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Forestry and the boreal fauna: matching management with natural forest dynamics

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Variation in assemblages of birds and carabid beetles in southern Finnish coniferous forest is described (1) within forest stands, (2) across the successional gradient from recently cut sites to mature forest, and (3) over a period of years. For birds, variation within a mature forest area was mainly due to nonsynchronous fluctuations of species and stochasticity in the site selection of individual breeding pairs. For carabid beetles, small-scale aggregations within a forest presumably reflected movement patterns of individuals. Both birds and carabids included some old-growth specialists and species inhabiting mainly, or exclusively, open habitats in young forest stages. The grain-patterning of silvicultural mosaics differ: birds put together their home ranges in a small-grained fashion, whereas for carabids the environment is coarse-grained. Maintenance of ecological heterogeneity at various scales relevant to different organisms in the taiga depends on how human-induced change and natural change compare with each other. The observed patterns are related to natural disturbance dynamics, and ecologically sound management approaches are discussed.

1. Setting the stage: ecological variation in the taiga

1.1. Scaling ecological variation

The appearance of 'biodiversity' as a basic issue in conservation reflects the realization that spatial and temporal variation is essential for the continuing functioning of ecological systems (see Wilson 1988, 1992). Thus, recording mere 'change' is but a starting point when evaluating ecological consequences of human activities. What matters is the relationship between human-induced change and change occurring naturally (Haila & Levins 1992); the question is, do human activities modify the dynamics of natural change? A major complication in addressing this question is that ecological processes operating on different scales cause different kinds of 'change' simultaneously (Levins 1973, Allen & Starr 1982, O'Neill et al. 1986, Levin 1992). These different scales should be considered simultaneously, but processes at each level should be maintained distinct from each other. One possibility, which we adopt in this paper, is to compare variation in groups of organisms which respond to processes on different scales. Defining adequate scales is primarily an empirical problem and depends on the ecological process in which one is interested (Addicott et al. 1987, Wiens 1989).

When investigating variation, one has to decide what are the relevant varying units, and what are their extensions, that is, what is the spatial and temporal resolution needed in the data. The measuring instrument and what is measured must match each other. In survey research a critical feature of the 'measuring instrument' is the sampling design (Rosen 1977, Wiens 1989, Levin 1992), which depends on assumptions about what units are worth observing and recording in the system studied (Haila 1988, 1992). An important distinction in ecological scaling is between individual-scale and population-scale processes (Wiens 1981, Birks 1986, Haila 1990). For instance, for recording local extinctions, observations must be made on the scale of local populations; shifts in the locations of reproducing individuals may represent ecologically interesting variations on the scale of individual behaviour, but this is a different issue (Smith 1975, Simberloff 1976, Haila & Hanski 1993, Haila et al. 1993a).

This paper is based on data concerning quantitative variation in two ecologically different groups of animals, namely birds and carabid beetles, in the southern Finnish taiga modified by forestry. The aim of the study is to understand ecological effects of modern forestry on the forest fauna. The data were collected in the years 1984–90, and the specific results as well as primary data are published elsewhere; the references are given below in the appropriate contexts. Here we characterize three aspects of variation in numbers in these groups: (1) within mature forest, (2) across the successional gradient between different forest age-classes, and (3) over a period of years.

After characterizing patterns of variation, we address the following broader questions:

1) How widely vs. narrowly are animals distributed across environmental types created by forestry?
2) What is the relationship between stochastic effects and environmental differences in explaining abundance variation in taiga animals?
3) How do individual and population scales relate to each other in the abundance variation in taiga animals?
4) What are the implications of our results for developing ecologically sound forest-management practices?

The questions we ask relate to the relationships between vegetation dynamics and the fauna in boreal forests. Before proceeding to the data, we give a brief characterization of natural disturbance processes in the taiga and formulate some hypotheses about how these might influence the fauna.

1.2. Natural disturbance and the fauna in the taiga

Extant animal communities in a particular landscape have been shaped by recurring disturbances that change conditions locally, at a characteristic average frequency, and trigger succession in vegetation (Watt 1947, Levin & Paine 1974, Connell 1980, Pickett & White 1985, Levin 1992). In northern Europe, such disturbances have occurred on three major scales (Birks 1986, Delcourt & Delcourt 1988, 1991, Shugart et al. 1992): (1) glacial cycles have shaped the extant species pool, (2) successions following regular major disturbances, particularly forest fires, have modified the distribution of life-history types within the species pool, and (3) mosaic processes (Whittaker & Levin 1977), connected with recurrent small-scale events such as the dying of single trees or variation in litter quality, have influenced the availability of particular niches in space and time.

Virgin taiga has been characterized as a 'fire ecosystem' in which vegetation dynamics are influenced mainly by frequent forest fires which follow a 'natural fire rotation' (Heinselman 1973, Rowe & Scotter 1973, Kuleshova 1981, Wright & Bailey 1982; data from northwestern Europe summarized by Zackrisson 1977, Haapanen & Siitonen 1978, Tolonen 1983, Engelmark 1984, 1987). Forest fires create a mosaic landscape of different-aged forest stands (see Loucks 1970, Wright 1974, Shugart 1984). Most plant species characteristic of early succession are probably present on burned sites right from the beginning as seeds or root-systems (Kujala 1926, Sarvas 1937). Thus, the regenerating vegetation shows great heterogeneity both on a fine scale, among different sites within one burn, and on a regional scale, among different burns (Miles 1987). However, floristic diversity of coniferous forest peaks quite early after the disturbance and decreases with increasing age (Esseen et al. 1992). The change in forest structure is thus non-linear in time, being rapid in the beginning but slowing down later. A mature forest is relatively stable at the stand level, but spatial heterogeneity is maintained by mosaic processes operating on a small scale within stands.

The 'fire ecosystem' view of taiga regeneration is well substantiated. Thus, although more data are needed as to details, for instance variation in fire frequencies in different types of forest, some qualitative predictions are warranted about the dynamics of animal populations in fire-driven taiga (Heinselman 1981, Fox 1983). First, primeval taiga has been characterized by a great degree of spatial heterogeneity. This implies that numerically dominant organisms have generalized habitat requirements or live in habitats that are continuously available. In addition, the 'adversity selection' of Greenslade (1983) may have furthered generalism. Second, types of species dwelling in different forest stages presumably vary with the age and stability of the forest types they inhabit, roughly along an '*r–K*' continuum (Parsons 1987). Early stages are characterized by efficiently colonizing, ephemeral open-country species, and old stages by more persistent species, adapted to permanent habitats. Third, continuity of the habitat is considered to be critical, particularly for organisms requiring specific microhabitats produced by mosaic processes operating on a small scale. This might be true, for instance, of species adapted to decaying wood. All taiga organisms do not necessarily show good dispersal ability; natural history data on endangered taiga insects suggest that some of them may be poor dispersers and occur in persistent populations in particular microhabitats (J. Muona, pers. comm.; Siitonen & Martikainen 1993).

The relationship between spatio-temporal scales of silvicultural and natural disturbance is decisive for assessing the effect of forestry on taiga animals. Researchers with a background in forestry often assume that, for instance, clear-cutting is a good substitute for natural wildfires which are nowadays efficiently extinguished (Kuusela 1990). This presumed similarity is, however, not true for several groups of forest animals, and requires systematic assessment: we return to this issue in the discussion.

2. Study area, materials and methods

The taiga can be divided into latitudinal subzones (see Hare & Ritchie 1954, Chernov 1975, Hämet-Ahti 1981, Tuhkanen 1984, Delcourt & Delcourt 1991). The phytogeographic zonation of the northwestern European taiga was described by Ahti et al. (1968) and Hämet-Ahti (1981), and corresponding zoogeographic zonations were discussed by Järvinen & Väisänen (1973, 1980).

Our study sites were located at the border between the south- and mid-boreal zones in northern Häme in three areas: in Seitseminen National Park, Helvetinjärvi National Park and in the surroundings of Hyytiälä Forest Research Station; these areas are about 50 km apart (at approximately 62°N, 23°E). The forests are conifer-dominated and relatively barren; general descriptions appear in Haila et al. (1987) and Niemelä et al. (1988). In the following we use the term 'type of forest' in a broad sense when referring to variation in forest structure and composition.

Data on the two animal groups were collected as follows: Bird data originate from two study schemes within and in the vicinity of Seitseminen National Park: (1) We have done censuses in a 36-ha study plot, called the 'forest plot' below, within the national park in 1985–90 (described in Haila et al. 1989). About one-third of the plot is covered by spruce-dominated old-growth forest, with other parts comprising younger stands and small peatlands. We divided the plot into 21 blocks, called 'habitat blocks' below, on the basis of tree-species composition and height, and use the blocks (in the manner specified below) as units for comparing variation within the plot. (2) We also censused 12 fragments (area 0.7–4.4 ha) of spruce-dominated mature forest (<100 years old), affected by management, and the surrounding sapling stands, in 1986–88 (described in Raivio & Haila 1990, Haila et al. 1993a). In the forest plot we used territory mapping, and in the fragments and surroundings a version of territory mapping in which we used observation frequencies in different habitat configurations for comparing bird abundances (for details, see the primary publications listed above). In addition, in 1987-90 in the forest plot in Seitseminen, we monitored movement patterns and space use of chaffinch males by radio telemetry (study scheme no. 1 above) (Hanski et al. 1992).

Carabid data were collected with pitfall traps according to three study schemes (one permanent trapping site plus two surveys covering a wider region): (1) The permanent site was in a spruce-dominated old-growth forest (most canopy trees >140 yrs.) in Musturi State Forest Reserve (Niemelä et al. 1992). In 1985, 300 traps, and in the following years (1986–1990) 64 traps were operated continuously through the growing season (May–October). (2) The first larger-scale survey, conducted in 1984–85, covered 35 mature, mostly unmanaged forest fragments and their managed surroundings cut 20–60 yrs. ago (Niemelä et al. 1988). (3) The second survey, conducted in 1989, included four mature-forest sites and successional sites at 0, 2 and 10 years post-cut (Punttila et al. 1991).

For describing assemblage-level variation in and between the samples we used within-site (alpha) and between-site (beta) diversity (Whittaker 1977). Rarefaction (Simberloff 1978) was used for estimating alpha-diversity, and the Czekanowski index of percentage similarity (after log transformation) (Wolda 1981, Pesenko 1982) and the Bray-Curtis index of similarity for estimating beta-diversity (Ludwig & Reynolds 1988). The use of the indices and pooling of data for different comparisons is described in appropriate contexts below.

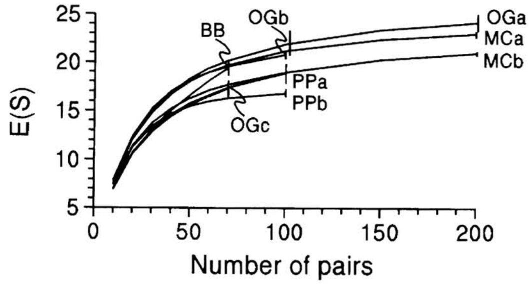

Fig. 1. Species richness ($E(S)$) of bird assemblages estimated by rarefaction in the eight 'habitat blocks' in the 36 ha 'forest plot' in Seitseminen National Park (Haila et al. 1989: fig. 1). — OGa, b, c = old-growth forests, PPa, b = pine plantations, BB = birch bog, MCa, b = mixed coniferous forest.

3. Patterns of spatial and temporal variation

3.1. Breeding birds

3.1.1. Variation within mature forest

The mapping data from the forest plot in Seitseminen allowed us to investigate diversity variation in the song-bird assemblage among stands within the plot. For the comparisons we pooled observations from each habitat block with a total area of at least 1.5 hectares over the six census years, including all pairs that maintained part of their singing territory in that block. There were eight such habitat blocks in the plot, belonging to six habitat types as defined in Haila et al. (1989: fig 1); the peat bog within the plot was not included in the comparison. However, species that could not reasonably be attributed to individual habitat blocks because of their wide-ranging movements were excluded from the analysis. Such species included tetraonids, waders, the black woodpecker *Dryocopus martius*, the mistle thrush *Turdus viscivorus* and the jay *Garrulus glandarius*. A total of 27 species were included in the comparison.

Rarefaction analysis of the alpha diversity of the pooled data sets showed that among the habitat blocks the open, pine-dominated stand had less and one of the old-growth stands had more species than the others (Fig. 1). Note that this comparison included both young and mature stands.

However, there was variation in species composition between the forest types. We evaluated this by calculating percentage similarity values of pooled data sets of the habitat blocks covered by mature, at least 80-year-old, forest (five blocks): three tall (>25 m) and spruce-dominated, one tall (about 20 m) and mixed coniferous, and one tall and pine-dominated (see Haila et al. 1989: fig. 1). The Czekanowski similarity values (max. 1.0) are given in the tabulation below:

	Tall spruce			Tall
	(1)	(2)	(3)	mixed
Tall spruce (2)	0.89			
Tall spruce (3)	0.74	0.75		
Tall mixed	0.85	0.91	0.79	
Tall pine	0.77	0.84	0.81	0.88

Overall, the values were relatively high, varying between 0.74 and 0.91, the greatest difference being between the spruce block (3) and the others, and between the pine-dominated block and the others. The latter difference was understandable: it is well known that bird-assemblage composition is greatly influenced by the dominant tree. The former difference occurred because a spruce block (3) had previously been managed and comprised almost exclusively tall spruces, whereas the other two spruce blocks were parts of an old forest reserve and had not been managed. It was noteworthy that this difference in management history was reflected in bird-assemblage composition equally as in the difference of spruce vs. pine.

3.1.2. Variation across the successional gradient

The forest plot in Seitseminen also included relatively young forests (one block each): medium-tall (15 m) mixed coniferous stands, pine-sapling stands (height <10 m), and birch-sapling stands (Haila et al. 1989: fig. 1). In the following tabulation we give Czekanowski similarity values for comparisons between pooled data sets of these blocks:

	Mixed coniferous	Pine sapling
Pine sapling	0.89	
Birch sapling	0.73	0.72

The pooled data sets of medium-tall mixed coniferous and pine-sapling blocks differed from each other about as much as did the data sets of mature forest stands, but the data set from the birch-dominated block differed somewhat more from the other young blocks.

Raivio & Haila (1990) presented an overall comparison between bird assemblages in old-growth forests vs. successional mosaics. Species richness, standardized for sample size by rarefaction, was similar, but birds were almost threefold more numerous in mature forest than in sapling areas, calculated per census effort.

However, the composition of the bird assemblages in mature vs. young forests showed great differences. A total of 36 species were numerous enough for classification according to the variation in their numbers along the successional gradient. Specialists of old-growth forests included five species, all of them quite scarce, and another 12 more numerous species were restricted to mature forest. Scarce specialists of open habitats included 11 species. The remaining eight species were considered generalists, six of them occurring mainly in mature, and two in young forests (for the criteria used, see Raivio & Haila 1990). In the following tabulation we compare the total proportions of the species belonging to specialists/generalists of sapling mosaics/mature stands in four forest age-classes, approximated by tree height (A, low saplings, <5 m, groups 1, 3, 4; B, tall saplings, 5–7 m, groups 7, 9; C, young forest, 10–15 m, groups 6, 8; and D, old forest. Data on and descriptions of groups in Raivio & Haila (1990: table 2):

Forest class:	A	B	C	D
Mosaic specialists	0.11	0.11	0.09	0.01
Mosaic generalists	0.68	0.59	0.45	0.10
Mature generalists	0.16	0.23	0.38	0.44
Mature specialists	0.04	0.05	0.08	0.41

The interesting feature in this comparison is that ‘mosaic specialists’ make up 11% of the total assemblage in low sapling stands, whereas ‘mature forest specialists’ form 41% of the assemblage in old forests. Thus, in the forest bird fauna as a whole, the component of mature forest is relatively much more conspicuous than that of young forest stages. Generalists form the majority of bird assemblages in the two types of sapling stands and in young forests (84, 82 and 83 %, respectively), whereas in the old forest, generalists constitute only about half of the species. This implies that the old-forest species make a relatively more important contribution to turnover along the habitat gradient determined by forest age than do species of young forest stages which, on the other hand, form a proportionally minor component in the fauna.

3.1.3. *Annual variation*

Over the six years in the 36-ha forest plot in Seitseminen we observed 42 bird species; this figure includes the two early-breeding *Loxia* species, but they are excluded from the following analysis because as early breeders their nesting was completed before our field work started. A total of 38 species included at least part of the plot within their breeding territory in one of the years, and another 18 species were present every year. The numbers of breeding species each year were 24, 32, 25, 27, 27, and 22 from 1985 through 1990, respectively. Overall, this assemblage included about 20 species present every year, a dozen species present in half of the years, and half a dozen species present in one or two years.

The total number of pairs, with only such territories included of which more than half was located within the 36-ha plot, was fairly stable: 102, 124, 105, 137, 112 and 135, in 1985 through 1990, respectively. Most of the variation was due to a few abundant species, as shown by the following examples (numbers of pairs in 1985 through 1990 in parenthesis after each species name): The siskin *Carduelis spinus* (14, 10, 8, 12, 9, 14) possibly fluctuated in concert with the spruce-seed crop which it feeds upon. The goldcrest *Regulus regulus* (11, 11, 3, 13, 11, 9) was scarce in 1987 probably because of its high mortality in the exceptionally cold winter of 1986/87. The chaffinch *Fringilla coelebs* (14, 16, 15, 15, 12, 23) was unusually abundant in 1990. The willow warbler *Phylloscopus trochilus* (5, 5, 9, 17, 12, 13) was scarce in 1985 and 1986, but unusually abundant in 1988. On the other hand, some species such as the tree pipit *Anthus trivialis* (6, 6, 6, 6, 5, 5) showed a stable number of pairs in the plot over the years. These data will be more thoroughly analyzed later (Haila, Hanski and Raivio, unpubl.).

Czekanowski percentage similarity in the assemblage composition in single habitat blocks between the years offers a measure of temporal variation. In the largest habitat block of the forest plot (a spruce-dominated old-growth stand of 6.5 hectares; spruce block (1) in the comparisons above) the year-to-year similarity varied between 0.68 and 0.84, median 0.76. Thus, the composition of the assemblages varied somewhat more from year to year in a single block than did the composition of pooled data sets of different blocks (0.74–0.91, median 0.83; see p. 191), despite variation in forest type.

The observed number of pairs and species in the largest habitat block varied over the years 1985 through 1990 as follows: 38/19, 55/22, 47/18, 51/19, 47/20, 51/14. Almost all species that claimed a territory within that block over the six years were present in 1986. In other words, a very high proportion of the pool of forest species may be present in a single year in a single forest block in the southern Finnish taiga, but variation occurs between the years.

In addition to population fluctuations, variation in numbers in single blocks might be due to 'sampling', i.e., to stochastic variation in territory locations from year to year (Preston 1960). The detailed radio-telemetry monitoring of territory locations of the chaffinch *Fringilla coelebs* (Hanski & Haila 1988, Hanski et al. 1992) showed that singing territory and home range differ. The former refers to the area announced and defended by singing, whereas the home range comprises a much larger area over which the male regularly moves during the breeding season. In the present study, the environmental spectrum utilized by the birds for foraging covers practically all habitat types available around their singing territories, including areas within the singing territories of neighbouring males. The overall implication is that male chaffinches make up their home ranges in a small-grained fashion as a combination of suitable habitat patches over an area several times larger than the singing territory (Hanski & Haila 1988, Hanski et al. 1992).

For other bird species breeding in the forest plot in Seitseminen our data are less detailed than for the chaffinch, but they show that the territory locations varied from year to year, as is demonstrated in fig. 1 of Haila et al. (1989); a similar pattern was shown by Palmgren (1987).

A detailed analysis of this pattern over the six census years is in progress (Haila, Nicholls, Hanski & Raivio, unpubl.). As an example, we give the numbers of 50 × 50 m squares occupied within the plot by the tree pipit over the six census years. The number of tree pipit pairs in the plot remained stable over the years, but only four out of 144 squares were occupied every year, with 29 occupied in at least four years (23 were occupied in 3 years, 22 in 2 years, and 40 in 1 year, whereas 30 were never occupied). It seems as if the species avoided some parts of the plot, and established territories in the rest of it at random. This pattern seems to correspond to the 'checkerboard' model of Wiens (1981), and implies that there is variation in the location of territories even though the regional population may remain stable (Preston 1960, Haila 1983, Haila et al. 1993a).

3.2. Carabid beetles

3.2.1. Variation within mature forest

Among the 300 traps functional in the old-growth forest in Musturi in 1985, single traps caught 0–29 individuals of up to 7 species. Likewise, variation in catches and species richness was considerable among blocks of 16 traps (4 × 4 adjacent traps). Blocks of 48 traps (6 × 8 adjacent traps) showed less variation and collected 343–437 individuals and 5.8–9.1 species in a sample of 100 individuals (rarefaction estimate; the differences were not statistically significant). In other words, variation in species richness of point-samples evened out when the sampling effort was spread over about 0.1 ha. The level of beta-diversity among sets of 48 traps in Musturi varied from 0.74 to 0.91 (Czekanowski-index). This variation correlated with a systematic change in topography, soil moisture, and density of foraging wood ants (*Formica aquilonia* and *F. lugubris*) across the grid (a detailed analysis of the data appears in Niemelä et al. 1992).

3.2.2. Variation across the successional gradient

We have two sets of data on variation in carabid numbers between mature and young forests regenerating after clear-cutting. First, the data collected in 1984 and 1985 from fragments of mature forest and their surroundings comprised 1986 individuals of 40 species (Niemelä et al. 1988). Samples from mature forests and young sapling stands (<20 yrs) showed great differences in alpha-diversity, as indicated by the rarefaction estimates ($E(S)$) for 50, 100 and 200 individuals shown in the following tabulation:

	Mature forests (n = 23)	Sapling stands (n = 12)
$E(S)_{50}$	9.8 ± 1.2	18.1 ± 1.9
$E(S)_{100}$	11.4 ± 1.3	23.7 ± 1.9
$E(S)_{200}$	13.3 ± 1.4	29.4 ± 1.6

However, their species richness differed significantly from that in the mature forests in only three of the sapling stands, two of them having a higher and one a smaller species richness than expected (see Niemelä et al. 1988). These comparisons suggest that the greater species richness in young plantations was due to variation among sites rather than to high diversity of local assemblages at individual sites.

Second, the data set collected from a series of sites regenerating after clear-cutting in 1989 (design in Punttila et al. 1991) comprised 15 118 individuals of 47 species. In comparisons of species richness we used data from four subsets (13 traps each) from each forest age-class out of the 100 included in the study. A comparison between the mature stands and the regenerating sites showed the same pattern as the previous data set: species richness was higher in the regenerating sites than in mature forest. Furthermore, the site cut the previous winter showed a lower species richness than sites cut two and ten years prior to our sampling (Fig. 2). Prescribed burning in the 2-year and 10-year-old sites may, however, at least partly explain their high species richness.

We analyzed the pattern of carabid diversity variation along the successional gradient by performing a cluster analysis based on the Bray-Curtis index of similarity for the two data sets. The sites appeared to cluster together according to the forest age. The three youngest forest-age classes (0, 2, and 10 yrs after cutting) formed the most distinct group, whereas the two older age classes of cut forest (10–20 and 20–60 yrs) clustered more closely to the mature forests (see

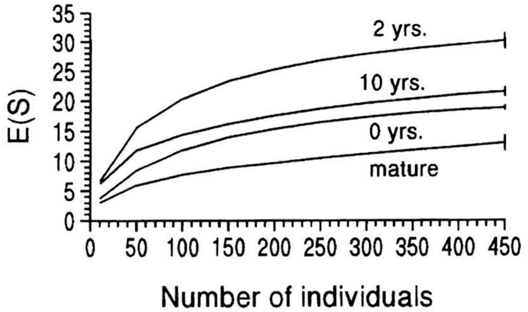

Fig. 2. Species richness (*E*(*S*)) estimated by rarefaction in the four forest age-classes (0 yrs, 2 yrs, 10 yrs since cutting and mature forest) for carabid data collected in 1989. Samples collected using identical sampling efforts (52 traps) in the age classes.

Niemelä et al. 1994). The clustering of the 0-year forests (cut in the previous winter) with young stands showed that several species inhabiting open stands had already colonized the areas during the first summer post-cut.

Forest management in southern Finland apparently does not change the dominance structure of the abundant species. The carabid fauna consists of very few abundant species, and *Calathus micropterus* and *Pterostichus oblongopunctatus* were among the three dominant ones in all forest age-classes (Table 1) (see also Niemelä 1993a). Especially in the mature forests and in the recently cut sites *C. micropterus* and *P. oblongopunctatus* were numerous, making up 50–80% of the catch. In carabids, a few species were abundant in all forest age-classes, in marked contrast to the pattern in birds. Two patchily distributed old-forest species (*Agonum mannerheimii* and *Notiophilus reitteri*), were found occasionally also in young-stage forests. On the other hand, a great number of species were recorded exclusively in young stages; they number 28 (1984–85 and 1989 data sets pooled).

The degree of carabid species turnover along the successional gradient was fairly low. Of the 38 species collected using comparable sampling effort throughout the gradient, ten were found in all forest age-classes. This is 67% of the species found in the mature forests. However, the proportion of forest species, as classified by Lindroth (1985, 1986) was clearly lower in the cut sites than in the mature forest (Table 2). These results are similar to findings based on data collected in a larger geographical region in 1984–85.

3.2.3. *Annual variation in carabid assemblages*

In the sample from the 64 pitfall traps operated in Musturi, carabid species richness remained fairly stable in 1985–90; the expected number of species in a sample of 100 individuals varied from 6.6 to 10.1 (differences not statistically significant). The value of the Czekanowski index over the years varied between 0.73 and 0.84, similar to the values for the 48-trap-blocks in the single year 1985 (see above).

Despite a six-fold difference between the lowest year and the highest year catch (Fig. 3), species turnover during the years was surprisingly low. A total of 20 species were caught during the six years, and the number of species in any single year varied between 11 and 16. Eight species were collected every year, and their proportion of the total catch was 98%. The dominance order

Table 1. Rank order of the three most abundant species and the combined proportion of *Calathus micropterus* (Ca mi) and *Pterostichus oblongopunctatus* (Pt ob) in mature forest (>100 yrs) and sapling stands (<60 yrs) in the data set collected in 1984–85 and in different age classes in the data set collected in 1989.

	1984–85		1989			
Species rank	mature	sapling	0 yr.	2 yr.	10 yr.	mature
1st	Ca mi	Ca mi	Ca mi	Pt ob	Pt ob	Ca mi
2nd	Pt ob	Tr se	Pt ob	Ca mi	Ca mi	Pt ob
3rd	No bi	Pt ob	Ag fu	Pt ad	Ha qu	No bi
Ca mi+Pt ob	52%	36%	81%	40%	42%	70%

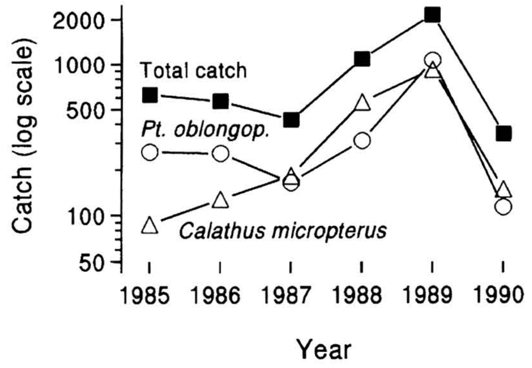

Fig. 3. The total catch of *Pterostichus oblongopunctatus,* and of *Calathus micropterus* in Musturi in 1985–90.

of the abundant species remained very stable, as well. *C. micropterus* and *P. oblongopunctatus* dominated the sample every year except in 1985 when *C. micropterus* fell to third most abundant species (Table 3). Each year these two species made up >50% of the catch, in 1989 rising as high as 92%. Fluctuations in total carabid samples were thus mainly caused by abundance variation in these two species (Fig. 3). This year-to-year variation in the carabid catches from Musturi was presumably related to weather conditions. Especially in the north, where the growing season is short, weather may be more important for carabid survival and reproduction than at more southern latitudes (Niemelä et al. 1989). For instance, during the cold and rainy summer of 1987 the catches of the more 'demanding' species (Lindroth 1985), such as *Carabus* spp. and *Cychrus caraboides* were exceptionally low. On the other hand, that year *C. micropterus* and *P. oblongopunctatus* were not particularly scarce (Fig. 3). From our data, however, one cannot infer whether the population fluctuations were directly related to weather or whether they were mediated through weather affecting other factors, such as prey.

Table 2. Carabid-species turnover across the forest age-classes in the 1989 data for identical sampling effort (52 traps) in all age classes. Number of species in each age class, number of species shared by the 0-year-old sites and the older ones, proportion of the shared species of the total in the older ones, and the proportion of forest species (Lindroth 1985, 1986) are given.

Forest age class:	0 yr.	2 yr.	10 yr.	mature
Species	19	34	22	15
Same as in 0 yr.	19	18	12	11
% same	100	53	55	73
% forest spp.	42	27	36	73

4. The closing act: conclusions and management implications

4.1. Forest structure and distribution of the fauna

Overall distribution patterns in birds and carabids appear quite similar. Numerically dominant species tend to be generalists, distributed broadly across the successional gradient. For birds, our data included a greater number of species of mature forest than of young and open forest biotopes, but for carabids the relationship was reversed. The abundant species in young vs. old forest-stages were different in birds, but the same in carabids. This is an understandable consequence of ecological differences between the groups: forest birds are sensitive to structural

Table 3. Percentage of the abundant carabid species (>5% of the catch for at least one year) among the six years (1985–90) and in the total catch in Musturi. Figures are rounded to the nearest integer (0 <0.5%, – species was not collected). — Abbreviations of the species names: Cal mic = *Calathus micropterus*, Car hor = *Carabus hortensis*, Cyc car = *Cychrus caraboides*, Lei ter = *Leistus terminatus*, Not big = *Notiophilus biguttatus*, Pte obl = *Pterostichus oblongopunctatus*.

	1985	86	87	88	89	90	Total
Cal mic	14	22	43	52	43	43	39
Car hor	1	1	–	0	0	5	7
Cyc car	14	19	3	8	2	10	7
Lei ter	16	1	1	4	2	3	4
Not big	6	3	10	4	1	3	3
Pte obl	42	45	39	29	49	33	42
Cami + Ptob	56	67	82	81	92	76	81

features of tree stands, whereas generalized forest carabids are not equally directly associated with any tree layer characteristic.

For carabids, between-site variation was greater in young than in old stands, which suggests that there may be more heterogeneity in vegetation relevant to ground-living arthropods in young than in old stands. This agrees with previous Finnish data on the effects of silviculture on populations of oribatid mites (Karppinen 1957), of soil-inhabiting spiders (Huhta 1971), and of various groups of ground invertebrates (Huhta et al. 1967, 1969). According to Helle & Mönkkönen (1986, 1990), bird assemblages in young successional forest stages vary also more than in old ones, but such a difference was only suggestive in our forest-plot data. Assessed by percentage similarity, variation in assemblage composition was similar for both groups between sites and between years. This is by no means self-evident and agrees with Preston's (1960) suggestion that local assemblages within a particular type of environment are constituted as random samples from the overall species pool residing in this environmental type. The composition of the pool, however, varies from year to year as a consequence of fluctuations in individual species.

However, when drawing conclusions from a comparison between birds and carabids, the differences in 'grain-pattern' between the groups need to be acknowledged (for the idea of environmental grain, see Levins 1968, Addicott et al. 1987). In birds, the uniformity of alpha-diversity over habitat blocks in our study plot was presumably due to the small "grain size" and mosaic-structure of the habitats. Bird individuals use the environment in a small-grained fashion and make up their home ranges from discrete habitat elements surrounding the territory. Species breeding in a habitat mosaic may include several different habitat types in their territory and, as a consequence, differences in habitat distributions among different species appear small (Haila & Hanski 1987).

In carabids the spatial variation within the Musturi old-growth stand is explainable by two complementary mechanisms: First, microhabitat differences within the grid are clearly important at the level of movement patterns of individuals. Because carabid beetles are aggregated within habitats (Loreau 1986, Luff 1986, Niemelä et al. 1986, 1992), chance factors affecting the location of aggregations may contribute to their total variation. Second, a few carabid species have narrow microhabitat requirements and show little spatial variation from year to year. For instance, *Agonum mannerheimii*, a denizen of wet, forested patches of the taiga (Niemelä et al. 1987), had a highly localized population within the Musturi trapping site. Similarly restricted local populations have been found elsewhere in our study area in Häme.

Thus, for carabid individuals the environment seems to be coarse-grained, i.e., they are most frequently caught in favourable microhabitat patches. The fact that pitfall trapping mainly gives an indication of variation in 'activity density', rather than in numbers, suggests that the individuals spend relatively more time in those patches than in the others (Niemelä 1990, Niemelä et al. 1992). Unfortunately, we do not explicitly know whether the patches with high densities are especially favourable in terms of such factors as increased reproductive output. This is an important question for further research.

The aggregated distribution pattern suggests that species interactions may be more important for the organization of carabid assemblages than indicated by their average densities over a whole range of environmental variation (Loreau 1992), although no direct evidence is available, and, overall, competition among carabids remains a dilemma (Niemelä 1993b). For some habitat specialists such as *A. mannerheimii*, the environment is probably coarse-grained on the population level. For denizens of open habitats this is very improbable; many of them, according to our indirect data on movement patterns, disperse very efficiently (Harri Tukia, unpubl.; see also Niemelä et al. 1994). Moreover, these efficiently dispersing open-habitat species may include habitat specialists. For instance, pyrophilous species rapidly invade burnt forest probably following chemical cues (i.e., no smoke, no beetles) (Holliday 1984).

The generalizability of these results to other taxa will be more thoroughly discussed in another context, but a low degree of habitat specialism seems to be true of birds and carabids of boreal forests. A basic differentiation is between young and mature forest-stages, both of which have specialized species. This generalization is valid also for ants (Punttila et al. 1991) and ground-living spiders (Pajunen 1988, Jennings et al. 1988, McIver et al. 1993). In beetles of decaying wood this contrast is even more dramatic (Väisänen et al. 1993).

4.2. From individual scale to population scale?

The discussion above dealt mainly with the issues on an individual scale. Surveys always record individuals. We suggest three different approaches to applying results from survey data at the level of local populations.

Territorially breeding birds are spread out in space, and it is prohibitively difficult to distinguish each local population in a uniform environment such as the boreal forest. This is further complicated in boreal forests by the low degree of natal philopatry, which means that it is difficult to determine the distances over which populations mix between generations. We suggest that a further elaboration of the territorial model of Lande (1988) might offer a bridge for overcoming this difficulty. His model takes potentially suitable territory sites on a regional scale as basic units and assumes that a local population can be characterized by two variables, (1) proportion of occupied sites among the potential ones, and (2) demographic efficiency which combines reproductive success and ability to disperse to a new suitable site. A fruitful starting point for such an elaboration would be to identify potentially suitable habitats for different species, for instance by exploring 'minimum habitat requirements' of each species (Haila et al. 1989, Raivio in preparation).

Second, for carabids it might be possible to assess habitat quality by comparing data on environmental variation with the numerical distribution and movement patterns of individuals of different species. After identification of important habitat characteristics, these can used to characterize habitat quality on a local population scale. Our results indicate that in coniferous forest, sites with abundant deciduous litter are good-quality 'resource spots' for many forest carabid species. Such 'spots' may serve as source patches from which individuals move into lower-quality patches nearby. Differences in the abundance or distribution of such 'resource spots' among different forest areas may cause differences in carabid abundance between forests (Niemelä et al. 1992).

Third, continuity of specific microhabitats is most likely an important characteristic of the environment on a population level for organisms specialized for those habitats ('mosaic-processes' of Whittaker & Levin 1977). The scale over which 'continuity' is determined depends on dispersal distances. Patches between which individuals readily disperse are effectively 'continuous' with each other. For generalist, migratory birds, 'continuity' is not likely to present problems in a heterogeneous landscape, because the birds have good dispersal ability and can 'bridge' spatial gaps. For sedentary birds the situation may be different if they do not, for instance, cross open areas.

Much less is known about the dispersal ability of mature forest carabids, although many species of open habitats are known to disperse efficiently by flight (Lindroth 1985, 1986, H. Tukia, unpublished). Continuity may be an important issue for some forest species which live in small populations in particular habitat types, for instance *A. mannerheimii* in southern Finland. Continuity is more likely to be a crucial feature of the environment for species dependent on decay processes in particular forest habitats, for instance for endangered saproxylic beetles (Rassi et al. 1992, Siitonen & Martikainen 1993). Such species may require extremely specific microhabitats during the decay process, as regards both tree and fungus species and environmental biotope characteristics (Kaila et al. 1994).

4.3. Forestry versus natural forest dynamics: critical issues

Modern forestry has brought about changes in the forest environment in at least three major respects: (1) changes in the size, configuration and spatial distribution of different types of forest stands (Mladenoff et al. 1993); (2) changes in the structural features of different types of forests and in 'edge effects' (von Haartman 1973, 1978, Järvinen et al 1977, Helle & Järvinen 1986, Angelstam 1992); and (3) loss of particular microhabitats, for instance snags and decaying wood (Heliövaara & Väisänen 1984, Esseen et al. 1992). Clear-cutting creates dynamics that are quite different from fire cycles (Hunter 1990, Hansen et al. 1991). Forest management has in recent decades aimed at the creation of uniform stands, which were assumed to maximize the productivity of the preferred timber. Uniform, single species stands are not, however, optimal for economic productivity; it is increasingly acknowledged that the productivity of forest ecosystems depends on heterogeneity on the level of soils, of tree species composition, and of stand configuration (Mladenoff & Pastor 1993).

Thus, forestry has certainly brought about changes in abundance relationships among birds and carabids in the region we have studied. The effects on Finnish birds of changing area proportions of different types of forest are well documented (Järvinen & Väisänen 1976, 1977, 1978, Järvinen et al. 1977, Helle 1984, 1985, Virkkala 1987, 1991, 1993). For carabids the same mechanism is highly likely (Niemelä et al. 1988).

The effects on birds of changes in the internal structure of forest habitats are also documented in several studies, beginning with the classic works of von Haartman (1973, 1978) (see Haila et al. 1980, Helle & Järvinen 1986, Virkkala 1990). Forest insects have felt the influence as well, but old data sets that would allow direct comparisons are lacking. Certainly, the patterns of distribution and abundance of forest animals have changed because of forestry. The next question is what are the basic processes involved? What are the causal pathways from change in the environment to changes in animal populations?

It is a platitude that different organisms respond to different habitat characteristics. It is less obvious that the spatial and temporal scales of the response often differ. The data we have discussed in this paper relate to the spatial scale — an assessment of the temporal dimension would require data that allow estimates of time lags in population responses, i.e., real long-term studies. A fruitful concept in evaluating spatial scales is 'grain size'. Birds and carabids perceive the patterns in the environment in different ways. A stand that is uniform for birds may be heterogeneous for carabids, because of variation in the field layer. Mosaic patterns are important for species in both groups, but it is important to conceptualize these adequately (see Kotliar & Wiens 1990). In assessing mosaic patterns, the whole annual (life) cycle ought to be considered; the requirements of juveniles vs. adults may differ, and their requirements may vary throughout the year (Esseen et al. 1992).

If our suggestion concerning the significance of mosaic patterns is valid, the importance of the 'large versus small' controversy fades: the composition and configuration of habitats within a forest preserve is an issue more important than its area. The typological idea of 'habitat fragmentation' is not particularly adequate in a continuously varying mosaic environment (Haila et al. 1993b). Our data suggest that a patch size of 5–50 ha is sufficient in our study area to preserve locally suitable environments for birds and carabids (Haila et al. 1987, Niemelä & Haila 1986). This is also *a priori* plausible because 5–50 ha seems to be the 'grain size' of natural differentiation of forest stands, due to variation in such elements as topography, microclimate, moisture and soil quality. But this conclusion is valid only provided that the same mosaic scale extends over a regional scale. Single patches of natural forest of this size within uniform expanses of managed monoculture would be of doubtful value as faunal preserves.

Thus, we are left with the general conclusion that has been reached by several forest ecologists: heterogeneity is needed on many scales simultaneously (e.g., Hunter 1990, Hansson 1992, Mladenoff & Pastor 1993). The problem is to make this general idea operational. An approach we advocate is to identify critical scales for a set of taxa, and use these as guidelines for management operations. An increasing knowledge of natural forest dynamics helps as an overall heuristics (Hunter 1990, Hansen et al. 1991), although an exact match between natural disturbance and forestry operations is unattainable, not only because forestry removes timber from the forest, but also because the large, exceptionally fierce forest fires of the past cannot be re-created (Hunter 1993).

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