy and artificial seed storage will not be sufficient to buffer against large-scale disturbances since acorns do not survive storage for more than 1 year (Bergquist and Isacsson 2002). Jays disperse acorns continuously, thus spreading them in time as well as space reducing the risk of losing all acorns to any singular, stochastic event like a pest outbreak. Continuous dispersal is advantageous if local population experience cyclic or chaotic environments (Holt and McPeek 1996).

(2) The service provided by the Jays is free. Although affected by urban sprawl and fragmentation, it is independent of the shifting goals and policies of conservation management. The cost for humans to take care of the plantation of oaks may be affordable in limited areas such as the National Urban Park, but would rise swiftly in larger areas (Hougner et al. 2006).

(3) Genetic diversity is one important aspect of ecosystem resilience and fragmentation of tree populations may have deleterious effects due to reduced gene flow (Bacles et al. 2006). Jays form linkages between areas and create a "genetic network", i.e. combining several different gene pools into one larger, more diverse pool with a dynamic exchange between nodes (cf. Hanski and Gilpin 1991). Recently it was shown that, at least for some temperate large woody species, seed dispersal is much more effective than pollen dispersal in maintaining genetic connectivity between patches (Bacles et al. 2006).

Conceptual model

Based on the result from the literature review and field experiments we have developed a comprehensible model for how the Jay-oak interaction works and how it can be managed. The approach described below has great potential for adaptive co-management (see for example Holling 1978; Gunderson et al. 1995) since it has a single unifying target, bridges administrative borders and is relatively easy to monitor and evaluate.

The landscape view of source and sink areas (Pulliam 1988; Dunning et al. 1992) and the species specific perception of the landscape (e.g. Dunning et al. 1992; Taylor et al. 1993; Farina and Belgrano 2004; Farina and Belgrano 2006) might be valuable for the understanding of Jay movements. The National Urban Park with its high proportion of oak trees is the main source for acorn dispersal in the area. A prerequisite for this dynamic to work is that the areas of low acorn production can provide the Jays with suitable breeding habitats. Thus acorn transportation will take place between different types of resource patches needed by the Jay, and the intensity will likely depend on difference in acorn production and the distance and type of land between the different patches. A simple model can be built to show how important spatial processes can be managed through a focus on a single species and its life history characteristics (see Fig. 3). Jays may fly up to 18 km to collect acorns and several sources suggest that the birds frequently cover distances up to 4 km (Cramp and references therein 1994). Areas within 100 m from acorn-bearing oaks are in this case of less interest because other organisms can carry acorns over these distances (Jensen and Nielsen 1986; Wauters and Casale 1996; Frost 1997; Ouden et al. 2005). Thus dispersal requires patches of suitable breeding territories within 4 km from the oaks in the NUP large enough to house a sufficient number of Jays to make the transportation of acorns meet the demand of new oak trees. Calculations based on the minimum area of suitable habitat and average seedling density show that one pair of Jays might contribute with 1,080 seedlings per year.‘

Based on knowledge of these basic conditions management can be shaped to explicitly target the maintenance of the oak-dominated landscape. We suggest the following procedure:

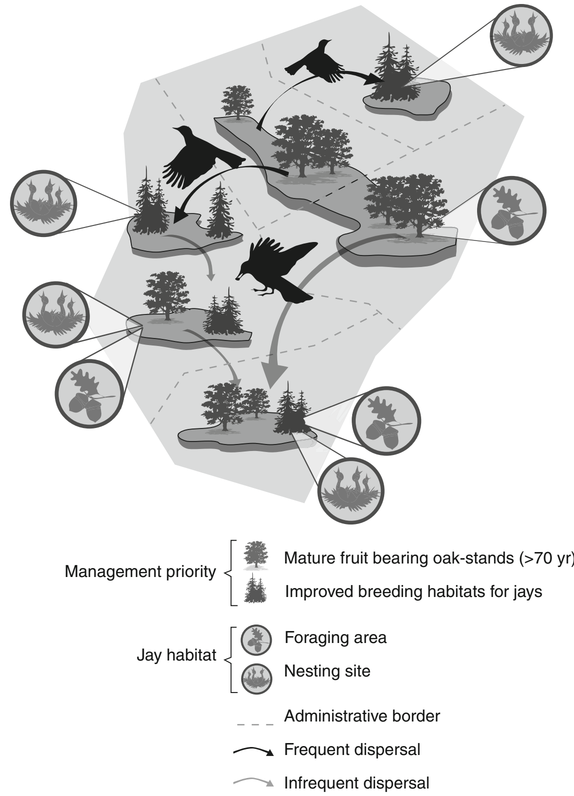

Fig. 3 Oak forest regeneration on a landscape scale is dependent on the presence of both foraging areas with mature oak trees and good nesting habitat sufficiently close to each other for a Jay to move between them. The figure is a simplified illustration of the study area with the National Urban Park in the middle. The green areas are separated by administrative borders and coordination is a prerequisite for efficient regional management. The different arrows indicate the frequency of exchange through the studied mobile link species

- Identify site-specific patch conditions, i.e. identify potential foraging and breeding sites.
- Identify landscape context, including characteristics of adjacent patches, distance between foraging and breeding patches and matrix composition.
- Establish a dialogue between mangers to coordinate efforts. The first issue is to identify common goals for the whole landscape, e.g. increase the amount of spruce to improve breeding conditions for Jays. The next step is to decide on a site-specific, spatially explicit management strategy that meets with management priorities, e.g. to ensure that there are sufficiently large areas of spruce within reach from the acorn-producing oaks.
- Each manager monitors the result of her/his management, e.g. through Jay surveys and oak seedling counts. The results should then be evaluated jointly in regular meetings.

The framework is yet to be tested in practice, but thanks to an on-going discussion with managers and interest groups the suggested process oriented approach and the preliminary findings from this study have already been used in a new management plan for the NUP to show the importance of a more landscape based approach to management (Bråvander and Jacobson 2006). It is also used as an argument and tool for collaboration over management borders.

Conclusions

Current recommendations for biodiversity conservation tend to focus on the need to conserve dynamic, multi-scale ecological patterns and processes that sustain the full complement of biota and their supporting natural systems (Poiani et al. 2000). However, many contemporary approaches to conservation seem intent only on protecting ecosystems from exploitation, and the selection of sites is based on the present state, e.g. European Union's nature conservation program Natura 2000. How the ecological values should be maintained is far less explicit.

We argue that the identification, and subsequent management, of key processes can often be an effective and easily monitored tool complementing other approaches to ecosystem management. The management of ecosystems should change focus from trying to control variability and natural pulses to maintaining options for desirable development for the future. Mobile links have been identified as an important part of this "natural insurance capital" when we face uncertain futures in constantly changing environments (Folke et al. 1996). The need and cost for human management could be much greater if existing ecosystem services are destroyed. Use of mobile links in management requires relatively small changes in management practices and offers several advantages. The Jay is but one of many examples of suitable mobile link organisms that can be found in the literature. Other examples are pollinators such as bees (Kremen et al. 2004), pollinating and seed dispersing flying foxes (Fujita and Tuttle 1991), and grazers such as bison (Knapp et al. 1999), and other ungulates (Bowyer and Kie 2006).

Regional planning and management implementation in urban settings have been shown to be difficult (James et al. 2000; Meffe et al. 2002). The many stakeholders in different administrative units impede successful management on a landscape scale. Strengthened collaboration and co-management over administrative borders is essential in order to maintain vital ecosystems and mitigate isolation effects on green areas. Mobile link species can unite managers around a common goal and thus act as a catalyst for improved regional management. Identifying organisms that connect administratively separated areas could potentially serve the same function as running water for watershed management, i.e. to align management with ecologically relevant scales. However, it should be remembered that systems are unique and that the importance of mobile links will differ between them. We suggest that the mobile link framework is useful in a specific management situation if the following steps can be taken:

- identify key spatial processes
- process assessment and analyses of its components
- choose an organism or functional group that is easily monitored
- use the procedure suggested in the model to plan and monitor management

Studies of processes such as seed dispersal reveal a landscape different from the isolated units presented on habitat maps. All organisms will perceive the landscape in their own way, and by trying to see the landscape through their eyes we can also gain a better understanding of the mechanisms underlying spatial processes. As for example in our case study it may be the relative location of two different essential resources that determines the strength and extent of a process. Thus, at least some vital spatial processes can be assessed when you know the different resource needs of certain species and the spatial properties of the landscape. We suggest that the potential for mobile link species to work as indicators of process strength could be and interesting avenue for future studies. We argue that a focus on species that uphold key ecosystem processes in landscapes has the potential to prevent ecosystem degradation and biodiversity loss in increasingly fragmented landscapes.

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