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A biogeographical hypothesis on the effects of human caused landscape changes on the forest bird communities of Europe and North America

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Ultimate factors underlying forest bird responses to human caused landscape changes are examined by comparing European and North American avifaunas, their history, taxonomic composition, and present day characteristic. Taxonomically, resident species show stronger affinities between the two continents than migrant birds. European avifauna is by and large of Palaeartic origin with only little Afrotropical or New World influence. By contrast, both Palaearctic and tropical elements are prominent in North American bird fauna. The taxonomical differences can be traced back to the Plio-Pleistocene history, and geographical configuration of the continental land masses. Human impact has also been of earlier origin and more drastic to European than to North American birds. The contemporary avifaunas of the two continents can be roughly grouped into three categories according to 'sensitivity' to human induced landscape changes. The western Palaearctic species group is not particularly sensitive to human impact due to preadaptations to the loss of habitats. For the American species group, the human induced framentation and habitat loss is an unpreceeded event which they have not had possibilities during their Pleistocene history to evolve adaptations to. The Siberian or Siberian-Canadian group of species is adapted to dynamic boreal landscapes but not to large-scale human caused alterations of habitats. Future population trends for the three species groups are outlined given the present trends in land use practices.

1. Introduction

There is one clear difference between the forest bird assemblages of Europe and eastern North America in overall population trends. North American assemblages of passerine birds contain many species whose breeding populations have at least locally declined coincidentally with the fragmentation of habitats (e.g. Robbins 1979, Whitcomb et al. 1981) whereas in Europe most passerines seem to do well in fragmented forest landscapes (Opdam et al. 1985, Haila 1986, Ford 1987, see, however, Virkkala 1990). Recent discussion has not resulted in a consensus concerning the reasons for decline in North American birds (Hutto 1988, Terborgh 1989, Askins et al. 1990, Robbins et al. 1990, Hussell et al. 1991). Discussion has largely focused on proximate factors such as breeding habitat fragmentation (Robbins 1979, Whitcomb et al. 1981, Lynch & Whigham 1984, Askins et al. 1990), deforestation in the tropics (Briggs & Criswell 1979, Rappole et al. 1983, Hall 1984), nest predation (Gates & Gysel 1978, Wilcove 1985) and nest parasitism (Whitcomb et al. 1981, Brittingham & Temple 1983) with little attention to the ultimate reasons in species life histories (see, however, McLellan et al. 1986, Hansen & Urban 1992).

A knowledge of ultimate factors such as basic ecological constraints is critical to understanding the proximate ones. For example, migratory habit can be seen as a basic constraint affecting, among others, the time available for breeding which, in turn, determines the renesting potential of species (see e.g. Mönkkönen & Helle 1987). The effects of nest predation and parasitism on reproductive output are, in turn, dependent on renesting potential.

Species' ecologies are not predestined but evolutionarily determined. The effects of human caused landscape changes on bird assemblages are dependent not only on their relative magnitude but also on adaptations that species have been able to achieve to face with such changes during on their history. Forest fragmentation, for example, affects the least forest bird species that have had time and opportunities to evolve life histories to cope with fragmentation (e.g. good dispersion/ colonization abilities). In this paper, we examine the ultimate factors behind the characteristics of species of temperate forest passerine birds in Europe and North America, and based on this knowledge propose a hypothesis on probable changes that will take place in community structure given the current land-use practices.

Geographical and temporal scales of patterns and processes are dependent (Pielou 1979, Wiens 1983). Since we are dealing with species assemblages on a continent-wide basis the time scale under consideration must also be large: hundreds of thousands of years. Much of our discussion is based on vegetation history since the history of passerine species is poorly known.

Species sharing similar history and life history characteristics are assumed to respond similarly to human induced landscape changes. To address the recent concern about the effects of habitat loss and fragmentation on long-distance migrants we focus on groups of species with common migratory strategies. The distinction between residents and migrants is important also with regards to the non-breeding season: resident birds have to cope with temperate zone landscape changes on a year-round basis, and migrants are affected by landscape changes along their migration route and in wintering grounds.

2. Taxonomy and the origin of the avifaunas

Taxonomically, bird species on the two continents that spend their whole lives in the temperate zone are more closely related to each other than are the long-distance migrants wintering in the tropics. Actually, Europe and eastern North America do not have any migrant bird genera in common, whereas 45 and 67% of the resident genera of North America and Europe, respectively, are Holarctically distributed (Helle & Mönkkönen 1990). Typical resident genera such as *Parus, Certhia, Regulus, Sitta, Corvus* and *Turdus* are common to the Palaearctic and Nearctic region, but the lack of prominent North American migrant genera from Europe and *vice versa* is striking (e.g. *Empidonax, Catharus, Vireo, Dendroica,* and *Icterus* in North America; *Phylloscopus, Sylvia, Oenanthe, Saxicola*, and *Ficedula* in Europe).

Table 1 depicts the composition of eastern North American avifauna based on the origins of the basic elements (see Mayr 1946, 1964). Two important patterns emerge. First, the Palaearctic element is most prominent in the boreal (coniferous forest) avifauna and its contribution decreases towards the south (see also Mayr 1946, Udvardy 1958). Second, the proportion of tropical migrants is lowest in the Palaearctic element (see also Keast 1980) consisting in total of only eight out of 42 species (19%). More than half of the species that belong either to North American or Pan/South American element winter in the Neotropic (totally 60 species). According to Rappole & Warner (1980) most Nearctic, long-distance migrants evolved from historically tropical or subtropical species. This explains their close fit to tropical communities during temperate winter (see Rappole et al. 1983) and is seen in their present life history characteristics (Mönkkönen 1992).

Tropical affinities of the North American avifauna are prominent. Most of the passerine species of eastern North America (76%) have either conspecific populations or congener species breeding in the tropics (see also Rappole et al. 1983).

Using the criteria of Mayr (1946, 1964), the contribution of the New World to European passerine fauna is far smaller than *vice versa*, since only 16 European species (the Wren, the Waxwing and buntings) have their origin in North America (none in South America). The European avifauna is also relatively distinct from the Afrotropical avifauna (Snow 1978). About 39% of European passerine species have conspecifics or congeners breeding in Africa. Remarkably few of the European passerines have an Afrotropical origin (3 species, see Snow 1978), while the number of species of European origin in Africa is larger (48). As well European long-distance migrants are mostly of Palaearctic origin. This clearly shows in their characteristics both on the breeding and wintering grounds (Mönkkönen et al. 1992). Their life histories do not differ much from those of more resident species (Mönkkönen 1992).

3. Pleistocene effects

The taxonomic differences between European and North American avifaunas stem from the geographical configuration of the continental land areas and historical events during the Pleistocene. In the Old World, the major land area lies at mid-latitudes (around 30°N), whereas in America land area rapidly diminishes at this latitude as one moves to the south. Furthermore, in Eurasia massive east-to-west mountain ranges, seas and deserts divide the temperate avifauna from the tropical. In North America, no such barriers exist.

The Pleistocene glaciations also had very different impact on vegetation and avifauna on the two continents. Continuous forests were almost completely eliminated from Europe north of the Mediterranean realm during the glaciations (e.g. Kurtén 1972, CLIMAP 1976). Forests persisted in the southern peninsulas of Europe, and probably also in small fragments further north. The diminishing forest area and disappearance of many tree species, and consequently, forest types (see e.g. Jahn 1991) obviously selected for habitat generalism and good colonizing ability among forest birds. At the same time the Saharan desert was even larger than it is today, and a drier climate in the Afrotropics shrunk the extent of tropical forest. Residency among forest birds was presumably favoured by the shortage of suitable wintering habitats in Africa. Major tropical elements were extirpated from European avifauna during glacial periods (Moreau 1972, Blondel 1990a). In eastern and central Siberia and China, extensive forest biomes persisted the vicissitudes of the glaciations (Kurtén 1972).

Table 1. Number (*n*), and percentage of the total regional avifauna, for eastern North American bird species belonging to Palaearctic, North American and Pan/South American faunal elements (see Mayr 1946) breeding in subboreal (deciduous), boreal (coniferous) and both types of forest. M = number of tropical migrant species (wintering completely south of the USA).

	Subboreal			Both			Boreal		
	n	%	M	*n*	%	M	*n*	%	M
Palaearctic	11	19	3	15	29	3	16	38	2
North American	35	60	18	28	54	18	22	52	10
Pan/South American	12	21	7	9	17	5	4	10	2

In North America, successive waves of Pleistocene glaciations resulted in a back-and-forth north to south movement of deciduous and coniferous forest belts. Both forest regions maintained a far more extensive presence than the European forests, and were always in close contact with the tropical forests to the south (CLIMAP 1976). Faunal exchange between the temperate and tropical areas of the New World has not been interrupted since late Tertiary (Mayr 1964). For North American bird species that had evolved in or adapted to continuous forests Pleistocene glaciations presumably did not cause any major problem of finding suitable refugia although the glaciations may have had a major role in the adaptive radiation of certain genera of forest birds (Mengel 1964). Migration to the tropics therefore has always been an available option for forest birds, and given the higher climatic seasonality in North America than in Europe, probably a profitable one.

4. The dynamics of natural forested landscapes

Since the last glaciation and before major human impact, both deciduous and coniferous forest zones were extensive and continuous on both continents (e.g. Brown & Gibson 1983). The dynamics of the forest landscape is different in deciduous and coniferous regions, however.

In the boreal zone, forests are frequently regenerated by forest fires. Historically an average (boreal forest) site burned with approximately a 50 to 100 year interval (Heinselman 1973, Zackrisson 1977, Haapanen & Siitonen 1978, Tolonen 1983). This resulted in heterogenous landscapes with a wide variety of different successional stages being available at any given time. Natural dynamics of boreal landscapes provided a spectrum of opportunities for birds to evolve behaviours which could range from fugitive (e.g. early successional species) to more specialized life styles (e.g. old forest dwellers).

Deciduous forests regenerate mainly through wind falls and mortality of individual trees (e.g. Röhrig 1991), since the major tree taxa in a temperate climate 'burn like damp asbestos' (Rackham 1986:72). The size of disturbance patches was never of the same magnitude as the boreal forest fires, which could burn hundreds of thousands of square kilometers during one fire (Wein & MacLean 1983). Consequently, the age structure of the deciduous forest was consistently uneven (Rackham 1986), whereas fire-originated boreal forest stands were more even aged at the forest stand level (e.g. Cayford & McRae 1983). Conditions in deciduous forests provided possibilities for specialization on specific aspects of the deciduous vegetation.

The number of possibilities actualized is, of course, dependent on the species surviving the Pleistocene effects and their phylogenetic properties. As shown, Nearctic forest associated bird species had better opportunities to find refugia in glacial landscapes than western Palaearctic birds. Furthermore, Nearctic avifauna was able to maintain their close contact with the avifauna of the Neotropics (see Hino 1990 for a eastern to western Palaearctic comparison). Consequently, one could expect that forest birds of the Nearctic region would show a wider range of life histories and a higher number of specialized species, whereas habitat generalism and colonizing abilities were selected for among western Palaearctic species.

5. The time scale of anthropogenic landscape changes

The human impact began on both continents after the Pleistocene glaciations, but at first the effects on landscapes were rather sporadic (Darby 1956, Williamson 1989). After that, rates and patterns of forest change and loss vary enourmously according to place, but certain general patterns are discernible. Fig. 1 schematically illustrates the time scale of human impact using selected sites from Europe and North America as examples.

A major change in European forests started as early as 10000–8000 years ago in the Mediterranean area (Blondel 1990b) and about 5000 years ago western and central Europe (Darby 1956, Thirgood 1981, Chambers 1993). In many regions, forest landscapes were changed to predominantly open cultivated ones with only fragmentary forests. It has been estimated that much

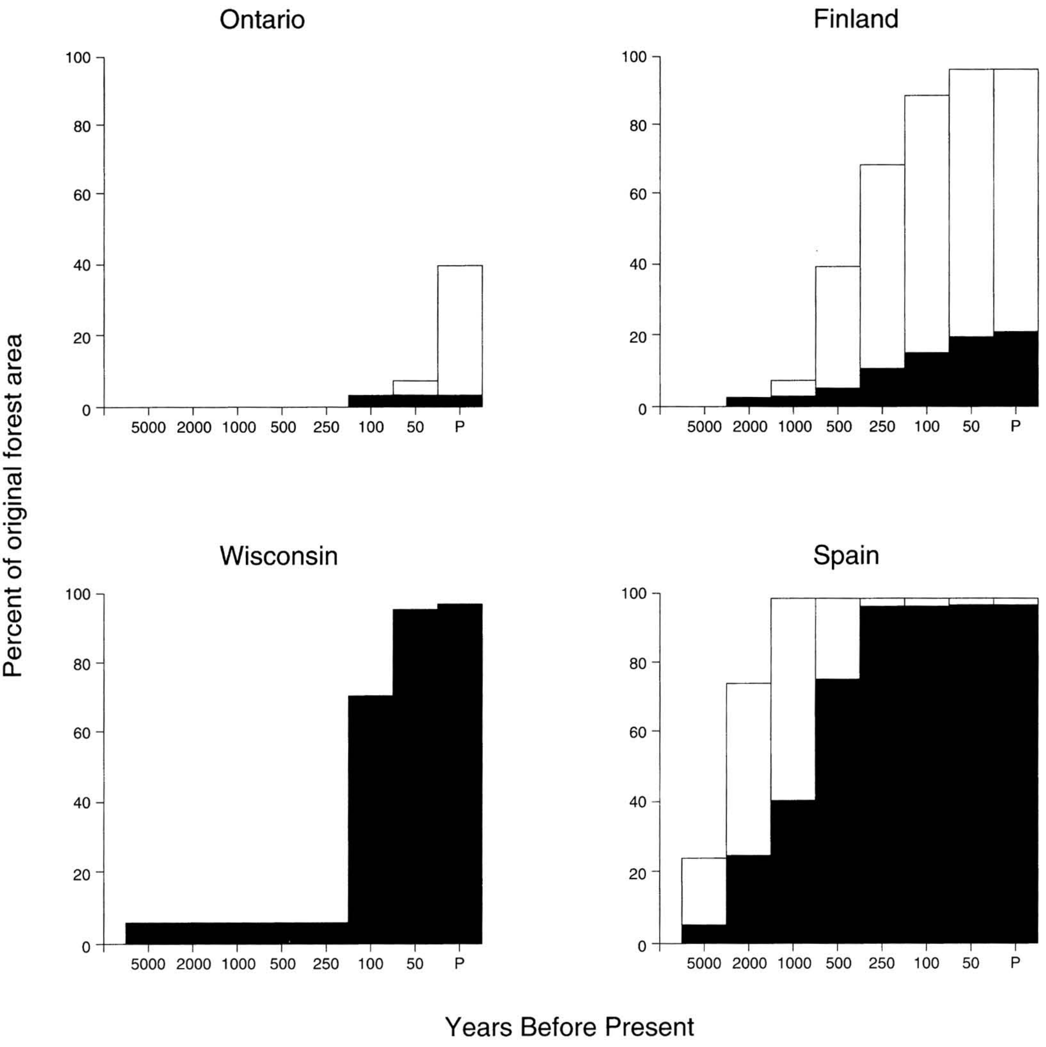

Fig. 1. The time scale of human caused forest habitat changes and loss in selected areas of Europe and North America. Black bar denote the proportion of totai forest area lost at a given time mainly due to agriculture. White area refers to the forest habitat area changed by man, but not lost, including land use practices like forestry, slash-and-burn cultivation, and grazing. Data for Spain is taken from Thirgood (1981) and for Wisconsin from Curtis (1956). Finnish figure is based on interpreted information for southern Finland given by Heikinheimo (1915), Darby (1956), Kalliola (1973) and Jutikkala et al. (1980). Figure for Ontario is based on unpublished data from Chapleau, Thunder Bay and Manitouwadge area gathered by D. Welsh.

of the present landscapes already existed 1000 years ago in western and southern Europe (Rackham 1980; Spain in Fig. 1).

Nowadays, barely one third of the once forested landscape (about 6 × 10^6 km^2) of Europe is covered with forests (Moreau 1972). Disproportionately more of the deciduous than coniferous forests have been lost, with probably one fifth of the deciduous forests remaining. Furthermore, these contemporary forests may well be structurally and spatially quite different from the original (see e.g. Rackham 1986).

In eastern North America, large scale forest destruction began 300 years ago. East of the Appalachian Mountains the largest changes have taken place within the last 100 years (Fig. 1, see also Williams 1989). In the eastern USA, approximately two thirds of the forest area was totally cleared during the 1800's with a considerable reforestation after the 1930's. Nowadays, about 60% of the forested area in presettlement times in the USA (10×10^6 km^2) is covered by forest (Powell & Rappole 1986). Our Wisconsin site obviously represents more heavily affected places (Fig. 1).

Human impact in the boreal zone on both continents is more recent than in southern forests (Fig. 1). Slash-and-burn cultivation and tar production resulted in a large scale forest clearing particularly in Finland between 1500 and 1900 (Kalliola 1955, Darby 1956). In the mid 1800's, a common shortage of fuel wood prevailed in southern and eastern Finland (Heikinheimo 1915). In Fennoscandia, intensive forest industry began in the late 19th century. The 20th century has been a period of mechanized forestry. Large scale harvesting of the New World boreal forest began only some 50 years ago. Forest habitat loss in the boreal forest zone has been less extensive than in the southern deciduous forest zone, and almost negligible in the Canadian boreal. Many of the boreal forest changes appear to be in proportional age structure, spatial patterns and forest types as most regions are still forested.

6. Contemporary avifaunas

The historical outlines just drawn can be compared with the knowledge of the present avifaunas of the two continents. The more homogenious origin of Palaearctic avifauna as a whole can be seen in their life history features. For example, differences in survival rate and reproductive effort between migrants and residents appeared to be more related to body size among European passerine species than in North America where migratory habit seemed to more directly connected with life histories (Mönkkönen 1992).

Eastern North American forest bird assemblages are characterized by a high proportion of long-distance migrants. In Europe, tropical migrants are predominantly early successional species and relatively scarce in mature forests both in the boreal and in more southern regions (Bilcke 1984, Helle 1988, Mönkkönen & Helle 1989); mature forests in Europe are characterized by residents (Helle & Fuller 1988). By contrast, in the eastern deciduous forest region of North America, migrants are rather scarce in early and mid successional stages (Helle 1988, Mönkkönen & Helle 1989). The boreal forest of the New World contain a high proportion of migrants irrespective of successional status of the habitat (Welsh 1987).

The vegetation history of continental forest biomes is expressed also in the diversity patterns of European and eastern North American forest bird assemblages (Mönkkönen, unpubl.). First, there are more forest bird species in continental and most regional species pools in the Nearctic than in the Palaearctic region. Second, Nearctic regional species pools are not only richer but also structurally more variable. Third, there is a greater between-habitat component of diversity in North American than in European forest bird assemblages. However, local breeding bird assemblages are about equally rich in species on both continents. In other words, the higher species diversity at higher spatial scales in the Nearctics is lost while entering the level of local communities (Mönkkönen, unpubl.). It can be inferred that Nearctic forest birds have clearly utilized the wider range of possibilities that have been available to them for the whole of Pleistocene and Holocene by becoming more specialized in their habitat preferences. European birds, in contrast, have gone through several 'bottle-necks' of habitat availability during the Pleistocene and are much less specialized as revealed by the relatively low between-habitat diversity in Europe.

The above inquiry into the evolutionary origin of continental avifaunas, and the history of forested landscapes suggest that contemporary avifaunas are not equally likely to be affected by human caused habitat and landscape changes of the present day and the future. The temperate avifaunas can be roughly categorized into three different groups according to their 'sensitivity' to human impact.

First, the European faunatype whose ice age refugia situated in western Palaearctic area has experienced fragmentation and loss of forest habitats, first 'natural' and later human induced, many times during the past two million years. Moreover, the Palaearctic origin (little tropical or Nearctic affinities) of the majority of this group contributes to its relative flexibility. Adaptations to human impact are obviously diverse among these bird species. This group consists of habitat generalists such as the Chaffinch (*Fringilla coelebs*), the Willow Warbler (*Phylloscopus trochilus*), and the Robin (*Erithacus rubecula*). The Chaffinch, for example, is a dominant species in forest bird communities all over the Europe irrespective of forest type.

The second group consists of species evolved in the New World environments. For these birds, the recent human caused deforestation and fragmentation is an unpreceeded event. Among these birds, there are many which have become ecologically specialized, and therefore, require large tracts of relatively natural forest. Species that evolved and specialized in the structurally diverse and spatially extensive deciduous forests of the Nearctics are supposedly particularly sensitive to human impact. Species such as the Woodthrush (*Hylocichla mustelina*), the Yellow-throated Vireo (*Vireo flavifrons*), the Cerulean Warbler (*Dendroica cerulea*), and the Hooded Warbler (*Wilsonia citrina*) as deciduous forest species are examples of the more sensitive species of this group.

Third, there is a component both in European and North American avifauna of northern origin which persisted in continuous forests of eastern Asia and Siberia over the glaciations (Siberian and Siberian-Canadian faunatype of Voous 1960). This component has not gone through the successive loss of forest area to an extend that has impacted the more western birds in the Palaearctic region. This third group is relatively more sensitive to the large-scale changes taking place in present boreal landscapes. As coniferous forest dwellers they can presumably tolerate landscape changes to a certain point due to their adaptation to the dynamic nature of coniferous forests. There are pairs of close relatives belonging to this group which inhabit the boreal zone in the Nearctic and Palaearctic region, respectively, such as the boreal chickadee (*Parus hudsonicus*) and the siberian tit (*P. cinctus*), and the gray jay (*Perisoreus canadensis*) and the siberian jay (*Perisoreus infaustus*), but also conspecifics (the three-toed woodpecker, *Picoides tridactylus*, the bohemian waxwing, *Bombycilla garrulus*, the pine grosbeak, *Pinicola enucleator*; for a more detailed comparison of the boreal avifaunas, see Haila & Järvinen 1990).

7. Population trends in retrospect and prospect

The composition of contemporary avifaunas of the three species groups outlined above, matches well with recent population trends in the Holarctic. In Europe, no consistent population declines among forest birds have been detected (Böhning-Gaese 1992, Marchant et al. 1990, Marchant 1992) with the exception of sedentary taiga birds in the north (Järvinen & Väisänen 1977, Helle & Järvinen 1986, Virkkala 1987). Migrant passerines have either remained relatively stable or increased particularly in the north (Järvinen et al. 1977). The most drastically reduced species of the taiga (e.g. *Picoides tridactylus, Parus cinctus, Perisoreus infaustus*) belong to Siberian fauna type of Voous (1960).

In eastern North America, specialized deciduous old forest dwellers have at least locally declined (for references see Introduction). This phenomenon is almost exclusively restricted to tropical migrants leading many authors to think that the cause of decline is in the tropics. However, taxonomic overview of these birds reveals that they belong to taxa that evolved in and experienced only unfragmented conditions during their Pleistocene and Holocene history. Hutto (1988) has described how the name of the group of birds that is reportedly declining has changed from 'migrants' to 'long-distance migrants' to 'forest-interior, long-distance migrants'. We further suggest that the name be reduced to 'forest-interior species'. Long-distance migration is rather a historical constraint among these birds, not necessarily directly linked with their decline. Some migrant species that have declined in the deciduous forests of North America have not done so in the boreal forests (see Hussell et al. 1991).

Assuming that present trends in land use do not change dramatically in the near future, which seems likely, the following changes are likely to occur: In the boreal forest zone on both continents, there will be little forest habitat loss, but the structure of individual forest tracts and entire landscapes will change. The forest industry's need for a continuous supply of 60–100 years old commercially valuable forest will stabilize age distributions. The need for access for harvesting efficiency will reduce the size of continuous forest blocks. There will be a proliferation of commercially valuable forest types, and loss of other ecosystems. Emphasis on 'clear' and 'healthy' stands will allow little natural death or decay. In other words, we will have more of the same with reduced forest diversity.

Much of this has already happened in the most intensively exploited areas of the boreal zone such as in Fennoscandia and is presently expanding in Canada and Russia. This development will cause population declines particularly in the New World boreal forests. The resident taiga bird fauna (Siberian-Canadian faunatype) will require a special conservation attention in the future also outside Fennoscandia given the present trends in boreal forest land use practices.

In the eastern North American deciduous forest zone, and particularly in more densely populated areas, forest habitats will continue to be lost and fragmented. Fragmentation will adversely affect birds that have evolved in and experienced only unfragmented conditions: the mature forest specialists. These species are all tropical migrants due to evolutionary history. The secondary effects of fragmentation, increased nest predation and parasitism, will continue to have a major impact due to the large number of mammalian as well as avian predators in North America. Habitat loss affects all forest birds.

For the majority of European forest birds there will be no drastic changes in general population levels provided that more forest habitats are not lost. The current avifauna is rather well adapted to fragmented landscapes due to its evolutionary origin, Pleistocene effects, and the long history of human caused fragmentation (see also McLellan et al. 1986).

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