

Effects of forest fragmentation on bird densities in northern boreal forests

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The structure of the forest in northern Finland has changed remarkably during the past few decades. The most dramatic changes are the increase of young (< 20 yrs) tree stands and the forest fragmentation. The change in the age structure of the forest has been beneficial to species of open land (e.g. *Oenanthe oenanthe*) and detrimental to species of old conifer forest. The increase in the amount of habitat edges has been advantageous to ecotone species such as *Sylvia borin* and unfavourable to species of the forest interior (e.g. *Turdus philomelos*). The breeding bird density increases with the age of the forest. The species diversity of the bird communities is lower in the bird communities in the forest edges than in the forest interior. The present forest fragmentation involves changes in both the age and the size of the tree stands, for which reason their effects should be studied simultaneously. Fragmentation is detrimental to *Phoenicurus phoenicurus*, *Ficedula hypoleuca*, *Fringilla montifringilla* and *Loxia species*, and beneficial to *Motacilla flava*, *Saxicola rubetra*, *Turdus iliacus* and *Sylvia borin*. The species that have decreased most strongly in recent decades are sedentary hole-nesters with an easterly distribution (e.g. *Picoides tridactylus*, *Parus cinctus*). The median weight of the species that have increased is 20 g and that of the species that have decreased is 56 g. Since the body size and territory size of birds are positively correlated, this supports the conclusion that forest fragmentation has played an important role in the changes in the bird populations. Although the majority of the changes in the bird populations in northern Finland during past decades are explained by the changes in the forest structure, other factors may be involved as well, e.g. population changes in southern Finland, environmental changes in the wintering areas and changes in predation pressure and interspecific competition.

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Introduction

The forests in northern Finland are western outposts of the Eurasian taiga. If unproductive forest sites are taken into account, almost 80 % of the total land area of northern Finland was earlier covered by forests. Since World War II, modern mechanized forestry has been practised in the northern forests, with extensive clear-felling, intensive preparation of the clearings and artificial reforestation. These are the most intensively exploited forests in Northern Europe, as is demonstrated by satellite pictures (Punkari 1984). The decrease in the area of virgin forests and fragmentation of uniform tracts of forest have been the most drastic changes and are well documented by the National Forest Inventories.

The recent changes in land bird populations in northern Finland are fairly well known, as are also the general effects of forestry on bird densities (Järvinen & Väisänen 1978, Väisänen 1983, Helle 1985a). A number of studies have examined the role of forest fragmentation in the recent changes in bird populations (Järvinen et al. 1977, Haila et al. 1980, Helle & Järvinen 1985) and the effect on bird life of anthropogenic environmental changes in general (e.g. v. Haartman 1973, Järvinen & Ulfstrand 1980).

This article on the impact of forest fragmentation

on bird densities in northern boreal forests is mainly based on studies conducted in northeastern Finland (Helle 1983, 1984, 1985a, 1985b). Special attention is paid to the question asked by Järvinen & Väisänen (1978): Are the changes in bird populations due to changes in the area of suitable habitats or due to changes in population densities within the habitats? An attempt is made to proceed further along this path. The effects of long-term climatic changes on bird populations lie outside the scope of the present discussion. The so-called amelioration hypothesis was earlier often used in explaining changes in the bird fauna (see e.g. Kalela 1949), but nowadays more importance is generally accorded to the effect of man on the ecosystems (e.g. v. Haartman 1973).

Fragmentation of forests

The age structure of the forest has changed remarkably during the past three decades in northern Finland. The proportion of tree stands aged less than 20 years has increased by 12 % units, whereas that of stands older than 100 years has decreased by 17 % units (Kuusela 1978, Anon. 1983). The stands are still clearly older, however, than those in southern Finland, as the proportion of forest aged more than 100 years amounts to 41 % in the north and to 9 % in the south. If felling continues at the present rate in northern Finland (about 500 km² clear-cut yearly; Anon. 1983), larger areas of old forest will soon be scarce and hard to find outside protected areas.

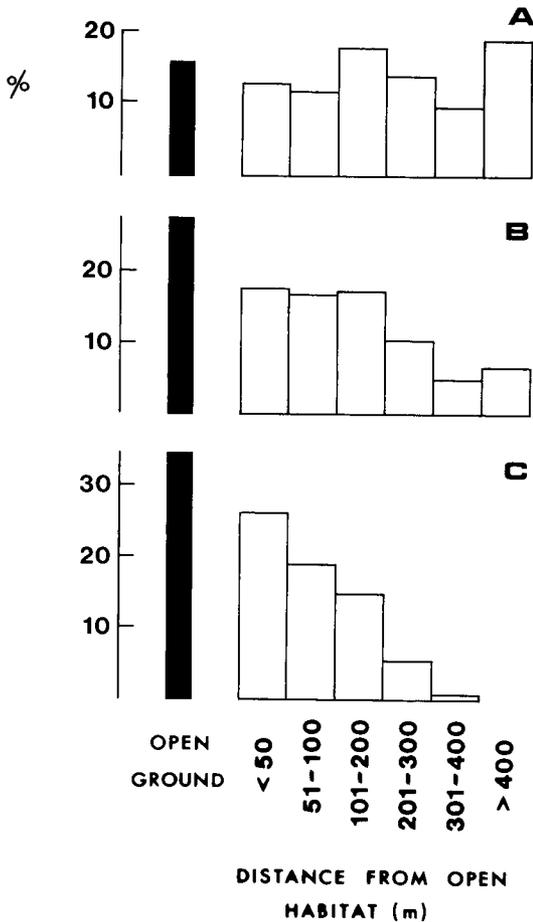


Fig. 1. Percentage distribution of 'the map survey points' (see text) in open habitats and in forest at different distances from open ground in the Oulanka National Park (A), outside the Park in 1955 (B) and outside the park in 1975 (C).

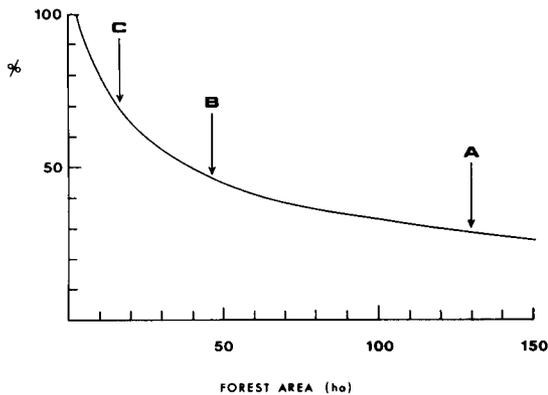


Fig. 2. Percentage of edge area (100 m in width) as a function of the total area of a circular habitat patch. The arrows (A-C) indicate the forest edge/total forest area ratios in the surveys presented in Fig. 1.

Large clear-fellings have converted areas of old forests into an archipelago of small peninsulas and islands of forest. Aerial photographs taken in 1955 and 1977 in Kuusamo (Northeastern Finland; 66°N, 29°E) were used to quantify the fragmentation. The Oulanka National Park (about 100 km²) and its surroundings (300 km²) were studied separately. The distribution of randomly chosen points (9 per km²) among open ground and forest habitats was studied and the distance to the nearest open land was measured from the points located in forest. The results (see Fig. 1) show that the areas around the Park became considerably more fragmented between the 1950s and the 1970s, and that even in 1955 they were more fragmented than the forest in the Park. The change in the surrounding areas is probably fairly typical of the whole of northern Finland.

The smaller the fragments studied, the higher is the proportion of forest edges in the total forest area (see Fig. 2). The edge/total area ratios of the map surveys confirm a drastic decrease in the size of stands over past decades (Fig. 2). The change in stand size cannot be measured correctly by this method, however, because the shape of the forest patches in Fig. 2 is taken as circular, whereas in reality the fragments are of irregular shape.

The quality of the stands has also changed during recent decades. The proportion of silviculturally good or satisfactory stands in the whole forested area has increased from 36 % in the 1930s to 60 % in the 1970s (Ilvessalo 1958, Anon. 1983). The rest of the stands belong to categories such as 'silvicultural measures neglected', 'trees unsuitable for site', 'over-aged', i.e. show features more or less characteristic of stands in natural condition. The number of dried-out standing trees is a good indicator of a stand in natural condition. Kalliola's (1966) maps clearly demonstrate a decline in such trees from the 1930s to 1960s.

Causes of changes in bird populations

Järvinen & Väisänen (1978) attributed the changes in land bird populations in northeastern Finland from the 1940s to the 1970s to: 1) changes in habitat areas and 2) within-habitat density changes. The latter alternative was not explicitly defined, but it evidently covered both density changes due to slight alteration of forest structure and 'strict' within-habitat changes (i.e. changes taking place in the population of a bird species in habitats which remained unchanged). In bird studies the habitat is (usually) only roughly defined (e.g. pine forest) and changes in the characteristics of such broadly defined macrohabitats are possible over a longer period. The 'within-habitat changes' *sensu* Järvinen & Väisänen (1978) can be divided into density changes due to alteration of the microhabitat and changes due to events outside the study area.

Effects of age and size of forest. Clear-felling considerably decreases the density of breeding birds. Two years after felling in northern Finland, total density amounts to about 30 % of that in mature forests (Helle 1985a). The density increases rapidly, however, the relationship between the bird density and the age of the forest being best described by a logarithmic function. Bird species diversity does not vary greatly in the course of forest succession in northern Finland (Helle 1985a). In view of the bird

density response to forest age, the recent change towards younger stands could be expected to have decreased the density. This has not happened, however (Väisänen 1983), the situation being more complicated than might appear, as will be seen later.

The general rule — the smaller the habitat fragment the higher the bird density — holds true in northern boreal forest patches as well (Helle 1984). Correspondingly, the edges of larger forests have a higher bird density than the interior parts of the same forests (see Table 1). According to the principle of the edge effect, the edges should contain more species than the interiors, but surprisingly they do not. The expected numbers of species in random samples of the same size (calculated by the rarefaction method; e.g. James & Rathbun 1981) show a clearly higher number of species in the forest interior than in the edges (Table 1). If the expected numbers of species in given areas are compared, an interesting phenomenon becomes evident (here the birds are assumed to be distributed evenly in the forests). The expected number of species per unit area differs less between forest edges and interiors than the expected number in random samples of the same numbers of pairs. This is due to the higher bird density in edges than in interiors. In fact, for this reason areas smaller than 60 ha have more species in the habitat edges than in the interiors (Table 1).

As regards the most abundant land bird species in northern Finland, the species benefited by the change in the age structure of the forests include: *Anthus pratensis*, *Saxicola rubetra*, *Oenanthe oenanthe* and *Emberiza citrinella*, and the species that have suffered from the change include *Phoenicurus phoenicurus*, *Turdus philomelos*, *Ficedula hypoleuca* and *Loxia* species (*curvirostra/pytyopsittacus*) (Väisänen 1983, Helle & Järvinen 1985). In the light of pure edge preference/avoidance, the increase of edge areas has profited *Turdus pilaris*, *T. iliacus*, *Sylvia borin*, *Muscicapa striata*, *Emberiza citrinella*, whereas *Turdus philomelos*, *Ficedula hypoleuca*, *Carduelis spinus* and *Loxia* species have suffered (Helle 1983; Helle & Järvinen 1985).

Effects of fragmentation; age and area effects combined. The fragmentation of forest includes both the previously mentioned components — the tree stands are younger and their size has decreased — and these should preferably be studied simultaneously. The relationship between the breeding bird density and the age and size of the stands according to data from northern Finland (Helle 1984, 1985a) is presented in Fig. 3, which reveals that both components of fragmentation are of importance. The regression model explains the slight increase in total bird density during recent decades in northern Finland reported by Väisänen (1983). The change in the age structure of the stands has been detrimental to birds (see previous subsection), but this has been compensated by

Table 1. Data on birds breeding in forest edges (>50 m from edges) and forest interiors (>200 m from edges) obtained from one-visit censuses in northeastern Finland. The stands are mainly coniferous forest of different age, the open land clear-felled areas (Helle 1983 and unpubl.).

	Edge	Interior	P
Pair density (pairs/km ²)	63	50	< 0.05
Species diversity (Shannon index)	3.00	3.19	< 0.05
Expected no. of species in a random sample of			
300 pairs	36.0	45.5	< 0.01
200 "	32.8	39.7	< 0.05
100 "	26.8	30.7	ns
Expected no. of species per			
500 ha	36.3	43.0	< 0.01
100 ha	21.7	22.1	ns
50 ha	15.2	14.7	ns
Total no. of pairs	466	389	
Total no. of species	39	48	
No. of species common to the samples	34		

the decrease in average stand size, which has been favourable.

Forest age/forest area patterns (as in Fig. 3) cannot be constructed for individual species, due to insufficient data. There is a neat relationship between the forest age preferences and edge preferences among the abundant bird species. The strongest edge preferences are shown by the species which have their highest population density in the bush phase of the forest succession, whereas the species of the youngest and oldest stages of the succession are 'interior' species, i.e. avoid edges (Helle & Järvinen 1985). The tolerance of fragmentation in the most abundant land bird species (deduced from their habitat preferences as regards forest age and edge) was compared with their recent population changes in northern Finland (Helle & Järvinen 1985). The

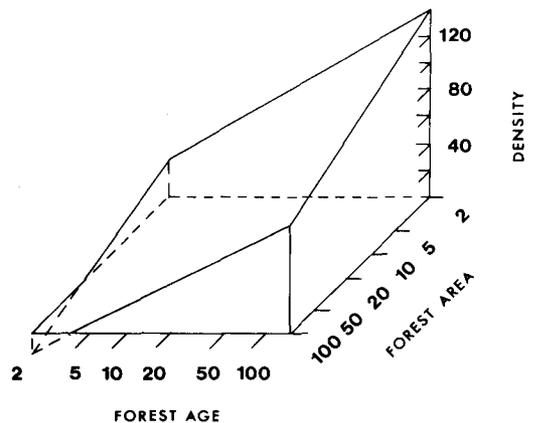


Fig. 3. Multiple linear regression of the density of breeding birds (pairs/km²) on the age (years) and size (hectares) of forest patches in moist forest sites in northern Kuusamo (N = 20, R = 0.672, P < 0.01).

Table 2. Classification of the most abundant bird species in the Kuusamo data by habitat choice (tolerance of fragmentation) and recent population change (Helle & Järvinen 1985).

	Population change in northern Finland since World War II	
	Decrease	Increase
Species favouring young phases of forest succession and/or habitat edges (= tolerant of fragmentation)	<i>Anthus trivialis</i> <i>Emberiza citrinella</i>	<i>Anthus pratensis</i> <i>Motacilla flava</i> <i>M. alba</i> <i>Erithacus rubecula</i> <i>Saxicola rubetra</i> <i>Oenanthe oenanthe</i> <i>Turdus pilaris</i> <i>T. iliacus</i> <i>Sylvia borin</i> <i>Phylloscopus trochilus</i> <i>Muscicapa striata</i> <i>Fringilla coelebs</i> <i>Carduelis flammea</i> <i>Emberiza rustica</i>
Species favouring old forest and/or habitat interior (= intolerant of fragmentation)	<i>Phoenicurus phoenicurus</i> <i>Ficedula hypoleuca</i> <i>Fringilla montifringilla</i> <i>Loxia curvirostris</i> <i>pytyopsittacus</i>	<i>Turdus philomelos</i> <i>Carduelis spinus</i>

population changes are well predicted by their tolerance of fragmentation, except in the southern species (see also Table 2). This means that the species abundant in northern Finland have followed the changes in habitat availability, whereas the southern species seem to be more dependent on other factors.

Other reasons for population changes. Some of the factors mentioned below are purely speculative. All of them can cause changes in bird populations in a given region, although no change in habitat areas has taken place (not even at macrohabitat level).

The number of sick and dead trees in a forest is much lower than, for example, 30 years ago (see also previous section). Such trees generally increase forest bird densities and species diversity (e.g. Nilsson 1979a, b). Järvinen & Väisänen (1978) related a within-habitat density decrease of *Parus cristatus* and *P. montanus* to forest fragmentation, which may limit the winter resources of these species. In addition, the decrease of dead and sick trees has probably contributed to the population crashes of these (and other old forest and/or hole-nesting) species. Järvinen & Väisänen (1978) connected some within-habitat density increases with the strengthening of the bush layer in forests — also a change in habitat microstructure.

Environmental changes outside the study area represent two different “mechanisms”. First, the population density of a species may change outside a given area and population pressure may affect populations in the area (irrespective of changes in habitat areas). A strong increase of spruce has been beneficial to the

species inhabiting spruce forests in southern Finland (e.g. *Turdus philomelos*, *Erithacus rubecula*, *Prunella modularis*), and for this reason they have increased in northern Finland also, although the abundance of spruce has decreased markedly there (Järvinen et al. 1977, Väisänen 1983). In general, ‘the overflow principle’ may be expected to work most clearly in the marginal areas of a species’ range and, on a local scale, in marginal rather than optimum habitats. Second, since the migratory birds breeding in northern Europe spend the major part of the year in their wintering areas (or on migration), environmental changes in those areas may be of importance (e.g. Järvinen & Ulfstrand 1980, Svensson 1985). The northern European population of *Phoenicurus phoenicurus*, for example, has suffered from changes in its wintering grounds in Africa (A. Järvinen 1981). Ulfstrand & Alerstam (1977) suggested that the same is true of many other migrants.

Changes in the habitat preference of a species may affect its population density. Studies on changes in habitat preferences are few (see however Stjernberg 1979 for *Carpodacus erythrinus* and Sorjonen 1980 for *Luscinia luscinia*) and there are none from the northern boreal area. Clear-felled areas in the north might provide some examples, since many species of open habitats have started to breed on them (Ahlén 1975, Helle 1985b). The population densities of *Numenius phaeopus* and *Saxicola rubetra* in clear-felled areas exceed the densities in their natural habitats in northern Finland (Helle et al. 1984), which may mean that such areas are optimum habitats in terms of offspring production. Detailed population studies are needed to answer these questions.

Other factors may lie behind the changes in bird populations, too. Väisänen (1983) supposed that the decline of falcons has contributed to the pronounced increases of many passerine birds of open habitats in northern Finland. Helminen & Väisänen (1980) suggested that the strong increase of migrants, especially *Phylloscopus trochilus*, in boreal forests during recent decades may have been detrimental to resident species of the foliage-gleaning guild (*Parus* spp.). Further studies are needed to test these hypotheses.

Conclusions

Comments on concepts. The expression ‘a given area’ has been repeated several times in this article. The scale of a study is of crucial importance: results from a very limited area, for example, may be totally misleading when generalized to a regional scale (see e.g. Wiens 1981). The same is true of time: short-term studies cannot be used to predict long-term changes. In this study the area amounts to about 100 000 km² and the time to several decades.

The different reasons for changes in bird populations mentioned in this paper — although presented as ‘independent’ factors — obviously interact in a complicated fashion. Changes in habitat preferences, for example, cannot be expected to occur without changes in habitat areas. To give another example, the amount of dead trees in the forest (and other natural microhabitat characteristics) is probably dependent on forest fragmentation. The larger the stand (forest island), the more likely it is to contain such features. To summarize, nearly all the reasons responsible for population changes in the northern boreal area may be directly or indirectly connected with the fragmentation of forests.

Changes in habitat areas and within-habitat density changes may be temporarily correlated. Reduction of a suitable habitat may increase the density of species favouring that habitat for a short period (see Criswell & Ganthey 1980, Whitcomb et al. 1981). Some northern boreal data support this idea, but the material is too scanty for stochastic variation to be ruled out (P. Helle, unpubl.).

Losers among land birds in northern Finland: the role of forest fragmentation. The effects of forest fragmentation have mainly been studied on the basis of the abundant species. The species most intolerant of fragmentation are of equal interest, not least from the viewpoint of nature conservation.

Fifteen of the 42 forest bird species studied by Väisänen (1983) have decreased significantly in northern Finland in recent decades. Järvinen & Väisänen (1978) noted that most of the population crashes are attributable to the reduction of the area of old pine forests. Six of the 15 decreased species are hole-nesters, 10 sedentary, 11 non-passerines and nine belong to the Siberian faunal element (six to the Palaearctic or European faunal element; Voous 1960, Siivonen 1979). None of these proportions deviates significantly from the proportions in the whole forest avifauna (42 spp.; Väisänen 1983: Table 1). The combination most ‘at risk’ has been a sedentary hole-nester of the Siberian faunal element, as all the species belonging to this category have declined severely (*Picoides tridactylus*, *Dryocopus martius*, *Parus cristatus*, *P. montanus*, *P. cinctus*).

As all the decreased species are nowadays scarce or rare, sufficient data are not available on their habitat selection and its relation to forest fragmentation (see however Helle & Järvinen 1985). Fragmentation has probably exerted an effect, as most of the population declines have been bigger than could have been expected from the reduction in the area of old forest (e.g. Järvinen et al. 1977). A positive correlation has been found between the body size and territory size of birds (e.g. Schoener 1968). Therefore, if the fragmentation of forest is a major factor affecting the bird populations, the species that have increased may be expected to be smaller than those

that have declined. The median body weight of the species that have increased significantly in northern forests is 20 g (15 spp.) and that of the decreasing species 56 g (15 spp.; $P < 0.10$; for the data see Väisänen 1983). The result seems to support the hypothesis regarding the effect of forest area put forward by Järvinen et al. (1977) and accords with that of Järvinen & Ulfstrand (1980) regarding ‘winning’ and ‘losing’ bird species in northern Europe during the past century.

Prospects. The effects of forest fragmentation probably vary from one biome to another. Changes in the density of breeding birds in the course of forest regeneration, for example, seem to vary geographically. In Central Europe, and evidently also in southern Finland, the density curve tends to have two peaks, the first in the bush phase and the other in older forest (Haapanen 1965, Ferry & Frochot 1970, Głowaciński 1972, 1979), whereas in the northern boreal area only the latter peak is present (see p. 36, Helle 1985a). Both of these patterns are found in North American studies, but Fox (1983) did not detect geographical regularities in these changes in his review.

The effects of forest fragmentation on bird occurrences have been studied most extensively in the deciduous forests of eastern North America (e.g. Robbins 1980, Lynch & Whigham 1984). Neotropical migrants — most of them ground-nesting, forest interior specialists — have been concluded to be the birds most severely disturbed by forest fragmentation in that region. This result clearly deviates from that obtained in northern Europe, where the sedentary species seem to be the least tolerant of fragmentation. In fact, *Phylloscopus collybita* is the only species among the decreasing forest birds in northern boreal forests that fulfils the conditions for a species very intolerant of forest fragmentation in North America. It is a ground-nesting tropical migrant preferring the forest interior (Tiainen et al. 1983). Information on forest fragmentation and bird densities from other parts of Europe could answer the question: Is the difference between North American and Northern European studies due to a difference in the bird fauna (different continents) or to the difference in latitude (coniferous vs. deciduous zone)? Such data are not available, as large areas in Central and Southern Europe were radically altered by man several centuries ago; primeval forests are rare, except in the more eastern parts of Europe.

Although several aspects of the ecology of forest fragmentation have been studied in the northern boreal area, a unifying theory has not yet been developed. This is mainly due to lack of data on the long-term effects of many forestry practices. The impact of clear-felling on bird densities is known, for example, but clear-felling is not the only aspect of forest renovation. Seed trees and shelterwood cut-

tings are used in more than half of all the felled areas in northern Finland, but the effects of these measures are poorly known (no quantitative data published).

The following questions seem to be the most important and interesting. How far does the edge effect extend (the extent is known to vary from species to species and from one habitat to another; see Gates & Mosher 1981)? Do the effects of forest fragmentation vary with the season (see Hansson 1983)? What ability have bird species to connect several small habitat patches to form a territory (see MacClintock et al. 1977, Whitcomb et al. 1981)?

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Selostus: Metsien pirstoutumisen vaikutuksesta Pohjois-Suomen pesimälinnustoon

Pohjois-Suomen metsäkuva on muuttunut voimakkaasti viime vuosikymmenten aikana. Huomattavimmat muutokset ovat metsien ikärakenteen nuorentuminen ja metsäkuvioiden koon pienentyminen (kuvat 1 ja 2). Periaatteessa muutokset Pohjois-Suomen lintukannoissa johtuvat alueesta itsestään (biotoopin pinta-alojen muutokset) tai ulkopuolisista tekijöistä. Metsien ikärakenteen nuorentuminen on lisännyt avomaalajien elintilaa (hakkuuaukeat, esim. kivitasku) ja kaventanut vanhaa metsää vaativien lajien mahdollisuuksia. Reunapiirien määrän kasvu on ollut edullista 'reunansuosijoille' (esim. lehtokerttu) ja epäedullista 'reunapakoisille' lajeille (esim. laulurastas). Metsänreunojen linnusto on yksilörikkaudesta huolimatta lajikohtainen kuin syvien metsien linnusto, mikä on vastoin ns. reunavaikutuksen periaatetta (taulukko 1). Koska metsien pirstoutuminen pitää sisällään sekä ikärakenteen nuorentumisen että kuviokoon pienentymisen, on luontevinta tutkia näiden yhteisvaikutusta. Tältä pohjalta tutkimustuloksia tarkastellen voimakkaimmin pirstoutumisesta kärsiviä (runsaslukuisia) lajeja ovat leppälintu, kirjosiippo, järripeippo ja käpylinnut ja siitä hyötyviä lajeja mm. keltävästäräkki, pensastasku, punakylkirastas ja lehtokerttu (taulukko 2). Kokonaislintutiheyden vaihtelua selittävä malli osoittaa sekä metsän iän että kuvion koon erittäin tärkeäksi (kuva 3).

Kaikkien runsaiden lajien kannanmuutokset Pohjois-Suomessa eivät selity alueen metsäkuvan muutoksilla. Muualta tuleva populaatiopaine on merkittävä muutamilla lajeilla (esim. punarinta) ja epäsuotuisat muutokset talveh-timisalueilla toisilla (esim. leppälintu). Muutokset saalis-tusaineessa ja lajien välisissä kilpailusuhteissa voivat myös vaikuttaa. Pirstoutumisvaikutusten pääpiirteet on selvitetty pääasiassa runsaiden lajien avulla. Luonnonsuojelun kan-nalta kiinnostavimpia ovat kuitenkin taantuneet lajit: onko niillä yhdistäviä piirteitä? Monet taantumiset koskevat kolopesijöitä, ei-varpuslintuja, paikkalintuja ja levinneisyys-deltään itäisiä lajeja. Rajuimmat ovat vähentyneet viime vuosikymmeninä levinneisyysdeltään itäiset, pohjoisessa talvehtivat kolopesijät (esim. pohjantikka, lapintiainen). Koska lintujen reviirokko on yleensä suhteessa ruumiinko-oon, voidaan viime vuosikymmeninä taantuneiden lajien olettaa olevan suurikokoisempia kuin runsastuneiden lajien, mikäli pirstoutumisella on ollut keskeinen merkitys.

Runsastuneiden lajien keskipaino on 20 g ja vähentyneiden 56 g, mikä tukee pinta-alatekijän merkitystä viimeaikaisissa kannanmuutoksissa.

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