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Focus

The role of landscape patterns and land-use history in the composition of bird assemblages in Mediterranean and boreal forest ecosystems

Lluís Brotons & Pasi Reunanen

Two questions are often stressed in landscape ecology: first, how landscape structure influences ecological processes; and, second, how changes in landscape structure affect such ecological processes through time. Here, our aim is to describe and discuss the role of natural and historical landscape patterns in boreal and Mediterranean forest biomes. Potentially, both areas are covered by forest to a large extent, but their ecological characteristics and past history differ remarkably. By using birds as example taxa, we discuss how habitat loss and fragmentation may have clearly different outcomes in seemingly similar habitats but in different geographical regions. We stress the role of four landscape characteristics as key factors affecting landscape structure and its development in time: 1) natural landscape pattern; 2) natural disturbance regime; 3) human-related disturbance regime; and 4) the history of human impact and its intensity. We compare these characteristics between the two forest ecosystems in order to investigate historical and current constraints on forest avifauna. Significant differences in current species responses to landscape patterns, such as forest fragmentation, seem to originate from past history and impacts on current species-pools. We emphasize the need to study landscape effects within a regional framework and suggest that both the natural and historical characteristics that have modified the ecosystem to its present state should be examined carefully. This approach will allow landscape planners better to estimate the regional effects of landscape changes on species-pools in the future. Landscape ecology should increasingly focus on such interactions if we aim at fully understanding how species respond to the spatial structure of habitats on a landscape scale.

Key words: landscape dynamics, disturbance regime, habitat mosaic, avifauna, Mediterranean and boreal forest.

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Landscape ecology is a relatively recent discipline which addresses the relationships between the spatial structure and the functioning of biological systems, including the effects of human beings. Two relevant questions are often stressed: first, how landscape structure influences ecological processes; and, second, how changes in landscape structure affect such ecological processes through time (Forman 1995).

When analysing landscape-scale effects on the distribution of organisms in space, general conclusions and extrapolations from one region

to another are often drawn without considering that underlying biological systems have different ecological constraints and past histories (Schmiegelow & Mönkkönen 2002). However, ecosystems may respond to similar disturbances in very different ways due to their specific ecological characteristics and/or historical landscape and land-use patterns (Sousa 1984).

All over the world, human activities are associated with habitat loss and the ensuing fragmentation of forest landscapes, which imply a decline in habitat area and an increase in interpatch distances. There is an increasing awareness of the direct and indirect consequences of habitat loss and fragmentation on trends in animal populations (Saunders *et al.* 1991, Andrén 1994). However, without a detailed knowledge of the natural landscape structure in a region, as well as the disturbance regime that modifies it and its past land-use history, it is difficult to assess the impact of landscape-scale disturbances, such as human-caused habitat fragmentation. For instance, landscape heterogeneity is often associated with local differences in abiotic conditions, or it is the result of historical disturbance (Pickett & White 1985, Zonneveld 1989). In systems in which human-originated perturbations mimic the local disturbance regime, effects of human-associated landscape change may be minimized. This is, in fact, the rationale behind the current practice in landscape-ecological forest-management guidelines in Nordic countries (Mönkkönen 1999).

By using two illustrative examples, we highlight the role of historical land-use patterns as determinants of current changes in forest biodiversity. The main question posed here is how the original forest species-pool has evolved in relation to the main constraints imposed by local biogeographical features and historical factors shaping the landscape character. Such an approach can be used as background information for better adjustment of the regional landscape management of local animal communities.

To exemplify the question presented above, we describe natural and historical landscape patterns of European boreal and Mediterranean forest biomes. Potentially, both areas are covered by forests to a great extent, but ecological characteristics and their land-use history deviate remarkably. We concentrate our discussion on boreal and Mediterranean biomes in Europe because they clearly present different past histories, which, from a European perspective, are situated in the two extremes of a continuum of human interference in forest ecosystems (Kirby & Watkins 1998). By using forest birds as an example group, we discuss how habitat loss and fragmentation may have clearly different outcomes in seemingly similar habitats but in different geographical regions. In boreal ecosystems, forest habitat loss and fragmentation are thought to be the main causes of an overall reduction in the presence and abundance of many bird species, especially those associated with mature forest stands (Haila & Järvinen 1990).

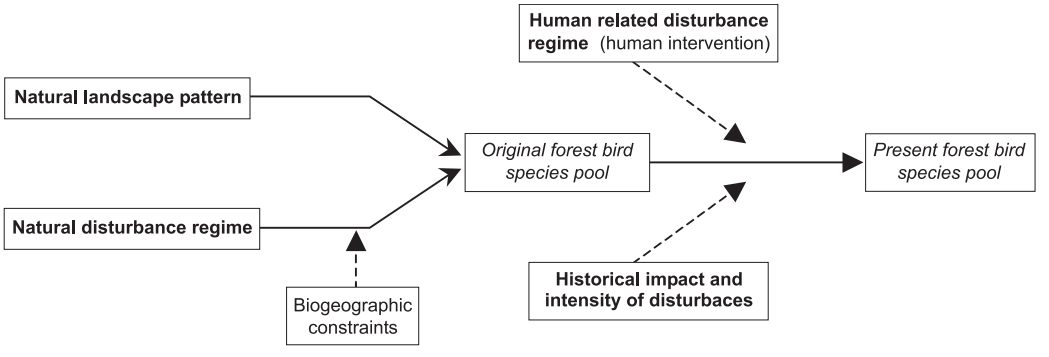

Figure 1. Schematic illustration of the key factors (in bold) affecting regional landscape characters and local forest-bird assemblages. The present species-pool results from natural and human-caused landscape changes but is also based on the structure of the original species-pool in the region.
Esquema il·lustratiu dels factors clau (en negreta) que afecten les característiques paisatgístiques regionals i les comunitats d'ocells forestals locals. El grup d'espècies actuals és el resultat dels canvis paisatgístics naturals i provocats per l'home però també es basa en l'agrupació d'espècies originals presents a la regió.

At present, in many areas covered by Mediterranean forest ecosystems (i.e. large areas in the Mediterranean Europe) habitat loss and fragmentation effects seem to be of lower intensity, and present concern is more focused on land abandonment and defragmentation processes that are associated with the loss of biodiversity on a regional scale (Rocamora 1997, Blondel & Aronson 1999).

We suggest four characteristics as key factors affecting landscape structure and its development: 1) natural landscape pattern; 2) natural disturbance regime; 3) human-related disturbance regime; and 4) its historical impact and intensity (Fig. 1). We briefly discuss the role of these characteristics in the two forest ecosystems in order to deduce historical and current constraints on the forest avifauna. Our aim here is not to present a detailed review of the main landscape features typical of Mediterranean and boreal ecosystems and their avifauna. Rather, we intend to discuss the role of the key factors as determinants of regional landscape responses of faunal groups with particular historical and biogeographical constraints. While abiotic conditions are acknowledged as having an important role in determining local species-pools, the historical background of landscape evolution seems often to have been neglected when interpreting faunal responses on the landscape level (but see Covas & Blondel 1998, Carrión 2002).

Natural landscape pattern

Local climatic conditions, prevailing soil types, and topography strongly conduct the development of vegetation types and, therefore, basically determine natural landscape heterogeneity. Due to a milder climate, richer soil types and variation in altitude, Mediterranean areas are markedly heterogeneous, and conditions change significantly within short distances (Blondel & Aronson 1999). This results in a variegated small-scale mosaic of different forest types and open areas such as "maquia" and "garriga" scrub formations. Natural small-grained heterogeneity of the forest landscape may impose limits to the potential ranges of species that need large continuous areas of forest or a coarse-grained landscape pattern.

In the boreal forest domain, the climate is harsh and the soil is, with a few exceptions, nutrient-poor, leading to geographically more homogeneous landscape patterns. Given that mountain ranges are not a common characteristic of the European boreal zone, altitude has a minor effect on the general landscape heterogeneity of the boreal biome (Hämet-Ahti 1981). Boreal forest landscape is formed, on the one hand, from practically stable habitat types, such as wetland areas and lake systems and, on the other hand, forest habitats. Hence, regional heterogeneity plays a less important role in boreal forest landscapes than it does in Mediterranean woodland mosaics (Sjöberg & Ericson 1997, Blondel & Aronson 1999).

Natural disturbance regime

Disturbances are a major driving force behind the maintenance of heterogeneity in natural systems (Sousa 1984, Brawn *et al.* 2001). In a successional dynamism, disturbances set the system back to early successional stages. The effect of disturbances on a given system depends on their intensity and extent. Gap dynamics are generated in both of the considered ecosystems by small-scale disturbance when forest is regularly replaced by openings of a single trees or groups of trees (Pickett & White 1985). However, fire is the most important disturbance agent in both ecosystems. In Mediterranean areas, wild fires turn large areas of forest into shrub-like formations (Trabaud 1981); recurrence of forest fires may vary to a great extent depending on relief and local conditions from less than 10 to 100 years, resulting in a mosaic of habitats in which forests of different age and tree composition and shrubby formations alternate in both space and time (Prodon *et al.* 1987). Forest fires and storm winds are the principal natural disturbances in a boreal-forest context (Esseen *et al.* 1997). The disturbance interval in boreal forests varies between 50 and 200 years (Zackrisson 1977, Bonan & Shugart 1989), but it can exceed 500 years in wet forests (Hörnberg *et al.* 1995). In addition, it must be kept in mind that the speed of forest succession in boreal latitudes is much slower and, thus, turnover time longer than in the south (Esseen *et al.* 1997). In both systems, successional turnover and disturbances over large areas are

intrinsic characters of the landscape, and have been incorporated into the dynamics of the avian community (Prodon *et al.* 1987). On the landscape scale and over long periods of time, the survival of the species in a habitat mosaic involves the existence of a disturbance regime that is unpredictable in time and space within a short time span but predictable in the long term.

Human-related disturbance regime

Humans have affected the composition and configuration of forest landscapes since ancient times. However, in terms of the time frame of the human influence, boreal and Mediterranean forest landscapes differ from each other to a great extent (Fig. 2). Agriculture, grazing and forestry are the most important human-induced perturbations in Mediterranean systems (Trabaud 1981). Agriculture can be considered as a permanent perturbation, whereas the other two are additional disturbances affecting many forested and non-forested habitats. These processes have created a mosaic-like landscape pattern of permanent agricultural habitats and more dynamic semi-natural areas. Traditional, low-intensity agriculture and forestry practices in the Mediterranean have significantly increased natural heterogeneity in the landscape in large areas of the region. Therefore, many species have to cope with habitat mosaics where resources are unevenly distributed in time and space (Blondel & Aronson 1999). Recently, there has been a tendency towards a large-scale, more intensive use of landscape for human activities, and this has greatly modified the semi-natural mosaic character of large areas, especially along the Mediterranean coast and more fertile agricultural plains.

In Fennoscandian boreal ecosystems low soil productivity has discouraged agriculture, which is concentrated on the most fertile soils in southern and middle boreal zones, whereas elsewhere forest harvesting and other forest-exploitation activities have dominated human intervention in the landscape. We can consider the role of human activities as landscape modellers having a low to moderate impact until recent times, during which industrial forestry activities have caused profound changes in the structure of forest landscapes. Industrial forestry profoundly alters the age structure of forest stands by decreasing the proportions of old forest in the landscape and increasing isolation among forest remnants (Haila 1994, Imbeau *et al.* 2001).

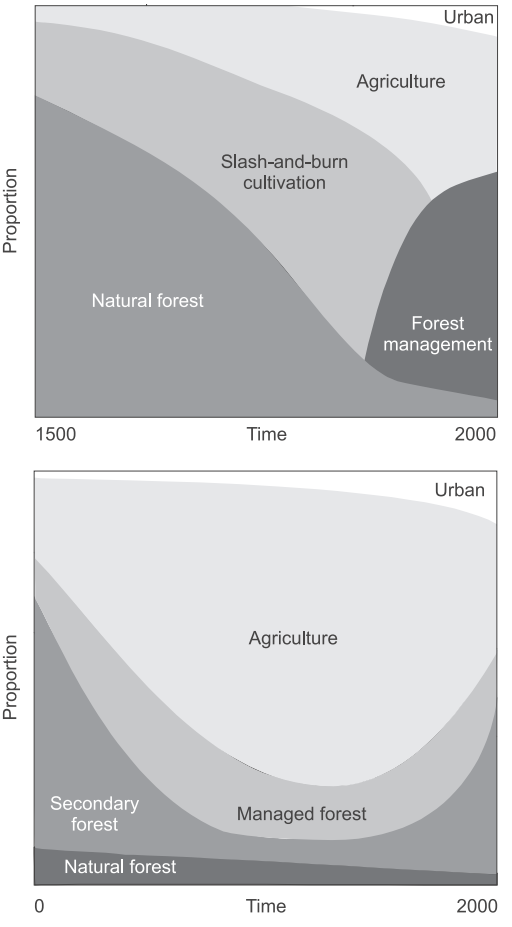

Figure 2. Schematic timeframe of major human-induced changes in boreal and Mediterranean ecosystems. The upper panel denotes boreal landscape, the lower Mediterranean. Note the different time scale. *Esquema cronològic dels principals canvis provocats per l'home en els ecosistemes boreals i mediterranis. El panell superior es refereix al paisatge boreal i l'inferior al mediterrani. Noteu l'escala de temps diferent.*

Time frame of human-related perturbation and its intensity

Mediterranean ecosystems have a long tradition of human activity, and this impact can be no-

ticed on different scales. Agriculture, grazing and forestry have generally been of low intensity, and in the course of time these disturbance agents have been incorporated into the landscape character (Fig. 2). Human activity has played such an important role in the shaping of the Mediterranean landscapes that human influence can be considered as a complex "co-evolution" between man and the ecosystem (Di Castri *et al.* 1981). As a result, it is very difficult, if indeed possible at all, to determine the original state of forested landscapes before human intervention (Quezel & Medail 2003).

In the boreal ecosystems, the history of intensive human exploitation of forest resources has been relatively short. For a long time forestry and agriculture had a minimal impact on these systems and, therefore, on the large scale they only fractionally changed the natural landscape pattern, having a minimal effect on the structure of boreal forests. However, slash-and-burn cultivation and agriculture had a remarkable effect on the local landscape composition and spatial arrangement of forested areas. The beginning of slash-and-burn cultivation and tar production dates back to the 16th century, and these activities were carried on until the end of the 19th century. Only recently, during the last century, and especially about 50 years ago, intensive large-scale forestry has become the key factor in shaping boreal landscapes in north-western Europe (Fig. 2). Intensive, industrialized forest exploitation has significantly altered natural landscape patterns in forested areas, and has created completely new, human-induced habitat configurations on a large scale (Franklin & Forman 1987).

Impact and-use history on forest-bird communities

Is it possible by examining historical landscape patterns to identify species that are affected by current human activities in the landscape? If present changes in landscape structure and composition depart significantly from the natural disturbance regime, we can argue that animal communities, including forest avifauna, are likely to be more affected by the changes than in those landscapes in which changes mimic natural landscape patterns and the pre-exisiting disturbance regime.

In order to answer the question, we need first to know the biogeographical context in which bird assemblages in the two ecosystems originated and later evolved. In addition to the differences in natural landscape pattern and natural disturbance regime, original forest avifauna is likely to differ significantly between European boreal and Mediterranean forest systems due to the strong influence of biogeographical events that have occurred in the two areas. During the last glaciations, forest retreated from most of continental Europe due to the prevailing, unfavourable low temperatures (Huntley & Bricks 1983, Zagwijn 1992). However, forested patches persisted in isolation in the Mediterranean area (Huntley & Webb 1988, Lang 1992, Quezel & Medail 2003). No large tracts of forest habitat persisted in the Mediterranean region during the quaternary, forcing forest faunas to adapt to a naturally fragmented landscape (Covas & Blondel 1998, Michaux *et al.* 2003, Kvist *et al.* 2004). These isolates formed a refuge for forest birds in the area and were very likely a source of colonizers in post-glacial Mediterranean and Central European forest landscapes. After the glacial period, a long history of forest fragmentation has continued in the Mediterranean areas with humans diminishing the total area covered by forests at the expense of agricultural and open areas. This period of human impact on habitat structure has had a significant influence on bird species assemblages. However, in the Mediterranean area, the historical human impact started c. 8000–10,000 years ago and resulted not so much in species extinctions as in dramatic changes in the distribution patterns of birds (Covas & Blondel 1998). Thus, the long history of forest fragmentation in Mediterranean areas, due to the natural character of the landscape, to biogeographical events, and to human-related activities, has lead to a present avifauna with very few, if any, species that are associated with large homogeneous tracts of mature forest (Covas & Blondel 1998). As an example, a recent extensive study of the effects of fragmentation on forest passerines in central Spain (Santos *et al.* 2002) found a negligible influence of isolation on the richness and distribution of bird species in forest fragments. The authors compared their results with those conducted in central and northern Europe and found that the Mediter-

ranean species-pool lacked many forest species susceptible to the effects of isolation. They argued that Mediterranean forests would, in fact, have lost most of the sensitive species a long time ago. As a result, present forest-bird communities in the Mediterranean area do not seem particularly sensitive to the current levels of fragmentation and isolation of forest remnants (Telleria & Santos 1992, Herrando & Brotons 2002), which fall well within the historical natural range of variation in the ecosystem.

On the other hand, due to the long historical period over which diverse habitat mosaics have developed in Mediterranean landscapes, a number of species have adapted and specialized on particular characteristics of dynamic landscapes, such as edge zones, non-forested habitats, and traditional agricultural landscapes (Blondel & Aronson 1999). Amongst these species we can cite species of high conservation concern (Tucker & Heath 1994) such as the Great Bustard *Otis tarda*, the Little Bustard *Tetrax tetrax* and the Lesser Kestrel *Falco naumanni*. Intensive agriculture and the afforestation of abandoned marginal agricultural areas dominate current land-use patterns in the Mediterranean. A process of land abandonment by humans works in parallel with natural forest succession and favours mostly forest-bird species (Preiss *et al.* 1997, Fig. 3). However, land

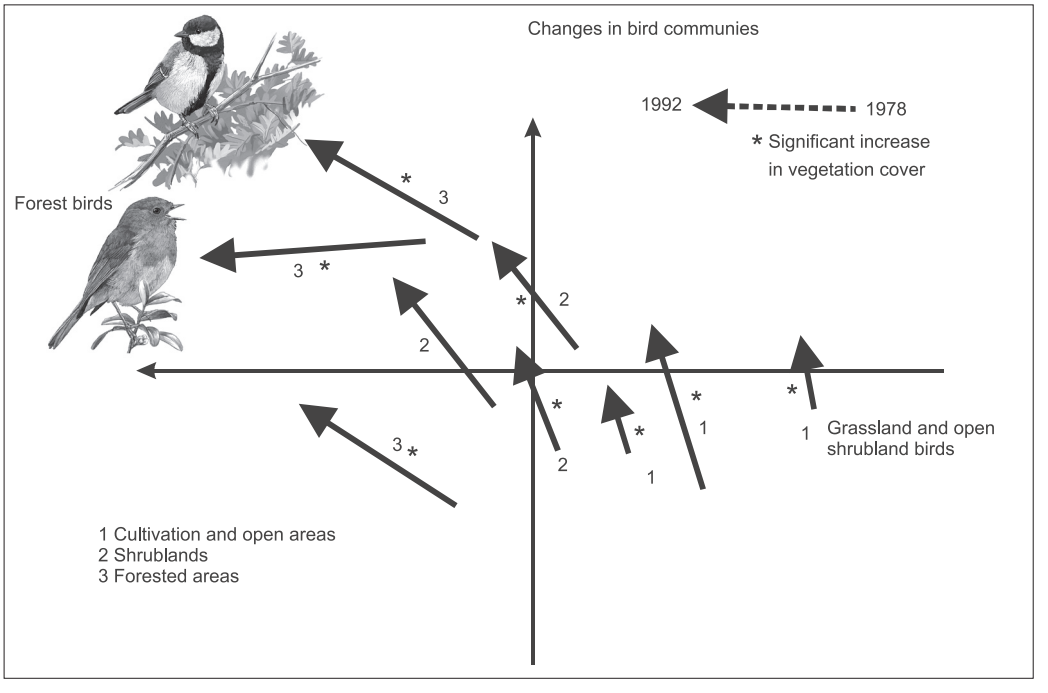

Figure 3. A recent increase in land abandonment has resulted in the expansion of generalist forest species (e.g. Short-toed Treecreeper *Certhia brachydactyla,* Robin *Erithacus rubecula*, Great Tit *Parus major*) at the expense of species dependent on open and shrub areas (e.g. Ortolan *Emberiza hortulana*, Tawny Pipit *Anthus campestris*). As expected, changes in avifauna in a Mediterranean area of southern France are parallel to landscape changes, and induce an expansion of forest-birds at expense of more open-land species. The axes represent results from multivariate ordination of bird communities by correspondence analyses showing the forest-bird community in the upper right corner of the graph (Figure modified from Preiss *et al.* 1997).
El recent increment de l'abandonament dels terrenys de cultiu ha provocat l'expansió de les espècies forestals generalistes (i.e. el Raspinell Comú Certhia brachydactyla*, el Pit-roig* Erithacus rubecula*, o la Mallarenga Carbonera* Parus major*) en detriment de les espècies que depenen d'àrees obertes i arbustives (i.e. l'Hortolà* Emberiza hortulana*, el Trobat* Anthus campestris*). Tal com es podia esperar, els canvis en l'avifauna de les àrees mediterrànies del sud de França són paral·lels als canvis paisatgístics i indueixen a l'expansió d'ocells forestals en detriment de les espècies de zones obertes. Els eixos representen els resultats de l'ordenació multivariant de la comunitat d'ocells obtinguda a partir d'una anàlisi de correspondències i mostra la comunitat d'ocells forestals en la part superior dreta de la gràfica (Figura modificada després de Preiss* et al. *1997).*

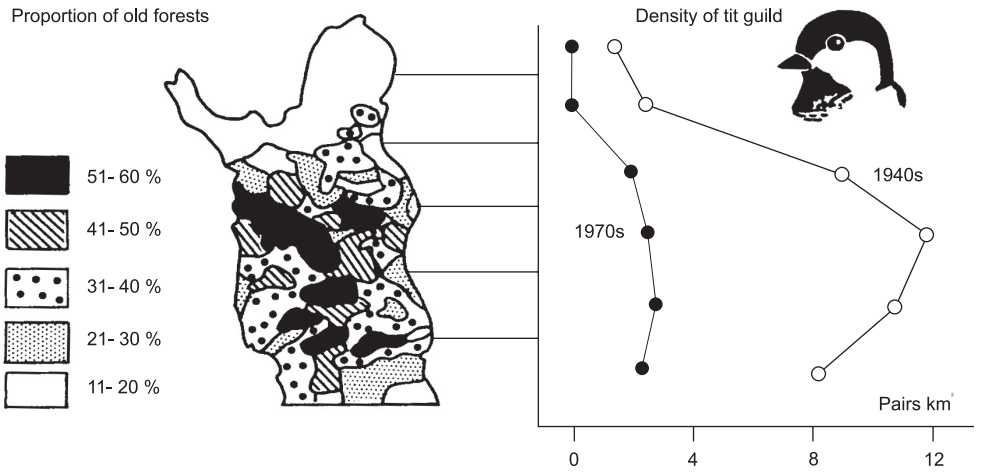

Figure 4. Large-scale forest management has altered stand age-structure and diminished the area of old-growth forests in boreal landscapes. In northern Finland (region represented in the map) densities in the tit (*Parus*) guild have declined significantly (proportions of decline shown in different filling patterns) due to habitat loss and fragmentation of old forests. (Figure modified from Järvinen & Miettinen 1987). Tit species are dominated by the Siberian Tit *Parus cinctus* and the Willow Tit *Parus montanus.*
*La gestió forestal a llarga escala ha alterat l'estructura dels arbres i ha disminuït la superfície de boscos madurs en els paisatges boreals. Al nord de Finlàndia (regió representada al mapa) les densitats de mallerengues (*Parus*) han disminuït significativament (proporcions de regressió observades en diversos patrons) a causa de la pèrdua d'hàbitat i la fragmentació dels boscos madurs. (Figura modificada després de Järvinen & Miettinen 1987). Les espècies de mallerengues més abundants són la Mallerenga de Lapònia* Parus cinctus *i la Mallerenga Capnegra* Parus montanus.

abandonment is detrimental to species which are adapted to heterogeneous mosaics of open and agricultural habitat types that are intrinsically linked to traditional agriculture and farming practices (Tucker & Heath 1994). As shown in a recent review on southern-European Mediterranean habitats, several species of open areas and extensive agricultural mosaics have already been affected by these changes (Rocamora 1997).

Fennoscandia was recolonized by forest species of Palearctic and Siberian faunal types (*sensu* Voous 1960) subsequent to the last glaciation (Taberlet & Bouvet 1994, Kvist *et al.* 2004); these recolonizers include species such as the Siberian Jay *Perisoreus infaustus* and the Siberian Tit *Parus cinctus* (Uimanienmi *et al.* 2000). During the glaciations, forested areas occupied by such species shifted latitudinally back and forth (Hewitt 1999) but did not undergo periods of habitat loss or the spatial subdivision of the habitat, as was the case with south-western European forests (Kurtén 1972, Zagwijn 1992). Since natural landscape patterns and the disturbance regime favour the maintenance of large forest tracts, and biogeographical and historical events have largely not isolated boreal forest areas, several bird species, particularly those of eastern origin, are likely to be very sensitive to the decline in the forest cover and fragmentation (Imbeau *et al.* 2001).

Forest species that are favoured by the natural disturbance regime, low regional heterogeneity in habitat, and low historical human activity are sensitive to large-scale, fine-grained changes in a landscape structure, such as the present intensive forestry practices in boreal forests. In northern Europe, old-forest species are sensitive to large-scale changes in boreal forest landscapes, and they have strongly declined during recent decades (Helle & Järvinen 1986, Haila & Järvinen 1990, Fig. 4). However, Virkkala (1991) found that large-scale population declines of resident birds in managed forest areas of northern Finland were not observed in large virgin forest remnants. This suggests that habitat loss and fragmentation of large tracts of forest negatively affects populations of forest-bird species associated with old forest. In Fennoscandian boreal forests, the change

in species-pool that occurred a long time ago in the Mediterranean may be taking place at present. Species sensitive to changes in habitat composition and to fragmentation, such as some woodpeckers, tits and the Siberian Jay (Uimaniemi *et al.* 2000), are declining. Gradually new species will colonize new forest habitats that have originated from the disturbance regime resultant from forest exploitation (Järvinen *et al.* 1977, Imbeau *et al.* 2001). Ongoing colonization of these habitats, often by more generalist species, may even replace native, especially resident and specialist, species and thus, affect the future bird community structure in the region.

Conclusions

The natural landscape pattern and the history of forest landscapes in Fennoscandia have resulted in a bird community which is to some extent sensitive to the spatial patterns derived from large-scale fragmentation and forestry activites (Imbeau *et al.* 2001). Several species are at present threatened because current landscape dynamics in Fennoscandian forests seem to exceed the natural range of variation (Imbeau *et al.* 2001), especially in terms of old-growth forests. In contrast, the natural landscape pattern and history in Mediterranean areas have originated a forest-bird community which is relatively well adapted to heterogeneous forest landscapes (Blondel & Aronson 1999). The current level of fragmentation in this zone lies within the historical ranges in which the avifauna has developed, and no forest species is seriously threatened due to present-day changes in the landscape (Carrión 2002). On the other hand, species adapted to traditional mosaic Mediterranean landscapes that are dominated by low-intensity perturbations are under threat due both to the intensification of cultivation (Brotons *et al.* 2004) and also to the abandonment of some agricultural areas (Prodon 1987, Preiss *et al.* 1997).

The effects of large-scale spatial patterns on ecological processes are directly, but in a complex way, related to the natural disturbance regime and human-induced alterations in the landscape structure (Dunning *et al.* 1992). Therefore, we should study landscape effects within a regional framework, and include both the natural and historical dynamics that have modified the ecosystem to its present state (Schmiegelov & Mönkkönen 2002). This is an essential starting point in understanding species responses to current changes in landscape structure. This approach will also help landscape managers to estimate the regional effects of landscape changes on species-pools, and make scenarios of possible future changes in species assemblage. In particular, a deep knowledge of the disturbance regime of a particular system may help to provide guidelines and tools to manage systems and favour many species of conservation concern (Bengston *et al.* 2000). The use of fire as a way to reset vegetation succession in Mediterranean landscapes affected by land abandonment, and forestry practices in northern European forests based on natural disturbance regimes described in natural habitats (Angelstram 1998), may be examples of this approach. We suggest that landscape ecology should increasingly focus on such interactions if we aim at fully understanding how species respond to spatial structure on a landscape scale.

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Resum

El paper dels canvis paisatgístics i dels usos del sòl sobre les comunitats d'ocells en els ecosistemes forestals mediterranis i boreals

En l'ecologia del paisatge sovint es debaten dues qüestions rellevants: en primer lloc, com l'estructura del paisatge afecta els processos ecològics, i, en segon lloc, com els canvis en l'estructura del paisatge afecten aquests mateixos processos ecològics al llarg del temps. La intenció d'aquest treball és descriure i discutir el paper de les fases naturals i històriques en els biomes forestals boreals i mediterranis.

Potencialment, ambdues àrees estan principalment cobertes per boscos, però les seves característiques ecològiques i la seva trajectòria històrica varien de forma remarcable. Utilitzant els ocells com a exemple, es discuteix com la pèrdua d'hàbitat i la fragmentació poden conduir a resultats clarament diferents en hàbitats aparentment similars, però situats en diferents regions biogeogràfiques. Es destaquen el paper de quatre característiques paisatgístiques: 1) els patrons paisatgístics naturals; 2) el règim de pertorbació natural; 3) el règim de pertorbacions causades per l'home; i 4) la història dels impactes humans i la seva intensitat com a factors clau que afecten l'estructura del paisatge i el seu desenvolupament en el temps. Es comparen aquestes característiques entre els dos ecosistemes forestals de cara a constatar les limitacions històriques i actuals sobre l'avifauna forestal. Les diferències significatives de la resposta de les espècies actuals cap als canvis paisatgístics, com ara la fragmentació forestal, semblen tenir un origen històric i condicionen les poblacions d'espècies actuals. Davant d'aquest fet, es recomana la necessitat d'estudiar els efectes paisatgístics a escala regional i se suggereix que cal tenir molt en compte tant les característiques naturals com històriques que han modulat els ecosistemes fins a la seva situació present. Aquesta aproximació ha de permetre als gestors tenir un millor coneixement dels efectes regionals dels canvis del paisatge sobre la comunitat d'espècies del futur. L'ecologia del paisatge hauria de tenir una rellevància cada cop més gran de cara a comprendre la resposta de les espècies a l'estructura espacial de l'hàbitat a escala paisatgística.

Resumen

El papel de los cambios del paisaje y de los usos del suelo sobre las comunidades de aves en los ecosistemas forestales mediterráneos y boreales

En la ecología del paisaje a menudo se debaten dos cuestiones relevantes: en primer lugar, cómo la estructura del paisaje afecta a los procesos ecológicos, y, en segundo lugar, cómo los cambios en la estructura del paisaje afectan a estos mismos procesos ecológicos a lo largo del tiempo. La intención de este trabajo es describir y discutir el papel de las fases naturales e históricas en los biomas forestales boreales y mediterráneos.

Potencialmente, las dos áreas están principalmente cubiertas por bosques, pero sus características ecológicas y su trayectoria histórica varían de forma remarcable. Utilizando las aves como ejemplo, se discute cómo la pérdida de hábitat y la fragmentación pueden conducir a resultados claramente diferentes en hábitats aparentemente similares, pero situados en diferentes regiones biogeográficas. Se destaca el papel de cuatro características paisajísticas: 1) los patrones paisajísticos naturales; 2) el régimen de perturbaciones naturales; 3) el régimen de perturbaciones causadas por el hombre; y 4) la historia de los impactos humanos y su intensidad como un factor clave que afecta a la estructura del paisaje y su desarrollo en el tiempo. Se comparan estas características entre los dos ecosistemas forestales con el objetivo de constatar las limitaciones históricas y actuales sobre la avifauna forestal. Las diferencias significativas de la respuesta de las especies actuales hacia los cambios paisajísticos, como la fragmentación forestal, parecen tener un origen histórico y condicionan las poblaciones de las especies actuales. Ante esta situación, se recomienda la necesidad de estudiar los efectos paisajísticos a escala regional y se sugiere que hay que tener muy en cuenta tanto las características naturales como históricas que han modulado los ecosistemas hasta su situación actual. Esta aproximación ha de permitir a los gestores que tengan un mejor conocimiento de los efectos regionales de los cambios del paisaje sobre la comunidad de especies del futuro. La ecología del paisaje debería tener una relevancia cada vez mayor de cara a comprender la respuesta de les especies a la estructura espacial del hábitat a escala paisajística.

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