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Abundance patterns in bird communities in old boreal forest in relation to stand structure and local habitat configuration

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In this sequel of a landscape level analysis (Edenius & Elmberg 1996) we relate abundance of species and functional groups of birds to stand structure and local habitat configuration in old naturally regenerated forests with a moderate but varying degree of human impact. Many species were rare, whereas the five most abundant comprised 54% of the total sample. No general pattern appeared among single-species regression models (abundance *versus* six habitat measures, N = 12), i.e. most were unique in their combination of variables and signs. Seven species produced models consistent with known habitat preferences, whereas the remaining were hard to interpret or contrary to expectation. Results for *Anthus trivialis* indicate that man-made and natural forest fragmentation affect abundance in opposite directions. Habitat configuration variables were more frequent than stand variables in single-species models, with 'distance to clear-cut or plantation' being the single most common. We found no correlation between territory size and the spatial level at which response patterns were found. Models for functional groups were similarly diverse, habitat configuration variables again appearing more frequently than stand variables. Only a few examples of a consistent multi-level pattern emerge when the present study is combined with Edenius and Elmberg 1996; i.e. a negative effect on abundance in *Turdus iliacus* and in 'Siberian species' on landscape as well as local habitat configuration level.

1. Introduction

Many previous papers address forestry-related effects on abundance, structure, and diversity of tropical and nemoral avian communities. When it comes to boreal forests, however, the topic has received less attention. This is particularly true for North America and Russia, as most relevant studies have been carried out in Finland and Sweden (cf. Welsh & Lougheed 1996). Yet, even from a Fennoscandian perspective at least two central issues remain largely unstudied.

First, do effects of changed habitat structure on lower spatial levels differ from those on landscape level? Only a few multi-level bird studies have been carried out (e.g. Virkkala 1991, Jokimäki & Huhta 1996), although a wealth of data from other biomes indicates that such analyses are essential to properly understand patterns and processes in ecological communities (birds reviewed by Wiens 1989). Acknowledging this, the present paper is a sequel of a landscape level analysis based on the same data set (Edenius & Elmberg 1996). In that study, we did indeed find significant effects of forestry-related habitat changes on species richness and relative abundance of some categories of birds, but not on others. Hence, we now explore whether relating bird abundance patterns to habitat variables at two lower spatial levels provides new insights or even changes the picture.

Secondly, functional groups are increasingly being used in conservation and forest management to shortcut a painstaking species-by-species approach (e.g. Zoneveld 1983, Morrison 1986, Väisänen et al. 1986, Solonen 1994). With respect to boreal Palearctic birds, several such species groups have already been defined based on response to habitat variables (see Methods), but their value remains largely untested.

Thus, the two principal objectives are: (1) to compare bird abundance patterns at stand level and local habitat configuration level with those previously found at the landscape level, and (2) to assess the value of some commonly used functional groups defined by others. All this is done under the assumption that the bird communities studied are structured on a yearly basis (see Methods) in response to habitat qualities which have been altered by human impact in the 20th century.

2. Material and methods

2.1. Study sites and independent variables

This study was carried out in six landscapes (equivalent to 25 × 25 km topographical maps) in the county of Norrbotten, northern Sweden. To avoid confounding effects of distribution limits and differing species pools we selected landscapes within the same biogeographical zone, i.e. the phytogeographical 'northern boreal subzone' (Ahti et al. 1968), which is dominated by coniferous forests where *Pinus silvestris* and *Picea abies* are the most common trees. Forests cover 57–69% of the six landscapes, almost all of the remainder being wetlands (i.e. mires, bogs and lakes). All landscapes have been affected in a similar fashion by slash-and-burn farming, livestock grazing and selective cutting in previous centuries (Hämet-Ahti 1983). Important characteristics of "modern forestry", i.e. clear-cutting, planting and fertilizing were here introduced only after the second world war. Recent impact of this modern forestry is high on three of the landscapes studied, low on the three others (see Edenius and Elmberg (1996) for details about how landscapes were selected).

All study sites were in old (80+ years) naturally regenerated forest, representing a gradient from old growth impacted by low-level firewood collecting to stands with moderate impact of selective cutting in the late 1800's. Thus, none of the study sites has been clear-cut, planted or otherwise subjected to regular present-day silvicultural methods, although these methods have been applied to a varying degree in the surroundings depending on landscape impact type and local conditions.

As all field work was done in one breeding season we strived to maximize the number of study sites, thus selecting 153 points along forestry roads. There were 33, 30, and 29 points, respectively, on low impact landscapes, 21, 20, and 20, respectively, on high impact landscapes. Census points were at least 500 m apart, but generally much farther separated, avoiding edges of plantations and clear-cuts. At each point we collected data on stand structure with a relascope from a randomly selected spot 50 m from the road. Living and dead standing saplings and trees were counted by species. A breast height stem diameter of 10 cm was used to separate 'saplings' from 'trees'. Only the latter are potentially important to the more demanding bird species when it comes to foraging and nest hole excavation. On the other hand, an abundance of saplings indicates a structurally more diverse and multi-layered forest if trees are also common (see below).

We chose independent variables that, for the region as a whole, have the following in common: (1) historically they have been more or less affected by local forest use (Linder & Östlund 1992, Edenius & Elmberg 1996), (2) they have been shown to affect composition of boreal avian communities (e.g. Haapanen 1965, Järvinen et al. 1977, Lynch & Whigham 1984, Väisänen et al. 1986, Virkkala 1990) or their prey (e.g. Jokimäki et al. 1998), (3) they can readily be translated into conservation-oriented modifications of silvicultural practices.

Thus, we used three variables to describe stand structure (# 1–3) and three to describe local habitat configuration (# 4–6): (1) basal area of standing saplings and trees (all tree species) (hereafter 'SBA'), to give a composite and general picture of stem density, canopy cover and layering, (2) basal area of trees only (see above) (hereafter 'BATT'), to describe stem density and canopy cover of trees, (3) basal area of deciduous trees and saplings ('BADT'), i.e. a composite measure referring to *Betula spp., Populus tremula*, and *Salix caprea* in order of decreasing prevalence, (4) distance to nearest forest edge ('DNCP'), i.e. to a clear-cut or a plantation, (5) distance to nearest natural edge ('DNNE'), i.e. to open water, mire or bog, (6) proportion of old forest within a 300 m radius ('POF300'), i.e. an area sufficiently large to contain a breeding territory of most species of forest bird in our study area.

As snags turned out to be sparse or lacking entirely at most sites, variables 1–3 represented living saplings and trees only in the subsequent analyses. Data on local habitat configuration were obtained from vegetation maps using the following stand definitions: 'clear-cut' = dominating tree height 0–2 m, 'plantations' = 2–10 m, and 'old forest' = tree height > 10 m. In practice, and in contrast to the first two classes, 'old forest' stands were naturally regenerated and they have never been clear-cut (i.e., of the same type as the study sites, see above).

Stand as well as local habitat configuration variables cover a wide range of conditions (Table 1), some of which deserve clarifying. First, our landscapes are naturally fragmented by wetlands in a fine-grained fashion, i.e. mean and range of DNNE are much lower than those of DNCP (see also Edenius & Elmberg 1996). Second, SBA, BATT, and BADT all show some remarkably low scores, but this is to be expected in patchily stocked semi-natural and old growth forest. In other words, some of the randomly selected spots at which the relascope measurements were made happened to be in clearings, in forest gaps or in patches of saplings.

2.2. Bird censuses and bird data

For the purpose of this study we assumed that territories and singing sites reflect some kind of habitat assessment and selection by the birds. As the vast majority of individuals in boreal forest bird communities is migratory (e.g. Solonen 1994, Schmiegelow et al. 1997), those encountered by us will have gone through such a selection process only days or weeks before our sampling.

We censused birds from 2 a.m. to 10 a.m. as two 5 minute point counts (Koskimies & Väisänen 1991, Bibby et al. 1992) within a six-day period (7–12 June 1994), less than 50 m from where the stand variables were measured. In brief, we stopped our car at the census point, waited a few minutes, and then counted all birds heard or seen from that point during a period of five minutes. Originally, birds within and outside a circle with a radius of 50 m were counted separately, but for the purpose of this study the two categories were subsequently pooled. To avoid double-counting, observations of bird species the song of which carries farther than 500 m were allocated to one point only. In boreal forests, even single-visit point counts are likely to detect at least 90% of the species and 60% of the breeding pairs at a given site (Järvinen & Lokki 1978). All censusing was done by the authors, and census person as well as visit order

Table 1. Stand structure and habitat configuration characteristics of study sites in old semi-natural boreal forests in northern Sweden.

Stand/configuration variable	Per site (N = 153)		
	Mean	Range	S.D.
Basal area of saplings and trees (m^2/ha) (SBA)	11.8	1–35	5.36
Basal area of trees (BATT)	8.6	1–24	4.52
Basal area of deciduous trees and saplings (BADT)	2.5	1–24	3.38
Distance to nearest forest edge (to clear-cut/plantation, in metres) (DNCP)	637	50–5 000	904
Distance to nearest natural edge (m) (DNNE)	226	50–850	186
Proportion of old forest within 300 m (%) (POF300)	77	1–100	20.5

Table 2. Occurrence of birds in point counts at 153 sites in old semi-natural forest in northern Sweden in 1994.

Species	Number of sites with occurrence	Total number of individuals observed
Aquila chrysaetos	1	1
Tetrao tetrix	5	5
Tetrao urogallus	3	3
Bonasa bonasia	1	1
Tringa ochropus	1	1
Tringa erythropus	16	20
Tringa nebularia	26	27
Columba palumbus	1	1
Cuculus canorus	113	145
Surnia ulula	1	1
Dendrocopos major	2	3
Picoides tridactylus	1	1
Dryocopos martius	7	7
Jynx torquilla	4	4
Corvus corax	32	42
Corvus corone	25	27
Pica pica	6	6
Garrulus glandarius	1	1
Perisoreus infaustus	10	26
Parus major	8	10
Parus cinctus	1	2
Parus montanus	14	18
Turdus viscivorus	22	26
Turdus pilaris	11	13
Turdus philomelos	94	98
Turdus iliacus	88	121
Turdus merula	1	1
Phoenicurus phoenicurus	119	185
Erithacus rubecula	38	43
Sylvia curruca	1	1
Phylloscopus trochilus	148	401
Phylloscopus collybita	2	2
Regulus regulus	23	24
Muscicapa striata	26	26
Ficedula hypoleuca	35	40
Prunella modularis	9	9
Anthus trivialis	67	89
Carduelis chloris	10	11
Carduelis spinus	95	166
Carduelis flammea	97	155
Pyrrhula pyrrhula	37	44
Pinicola enucleator	1	1
Loxia curvirostra	24	194
Fringilla coelebs	39	45
Fringilla montifringilla	143	368
Emberiza citrinella	7	7
Emberiza rustica	13	15
Total		2 437

of the sites on a landscape were reversed in the second census. We here use the highest number of individuals recorded at a site as a measure of abundance for that species. Due to interspecific differences in detectability we regard our estimates as indices of relative abundance, usually not comparable between species and, of course, not as true density measures.

We sampled birds right where the habitat variables were measured, reasoning that any pattern found would then be more likely to represent a causal link, i.e. birds responding directly to habitat qualities. In contrast, many previous Fennoscandian studies addressing the same topic have been based on a combination of site-wise habitat measures and bird data from line-transects covering a much larger area (e.g. Järvinen et al. 1977, but see Jokimäki & Huhta 1996).

Since we sampled later successional forest stages we here only use data for species having forest as their main habitat (*sensu* Solonen 1994). We refer to them as 'all forest species'. A census summary and a full list of recorded 'forest' species are found in Table 2. In addition to analyses of specific patterns we used four functional groups of birds defined and used by other workers, i.e. subsets of 'all forest species' (Appendix 1): (1) species with a long-term decreasing population trend in northern Finland (*sensu* Väisänen et al. 1986; hereafter 'decreasing species'), (2) sedentary species, which are thought to be sensitive to habitat loss through forestry (e.g. Fretwell 1972, Järvinen et al. 1977, Solonen 1994; hereafter 'resident species'), (3) species belonging to the Siberian or Siberian-Canadian faunal group (*sensu* Voous 1960; hereafter 'Siberian species'), which evolved in the boreal environment and may hence have strong habitat affinities (Mönkkönen & Welsh 1994), and (4) hole-nesting birds, i.e. primary or secondary nesters in cavities in tree trunks, species generally assumed to be declining as the trees they require become scarcer in managed forests. As can be seen from Appendix 1, the four functional groups are partly overlapping. Avian nomenclature follows Cramp et al. (1977–1994).

Because our data set consists of count data and contains many zeroes and low values, we used Poisson regression to explore relationships between bird abundance and habitat variables. The modelling work was done with generalized linear modeling in GLIM (Aitkin et al. 1989). For each species and functional group, separate models were employed for each of the independent variables, and the explanatory power of the variable in question was determined by the amount of change in deviance from the null model. Regression was done on untransformed habitat variables based on visual inspection of residual plots. Overdispersion, which is a potential problem in Poisson regression, was checked for, but was found to be a minor problem. However, parameter estimation for decreasing species was adjusted by Pearson's χ^2 to account for overdisperson (Crawley 1993). Analyses of functional groups included count data for all species in the group, but single-species modelling was attempted only for species occurring at 20 sites or more.

3. Results

Among the independent habitat variables, five out of 15 possible pairwise intercorrelations were significant, i.e. SBA versus BATT, SBA versus SBT, BADT versus DNCP, DNCP versus POF300, and DNNE versus POF300 ($P < 0.05$, $N = 153$, all variables except SBA were non-normally distributed and hence log-transformed before analysis).

Using the census criteria above (i.e. the maximum score out of two counts of 'all forest species') observations of 2 437 individuals of 47 species qualified for further analyses (Table 2). On average, there were 15.9 birds and 9.3 species per site (Table 3). Many species were rare; 26 (55%) occurred at less than 10% of the sites (i.e. 15 sites or less; Table 2). On the other hand, a few were very common. The five species recorded at the highest number of sites, i.e. *Phylloscopus trochilus, Fringilla montifringilla, Phoenicurus phoenicurus, Cuculus canorus*, and *Carduelis flammea* comprised 35% of the total sample. The five most abundant species in our sample were *Phylloscopus trochilus, Fringilla montifringilla, Loxia curvirostra, Phoenicurus phoenicurus,* and *Carduelis spinus,* which together made up 54% of the sample. By contrast and by functional groups, resident species comprised only 4.5% of the individuals recorded, and hole-nesting, decreasing and Siberian group birds 11.1%, 22.6% and 22.5%, respectively (Table 3).

Twenty species met the criterion for single-species modelling, i.e. they occurred at 20 sites or more. In twelve of these species we found a significant relationship with one or more of the habitat variables (Table 4, upper section). There were no general trends among the single-species models, i.e. most had a unique combination of variables and signs. However, *Corvus corax* and *Erithacus rubecula* were both more common when DNCP was short, whilst *Turdus iliacus* and *Fringilla montifringilla* showed the opposite trend. Further, the lack of general response patterns means that no 'new' functional groups were found.

If single-species models are sorted by independent variables, though, other patterns emerge. First, habitat configuration variables appear more often than stand variables (in ten and four species, respectively). Second, DNCP is the single-most frequently occurring variable, being positively associated with abundance in four species and negatively in three. BATT and DNNE appear in four models each, but also with inconsistent sign.

Functional group models are similarly diverse. All groups except resident species produced a significant model (Table 4, lower section), POF300 and DNCP being the most frequently occurring independent variables. POF300 was consistently and positively associated with abundance.

Table 3. Species richness (all forest species) and relative abundance (all forest species and four functional groups) at 153 study sites in old semi-natural boreal forest in northern Sweden.

Bird group	Sum	Per site (N = 153)		
		Mean	Range	S.D.
Forest birds				
No. of species	47	9.32	3–15	2.20
No. of individuals	2 437	15.93	4–47	5.76
Decreasing species				
No. of individuals	552	3.61	0–36	5.10
Resident species				
No. of individuals	110	0.72	0–6	1.10
Siberian species				
No. of individuals	549	3.59	0–11	2.14
Hole-nesting species				
No. of individuals	271	1.77	0–6	1.28

4. Discussion

4.1. Stand level and habitat configuration level patterns

Even though our analyses are based on indices of abundance rather than on true abundance measures (see 2.2) the species composition corresponds very well to previous studies in northern Norway, Sweden, and Finland, as does the general pattern of abundance among species and functional groups (Helle 1983, Virkkala 1987b, Haila & Järvinen 1990, Stokland 1994, Jokimäki & Huhta 1996). Hence, our bird sample is representative for the area and for boreal forests in the western Palearctic.

Some models in Table 4 are consistent with known habitat preferences for the respective species (Cramp et al. 1977–1994, Gjershaug et al. 1994, Hagemeijer & Blair 1997, Väisänen et al. 1998): (1) *Corvus corone* is associated with young and dense forest, (2) *Turdus viscivorus* prefers old well-stocked but not too closed stands, (3) in older forest *Phylloscopus trochilus* is more common where there are adjacent habitats of young forest or wetlands, (4) *Fringilla montifringilla* is more abundant in the interior of stands, and (5) *Anthus trivialis* is more common when clear-cuts and plantations are nearby, but it avoids edges of wetlands.

The models for *Phoenicurus phoenicurus, Carduelis flammea* and *Loxia curvirostra* may seem counter-intuitive or contradictory when viewed against known habitat preferences. In the case of *Phoenicurus phoenicurus* we are confident that the negative correlation with basal area of deciduous trees and saplings (BADT) is not due to avoidance *per se* of mature deciduous trees, but rather a side-effect of the species' regional association with old coniferous forests (e.g. Jokimäki & Huhta 1996, Edenius & Sjöberg 1997). The latter are relatively rich in snags and other suitable nest sites but have very few deciduous trees for entirely natural reasons. Ecologically plausible interpretations of the models for *Carduelis flammea* and *Loxia curvirostra* can indeed be conceived but will remain more speculative. For example, the latter species is a very early breeder and it is likely that we did not observe nesting birds but rather measured habitat utiliza-

Table 4. Poisson regression analysis of relationships between bird abundance and habitat variables at 153 sites in old semi-natural boreal forest in northern Sweden. Parameter estimates and signs for variables showing a significant (P < 0.05) change in deviance when added to the model are shown. Numbers within parentheses denote the relative order of variables in terms of the amount of deviance reduced. SBA = basal area of saplings and trees, BATT = basal area of trees only, BADT = basal area of deciduous trees and saplings, DNCP = distance to nearest clear-cut or plantation, DNNE = distance to nearest natural edge, POF300 = proportion of old forest within 300 m.

	SBA	BATT	BADT	DNCP	DNNE	POF300
Species						
Corvus corax				– 0.00049		
Corvus corone		– 0.1130				
Turdus viscivorus		0.1030 (1)			0.0020 (2)	
Turdus iliacus				0.00031		
Phoenicurus phoenicurus		0.0319 (2)	– 0.0651 (1)			
Erithacus rubecula				– 0.00471		
Phylloscopus trochilus						– 0.0054
Regulus regulus					– 0.0028	
Anthus trivialis				– 0.00059 (1)	0.0158 (2)	
Carduelis flammea				0.00032 (1)		– 0.0118 (2)
Loxia curvirostra	– 0.2368 (2)	0.3220 (1)		0.00011 (5)	– 0.0034 (4)	– 0.0487 (3)
Fringilla montifringilla				0.00014		
Functional group						
All forest species						0.0026
Decreasing species		0.0546 (1)	– 0.0515 (3)	– 0.00016 (4)		0.0124 (2)
Siberian species				0.00017		
Hole-nesting species						0.0033

tion by families and groups of individuals that may have nested someplace else.

Examples (3) and (5) above are thought-provoking and of more general ecological interest. Our results for *Phylloscopus trochilus* imply that species occurring in the interior of a stand may be affected by habitat configuration far outside the boundaries of their territory. Secondly, our data for *Anthus trivialis* (and to some extent for *Loxia curvirostra*) indicate that man-made and natural fragmentation (distance to nearest clear-cut or plantation (DNCP) and distance to nearest natural edge (DNNE), respectively) affect abundance in opposite directions. This is worth closer study, as boreal birds have so far only been analyzed with respect to fragmentation by forestry (e.g. Virkkala 1987a, Raivio & Haila 1990, Jokimäki & Huhta 1996, Schmiegelow et al. 1997, but see Edenius & Sjöberg 1997).

Also the models for *Turdus iliacus* and *Regulus regulus* seem contrary to expectation at first, as they are often seen as 'edge' and 'stand interior species', respectively (e.g. Helle 1983). However, as we actively chose census points away from forest edges, our results do not contradict the findings by Helle and others. Further, and now considering the range of DNCP and DNNE actually covered by us, both species are associated with *Picea abies* in the study region, which is here often the dominating tree close to wetlands. Hence, at least in the case of *Regulus regulus* the model makes sense because a common side-effect of proximity to wetlands is an abundance of *Picea abies* (cf. *Loxia curvirostra* above).

Human impact at our 153 study sites is generally limited to draining, selective cutting and other uses which do not transform the habitat as radically as modern silviculture usually does (e.g. clear-cutting, planting, thinning, monoculture). Nevertheless, most of our sites today probably have lower BATT (basal area of trees), BADT, POF300 (proportion of old forest within 300 m), and DNCP, but higher DNNE than would have been the case if they had remained in a more pristine stage. If our matrix of single-species models is extrapolated to such a hypothetical 'pristine scenario', *Corvus corax, Corvus corone, Erithacus rubecula, Phylloscopus trochilus,* and *Anthus trivialis* would have been less abundant than they are today, whereas *Turdus iliacus, Regulus regulus,* and *Fringilla montifringilla* would have been more common than they are at present. Along the same lines, human impact has favored *Turdus viscivorus, Phoenicurus phoenicurus, Carduelis flammea,* and *Loxia curvirostra* in some respects, but affected their abundance negatively in others. This scenario may serve to stimulate our thinking about the effects of fragmentation and different forms of forestry, but it is based on a snapshot in time and it must be balanced against other factors possibly affecting the abundance and distribution of boreal birds (long-term distribution changes, predation, competition for nest sites etc.). In this context it should be noted that the abundance of some species which are well known to have declined greatly due to present silvicultural practices (e.g. *Parus cinctus, Perisoreus infaustus, Picoides tridactylus* (Väisänen et al. 1998)) could not be analyzed because the timing of our censuses did not permit us to observe them in sufficient numbers.

A corresponding 'pristine scenario' for the abundance of functional groups shows that 'all forest species', Siberian species and hole-nesters have been affected negatively by the seemingly moderate anthropogenic impact during the last 100 year in the forests studied. The same can be said about the decreasing species although the third variable to enter the model points in another direction. However, the latter is probably an effect of the preferences of *Phoenicurus phoenicurus* and *Loxia curvirostra* for coniferous habitats (which comprise 67% of all individuals of decreasing species).

Thus, uneven abundance among species within a functional group may greatly reduce its value when it comes to describing and understanding boreal avian communities. This conclusion is supported also by our model for Siberian species; *Fringilla montifringilla* comprises 67% of the sample, and not very surprisingly its specific model is strikingly similar to that of the functional group. Resident species, finally, were so scarce in our sample (viz. 0.72 individuals per site) that this functional group too was of little use in our analyses. Although early breeders were probably underestimated by our sampling in June, by and large our results do not provide support for functional groups as a management tool for boreal bird communities (cf. Landres et al. 1988, Niemi et al.

1997). We agree with those who argue that responses to habitat change are largely species-specific (e.g. McGarigal & McComb 1995, Jokimäki & Huhta 1996).

Habitat configuration variables entered models more frequently than stand structure variables on the whole when specific and functional group models are both considered. However, we found no correlation between level of response and territory size. *Corvus corone* and *Phoenicurus phoenicurus*, which both have large territories, have models including stand variables only, and *Erithacus rubecula, Phylloscopus trochilus* and *Regulus regulus*, all with very small territories, have models including configuration variables only. Until the processes behind these patterns are clarified, we see many good reasons why several spatial levels must be incorporated if we are to understand variation in abundance among species as well as for devising management and conservation strategies.

4.2. Comparing patterns on different spatial levels

Our landscape scale analysis (Edenius & Elmberg 1996; block size 25 × 25 km, each with either high or low recent impact by modern forestry) produced results (tables 7b and 8b) of which some support and some contradict the patterns described in the present paper. Twelve species show significant models in the latter (Table 4), but only two of them in the landscape level ANOVA of effects of forestry impact. Moreover, patterns are inconsistent in both cases. *Anthus trivialis* is favored by human impact on habitat configuration level, but affected negatively on landscape level. *Carduelis flammea* has been affected both ways on the level of habitat configuration, and favored on the landscape level. Our only example of a consistent species-specific pattern is *Turdus iliacus*, which appears to have been affected negatively by changed tree species composition on the landscape level and by lowered DNCP on the level of habitat configuration. Among functional groups, Siberian species is the only one showing a significant multi-level pattern: a negative effect of forestry, i.e. of area reduction on landscape level and of fragmentation of old forest stands on the level of habitat configuration. Again, this may to a large extent be the effect of a single species, *Fringilla montifringilla,* which dominates the sample on both levels. Just like Jokimäki and Huhta (1996) we conclude that bird responses to human impact are inconsistent, scale-dependent, and species-specific, and that few general patterns emerge.

Virkkala (1991), Helle and Järvinen (1986), Väisänen at al. (1986) as well as Jokimäki and Huhta (1996) stress that processes on yet higher spatial levels, i.e. regional and continental, may be important to the structure of boreal bird communities. We agree; the high abundance of *Loxia curvirostra* in 1994, in turn affecting some of our models, serves as a good example of a long-distance influx affecting local populations.

Two conclusions bearing on the conflict between timber extraction and biodiversity preservation in boreal forests emerge from this study. First, the local effects of "pre-modern" forest management in naturally regenerated stands seem less drastic than when intensively managed plantations are compared with old growth (Virkkala 1987a *versus* Nilsson 1979 and Raivio & Haila 1990). Second, the moderately intensive silvicultural practices adopted at our study sites can be combined with fairly ambitious goals of retained avian biodiversity.

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Sammanfattning: **Talrikhetsmönster hos fåglar i gamla boreala skogar i förhållande till beståndsstruktur och lokal habitatkonfiguration.**

I denna efterföljare till en tidigare studie på landskapsnivå (Edenius & Elmberg 1996) relaterar vi skogshäckande fåglars talrikhet vid 153 invente-

ringspunkter i mellersta Norrbottens län till beståndsstruktur och lokal habitatkonfiguration. De undersökta skogarna är gamla och naturligt föryngrade, och visar varierande men måttlig mänsklig påverkan av bland annat äldre tiders skogsbruk och dikning. Nästan alla tidigare studier med liknande frågeställning har istället jämfört rena urskogar med intensivt skötta produktionsskogar. Totalt registrerades 2437 fåglar av 47 arter (Tabell 2), och i genomsnitt noterades 15,9 individer och 9,3 arter per inventeringspunkt (Tabell 3). Många arter var ovanliga, medan de fem vanligaste (rödstjärt, lövsångare, grönsiska, mindre korsnäbb och bergfink) tillsammans utgjorde 54% av alla inräknade individer. Inga generella mönster framträdde i de artvisa regressionsmodellerna (N = 12); tvärtom var de flesta modeller säregna vad gäller ingående variabler och dessas tecken (Tabell 4). För kråka, dubbeltrast, lövsångare, bergfink, trädpiplärka, rödstjärt och kungsfågel erhöll vi modeller som stämmer väl överens med tidigare dokumenterade habitatpreferenser, medan övriga fem gav oväntade eller svårtolkade resultat. Vi fann att trädpiplärkans talrikhet påverkas på motsatta vis av antropogen och naturlig skogsfragmentering, vilket är särskilt intressant i generella bevarandebiologiska termer. På det hela taget förekom habitatkonfigurationsmått oftare än beståndsstrukturmått i de artvisa modellerna, och av de förra var 'avstånd till hygge eller ungskog' allra oftast förekommande. Vi fann inget samband mellan revirstorlek och den rumsliga nivå på vilken de artvisa modellernas variabler hörde hemma. Man hade annars kunnat förvänta sig att arter med stora revir framför allt borde påverkas av förändringar på den högre rumsliga skalan (habitatkonfiguration), medan arter med små revir mest skulle påverkas av beståndsstruktur. Regressionsmodellerna för funktionella grupper var också de sins emellan olika och med få gemensamma drag. Även här var habitatkonfigurationsmått oftare förekommande än beståndsstrukturmått. När resultaten från denna studie fogas till de vi tidigare erhöll på landskapsnivå (Edenius & Elmberg 1996) framträder förvånansvärt få genomgående mönster. De tydligaste exemplen är att rödvingetrast och 'Sibiriska arter' (*sensu* Voous 1960) genomgående påverkats negativt av de förändringar i habitat- och landskapsstruktur som skett, i huvudsak på grund av skogsbruk.

References

Ahti, T., Hämet-Ahti, L. & Jalas, J. 1968: Vegetation zones and their sections in northwestern Europe. — Ann. Bot. Fennici 5: 169–211.

Aitkin, M., Anderson, D., Francis B. & Hinde, J. 1989: Statistical modelling in GLIM. — Clarendon Press, Oxford.

Bibby, C. J., Burgess, N. D. & Hill, D. A. 1992: Bird census techniques. — Academic Press, London.

Cramp, S., Simmons, K. E. L. & Perrins, C. M. 1977–1994: Handbook of the birds of Europe the Middle East and North Africa. The birds of the Western Palearctic. Volume 1–9. — Oxford University Press.

Crawley, M. J. 1993: GLIM for ecologists. — Blackwell, London.

Edenius, L. & Elmberg, J. 1996: Landscape level effects of modern forestry on bird communities in north Swedish boreal forests. — Landscape Ecology 11: 325–338.

Edenius, L. & Sjöberg, K. 1997: Distribution of birds in natural landscape mosaics of old-growth forests in northern Sweden: relations to habitat area and landscape context. — Ecography 20: 425–431.

Fretwell, S. D. 1972: Populations in a seasonal environment. — Princeton University Press, Princeton, N. J.

Gjershaug, J. O., Thingstad, P. G., Eldöy, S. & Byrkjeland, S. (Eds.) 1994: Norsk fugleatlas. — Norsk Ornitologisk Förening, Klaebu.

Haapanen, A. 1965: Bird fauna of the Finnish forests in relation to forest succession. I. — Ann. Zool. Fennici 2: 153–196.

Hagemeijer, E. J. M. & Blair, M. J. (Eds.) 1997: The EBCC Atlas of European breeding birds: Their distribution and abundance. — T & AD Poyser, London.

Haila, Y. & Järvinen, O. 1990: Northern conifer forests and their bird species assemblages. — In: Keast, A. (ed.), Biogeography and ecology of forest bird communities: 61–85. SPB Academic Publishing bv, The Hague, The Netherlands.

Helle, P. 1983: Bird communities in open ground-climax forest edges in northeastern Finland. — Oulanka Reports 3: 39–46.

Helle, P. & Järvinen, O. 1986: Population trends of North Finnish land birds in relation to their habitat selection and changes in forest structure. — Oikos 46: 107–115.

Hämet-Ahti, L. 1983: Human impact on closed boreal forest (taiga). — In: Holzner, W., Werger, M. J. A. & Ikusima, I. (eds), Man's impact on vegetation: 201–211. W Junk Publishers, The Hague, The Netherlands.

Jokimäki, J. & Huhta, E. 1996: Effects of landscape matrix and habitat structure on a bird community in northern Finland: a multi-scale approach. — Ornis Fennica 73: 97–113.

Jokimäki, J., Huhta, E., Itämies, J. & Rahko, P. 1998: Distribution of arthropods in relation to forest patch size, edge, and stand characteristics. — Canadian Journal of Forerst Research 28: 1068–1072.

Järvinen, O., Kuusela, K. & Väisänen, R. A. 1977: Effects of modern forestry on the numbers of breeding birds in Finland in 1945–1975. — Silva Fennica 11: 284–294. (In Finnish with summary in English).

Järvinen, O. & Lokki, J. 1978: Indices of community structure in bird censuses based on a single visit: effect of variation in species efficiency. — Ornis Scandinavica 9: 87–93.

Koskimies, P. & Väisänen, R. A. 1991: Monitoring bird populations. — Zoological Museum, Finnish Museum of Natural History, Helsinki.

Landres, P. N., Verner, J. & Thomas, J. W. 1988: Ecological uses of vertebrate indicator species: a critique. — Conservation Biology 2: 316–328.

Linder, P. & Östlund, L. 1992: Changes in the boreal forests of Sweden 1870–1991. — Svensk Botanisk Tidskrift 86: 199–216. (In Swedish with an English summary).

Lynch, J. F. & Whigham, D. F. 1984: Effects of forest fragmentation on breeding bird communities in Maryland, USA. — Biol. Conserv. 28: 287–324.

MacGarigal, K. & McComb, W. C. 1996: Relationships between landscape structure and breeding birds in the Oregon coast range. — Ecol. Monogr. 65: 235–260.

Morrison, M. L. 1986: Bird populations as indicators of environmental change. — In: Johnston, R. F. (ed), Current Ornithology: 429–451. Plenum Press, New York.

Mönkkönen, M. & Welsh, D. A. 1994: A biogeograhpical hypothesis on the effects of human caused landscape changes on the forest bird communities of Europe and North America. — Ann. Zool. Fennici 31: 61–70.

Niemi, G., Hanowski, J. M., Lima, A. R. & Weiland, N. 1997: A critical analysis on the use of indicator species in management. — Journal of Wildlife Management 61: 1240–1252.

Nilsson, S. G. 1979: Effect of forest management on the breeding bird community in southern Sweden. — Biol. Conserv. 16: 135–143.

Raivio, S. & Haila, Y. 1990: Bird assemblages in silvicultural habitat mosaics in southern Finland during the breeding season. — Ornis Fennica 67: 73–83.

Schmiegelow, F. K. A., Machtans, C. S. & Hannon, S. J. 1997: Are boreal birds resilient to forest fragmentation? An experimental study of short-term community responses. — Ecology 78: 1914–1932.

Solonen, T. 1994: Structure and dynamics of the Finnish avifauna. — Memoranda Soc. Fauna Flora Fennica 70: 1–22.

Stokland, J. N. 1994: Biological diversity and conservation strategies in Scandinavian boreal forests. — Ph.D. Thesis, Department of Biology, University of Oslo.

Virkkala, R. 1987a: Effects of forest management on birds breeding in northern Finland. — Ann. Zool. Fennici 24: 281–294.

Virkkala, R. 1987b: Geographical variation in bird communities of old intact forests in northern Finland. — Ornis Fennica 64: 107–118.

Virkkala, R. 1990: Ecology of the Siberian Tit Parus cinctus in relation to habitat quality: effects of forest management. — Ornis Scand. 21: 139–146.

Virkkala, R. 1991: Spatial and temporal variation in bird communities and populations in north-boreal coniferous forests: a multiscale approach. — Oikos 62: 59–66.

Voous, K. H. 1960: Atlas of European Birds. — Nelson, London.

Väisänen, R. A., Järvinen, O. & Rauhala, P. 1986: How are extensive, human-caused habitat alterations expressed on the scale of local bird populations in boreal forests? — Ornis Scand. 17: 282–292.

Väisänen, R. A., Lammi, E. & Koskimies, P. 1998: Muuttuva pesimälinnusto (Finnish bird atlas, in Finnish). — Otava, Helsinki.

Welsh, D. A. & Lougheed, S. C. 1996: Relationships of bird community structure and species distributions to two environmental gradients in the northern boreal forest. — Ecography 19: 194–208.

Wiens, J. A. 1989: The ecology of bird communities. — Cambridge University Press. Cambridge.

Zoneveld, I. S. 1983: Principles of bio-indicators. — Environmental Monitoring Assessment 3: 207–217.

Appendix 1. Sub-groups of forest birds used as dependent variables. From the original classification cited, only birds occurring in the present study are listed.

'Decreasing species' = species with a long-term decreasing population trend in northern Finland *sensu* Väisänen et al. (1986)
Tetrao urogallus
Picoides tridactylus
Dryocopus martius
Garrulus glandarius
Perisoreus infaustus
Parus cinctus
Parus montanus
Turdus viscivorus
Phoenicurus phoenicurus
Anthus trivialis
Loxia curvirostra

'Resident species' = resident species *sensu* Solonen (1994)
Tetrao urogallus
Bonasa bonasia
Picoides tridactylus
Dryocopus martius
Corvus corax
Perisoreus infaustus
Parus major
Parus cinctus
Parus montanus

'Siberian species' = species belonging to the Siberian-Canadian faunal group *sensu* Voous (1960)
Bonasa bonasia
Surnia ulula
Picoides tridactylus
Perisoreus infaustus
Parus cinctus
Turdus pilaris
Turdus iliacus
Fringilla montifringilla
Pinicola enucleator
Emberiza rustica

'Hole-nesting species' = species nesting in cavities in tree stems (Jokimäki & Huhta 1996).
Surnia ulula
Dendrocopos major
Picoides tridactylus
Dryocopus martius
Jynx torquilla
Parus major
Parus cinctus
Parus montanus
Phoenicurus phoenicurus
Ficedula hypoleuca