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The spacing of mature forest habitat in relation to species-specific scales in managed boreal forests in NE Finland

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Modern forestry alters the structure of boreal forest landscapes, and this affects several forest species with different habitat requirements. Quantitative analyses of the structure of real landscapes are scarce, although this information will be needed in landscape-level planning and management applications. We investigated the occurrence and configuration of mature forest (> 80–100 year) in relation to five different extents (ranging from 20 to 7 854 ha) of circular landscapes around random points in managed forest environment in NE Finland. The habitat type was coarsely chosen according to requirements of certain resident birds and mammals. We present an approach where species-specific home-range scales are related to the observed environmental heterogeneity pattern for assessing the potential of actual landscapes to maintain these species. As a result we found that there is a minority of landscapes where total area of mature forest was comparable to species' home ranges. Irrespective of the scale examined, the average proportion of habitat in a landscape was approximately 15%. Besides that the mature forest was physically fragmented already on a scale relevant to individual animals, the variation in habitat proportion between landscapes decreased rapidly when the landscape extent was increased. This decrease of variation occurs on surprisingly small scales; the forest landscape structure is unintentionally altered due to small-patterned land ownership, even age distribution of managed stands, and small variation in regeneration patch size. In terms of related landscape metrics, we also compare our results with patterns achieved in randomly generated neutral landscape models.

1. Introduction

The central task in the conservation of biological diversity is to comprehensively maintain viable populations of naturally existing species in the foreseeable future. This applies also to managed forest environments; although, inevitably, in managed forests, solutions must acknowledge intrinsic characteristics of areas and diverge spatially (Mykrä & Kurki 1998).

Even though forest structure at stand level and its alteration seem to be most important for the majority of boreal forest species (e.g. Esseen *et al.* 1992, Raivio 1992, Haila 1994, Siitonen & Martikainen 1994, Petterson 1997, Wikars 1997), the population viability of a number of species is also critically connected to the structure of forest landscapes (Angelstam 1992, Hansson 1992, Andrén 1994, Kurki *et al.* 2000). Composition and configuration of forest landscape may affect these species either directly, through distribution of resources and habitats, or indirectly by altering inter-specific interactions in communities modified by changed landscape structure (e.g. Angelstam 1992, Dunning *et al.* 1992, Wiens *et al.* 1993, Kurki *et al.*1998).

Although the ecological effects of boreal forest management were studied intensively in Fennoscandia during the past two decades, quantitative information on present forest landscape structure and also reliable estimates of natural large scale variation in former forest landscapes seem to be scarce. The characteristics of natural forest landscapes in Fennoscandia are well described in the recent review of Esseen *et al.* (1997). However, they also state that there is no quantitative data available regarding landscape level heterogeneity in the past. The knowledge of natural stand level characteristics has accumulated splendidly during recent years, but it is also necessary to understand the larger scale conditions to which forest species have adapted. The best documented changes in Fennoscandian forests caused by commercial forestry are the loss and fragmentation of natural old-growth forests together with the simultaneous proportional increase of younger successional stages, and the rarity of forests with a significant old deciduous component (Hansson 1992, Östlund *et al.* 1997). In Finland at present, about 20.3% of productive forest land are forests older than 100 years, and 9.1% are older than 140 years. When the two northern provinces of Oulu and Lappi (which represent 42.6% of forest land in the country) are excluded, the corresponding percentages for southern Finland are 12.5 and 1.6, respectively (Anon. 1996).

The loss of forests with old-growth characteristics has been shown to have deleterious effects on many forest-dwelling species in different taxa in Fennoscandia (Helle & Järvinen 1987, Virkkala 1987, 1991, Rassi *et al.* 1992, Angelstam & Mikusinski 1994, Siitonen & Martikainen 1994, Edenius & Elmberg 1996, *see* also Esseen *et al.* 1997). In this paper, we examine the managed forest landscape structure in relation to coarsely defined requirements of certain resident forest dwelling mammals and birds. For this purpose, we want to draw a distinction between natural old-growth forests of long continuity and a broader class of mature managed stands. Natural old-growth forests are nowadays rare, and being an obligatory habitat for many specialist species they always have a high conservation value as such. In spite of that, and regarding the occurrence of some of the declining species in relation to conditions prevailing particularly in managed forest landscapes, there is a positive statistical relationship between the fulfilment of habitat requirements and coverage of mature stands. This division between natural old-growth forests and mature or 'old' managed forests is partly congruent with the difference in mentioned direct and indirect mechanisms that are behind population declines of forest species. Threatened and declining species are either tightly dependent on some particular resource combination materialising itself nowadays only in sparse natural forests, or their population declines are due to altered inter-specific interactions following structural changes in communities at larger scales (Kurki *et al.* 1997). Although, this is a rather broad generalisation because both the degree of specialisation and ability to respond to and compensate community changes varies greatly from species to species. It is also probable that most of the population declines result from both direct and indirect reasons.

We investigated the occurrence and configuration of mature forest (growing stock volume

> 100 m^3 ha^{-1}) in relation to spatial scale in a managed forest region in north-eastern Finland. The habitat type definition and this approach are based on Finnish and Scandinavian literature, which emphasises the positive relationship between the occurrence of mature forests and several forest dwelling vertebrates (Helle 1985, Rolstad & Wegge 1987a, 1989, Virkkala 1987, 1991, Angelstam 1992). In this study, we obtained a general picture of the distribution and abundance of mature forest habitat in managed forest landscapes in that region, and we interpret our results in relation to literature-based information concerning home range scales of flying squirrel (*Pteromys volans*), siberian tit (*Parus cinctus*), siberian jay (*Perisoreus infaustus*), three-toed woodpecker (*Picoides tridactylus*) and capercaillie (*Tetrao urogallus*) (Haftorn 1973, Kokhanov 1982, Haila 1983a, Rolstad & Wegge 1987a, 1987b, Virkkala & Liehu 1990, Helle *et al.* 1994, Mönkkönen *et al.* 1997, Reunanen & Nikula 1998, Hanski 1998). On the individual level the home ranges of all these species contain certain specific resources (Rolstad & Wegge 1987b, Hågvar *et al.* 1990, Virkkala & Liehu 1990, Virkkala *et al.* 1991, Stenberg 1996, Hanski 1998, Reunanen & Nikula 1998), which on the one hand are not prevalently present in this artificially pooled > 100 m^3 ha^{-1} habitat, and on the other hand, certainly occur to some extent in the matrix, too. Moreover, as it is evident that individuals do not require area *per se*, but that area requirements of individuals are a function of the occurrence of relevant resources (Haila *et al.* 1989), we do not claim that the examined habitat exclusively represents the requirements of the discussed species. Nevertheless, the occurrence of these species can be assumed to be at least concentrated on the examined habitat class in the study area. Furthermore, irrespective of theoretical problems falling on the term "area requirements", it is evident that individual level operational scale differs between these species. Our aim is to portray an approach where information on species-specific scales is related to the observed environmental heterogeneity pattern for assessing the potential of actual landscapes to maintain these species. In the discussion we also compare our results with patterns achieved in randomly generated neutral landscape models.

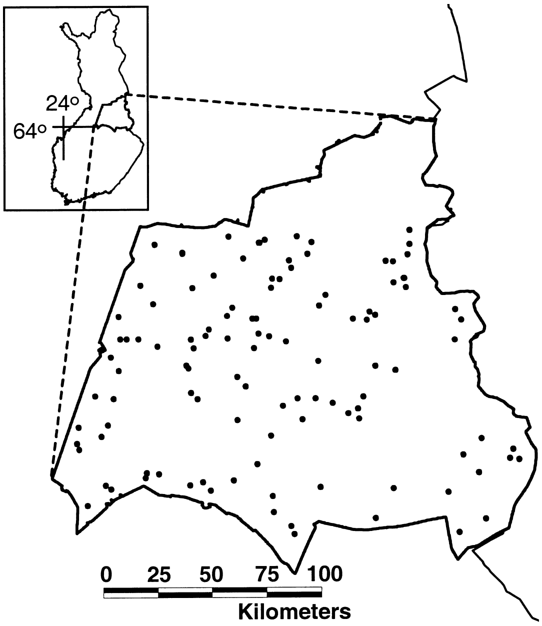

Fig. 1. Kainuu forestry centre in northeastern Finland. Dots on the map depict the spatial distribution of randomly located circular landscapes.

2. Material and methods

2.1. Study area

Our 24 000 km^2 study area (Kainuu forestry centre) (Fig. 1) is located in northeastern Finland and lies in the northern boreal zone (Ahti *et al.* 1968). Of the total area, water covers about 11%, and 5% of the land area is covered by agricultural land and human settlements. The rest, approximately 84% of the total area, is 'forestry land', which is further divided, according to the forest management terminology, into 'forest land' (81%), 'scrub land' (12%) and 'waste land (7%). The 'forestry land' in the study area is highly dominated by coniferous forests and bogs. More than two fifths (43.8%) of forest land are privately owned whereas 39.6%, 13.6% and 3.0% are owned by the state of Finland, forest companies, and other owners, respectively. Nature reserves compose 3% of land area (Anon. 1996, Anon 1998).

Modern forestry, based mainly on clear-cutting and artificial regeneration, started more widely after World War II, and thus far at least

65% of the ‘forest land’ has been regenerated once. During this period there has been a decreasing trend in the size of regeneration areas. Their typical size has varied from one hectare to some tens of hectares, and nowadays more than 80% of cutting areas are smaller than 10 ha. The rotation time in the study area averages 100 years.

2.2. Landscape data and analyses

We used classified Landsat images produced by the National Forest Inventory (NFI) (Tomppo 1993, 1996) to examine the occurrence of mature forest. For each pixel on forested land (25 m × 25 m land element) NFI produces an estimate of growing stock volume separately for Scots pine (*Pinus sylvestris)*, Norway spruce (*Picea abies*), birches (*Betula* spp.) and other species as a combined class. Digital maps of non-forest lands (peat land, water area, agricultural land, roads and settlements) are used to separate non-forest areas from forest land (Tomppo 1993, 1996).

We reclassified the landscape data by summing the growing stock volume of different tree species for each pixel and defining pixels that had timber volume over 100 $m^3 ha^{-1}$ as ‘mature forest’. In other words, the data were bisected to mature forest and everything else. The 100 $m^3 ha^{-1}$ division limit refers approximately to class midpoint of the average total volume of young thinning forests (58 $m^3 ha^{-1}$) and advanced thinning forests (131 $m^3 ha^{-1}$) in the study area (Tomppo *et al.* 1998). Furthermore, timber volume correlates well with the age of the forest stand and the criteria used in our study is about in the class midpoint of the average timber volumes of age classes 61–80 years (80 $m^3 ha^{-1}$) and 81–100 years (113 $m^3 ha^{-1}$) (Tomppo *et al.* 1998).

After reclassifying the landscape data, we randomly selected 120 points (Fig. 1) avoiding only large lakes and towns in the study area, and formed circular landscapes around them using five different radii: 250, 500, 1 000, 2 000 and 5 000 metres. Corresponding areas covered were approximately 20, 79, 314, 1 257 and 7 854 hectares. In seven cases landscape data did not cover the whole area inside the largest radius. They were therefore omitted, and the data were only used from 113 points. The area of mature forest (CA), number of mature forest patches (NP), mean patch size (MPS; ha), mean nearest neighbour distance (MNN; m) and largest patch index (LPI; $(\text{area}_{\text{largest patch}}/\text{area}_{\text{landscape}}) \times 100$) were computed for each landscape using FRAGSTATS (McGarigal & Marks 1995).

2.3. Individual level operational scale of species

The information on territory sizes and individual level home range scale of flying squirrel, siberian tit, capercaillie, siberian jay and three-toed woodpecker were surveyed mainly from Fennoscandian literature, which makes it applicable also in this particular study area. The information on territory size of flying squirrel is based on recent radio-tracking data from southern Finland (Hanski 1998), and from studies conducted in the same region that we used in this study (Mönkkönen *et al.* 1997, Reunanen & Nikula 1998). According to these studies, flying squirrels require some 0.5–3 ha of favourable habitat to be able to establish a territory. Total activity areas of an individual, however, may be even 5 to 10 times greater. According to Hanski (1998) the average for this is 6.5 ha. The territory size of siberian tit is reported to range from 15 to 20 ha in coniferous forest habitats (Haftorn 1973, Virkkala & Liehu 1990). The home range size of an individual capercaillie varies from some tens of hectares to more than 100 ha, but in the case of this species more important is that a minimum requirement for a viable lek is around 300 ha of suitable habitat (*see* Rolstad & Wegge 1987a, 1987b, Helle *et al.* 1994). Comparable published information on siberian jay and three-toed woodpecker seems to be surprisingly hard to find. In the case of the former, we rely on Kokhanov (1982). The mean size for five studied territories in the Kola Peninsula was 52 ha and the range varied from 45 to 57 ha. For the latter species, the only piece of information concerning the home range scale seems to be the one presented by Haila (1983a) in his study on colonisation of islands by land birds in the lake Inari in northern Finland. He conducted land bird censuses on 41 islands with a size range of 0.5–885 ha. The three-toed woodpecker occurred only on three islands, the smallest of them being 99 ha.

The other two were 680 and 885 ha. Habitat types comparable with these 'woodpecker islands', however, occurred in substantial proportions on many of the smaller sized islands. Also, in the case of other species his results were in accordance with the abovementioned studies. The smallest islands from where siberian tit, siberian jay and capercaillie were found, were 17, 67 and 290 ha, respectively. Haila observed individual capercaillies also on islands sized 22 and 54 ha, but the one with 290 ha area was smallest with more than one (3) individual. This may indicate lekking and/or nesting.

The three smallest landscape extents used in this study (20, 79 and 314 hectares) are almost equivalent with the home range scale hierarchy among these species. In the examination, landscape extents were associated to species operational scales and the fulfilment of each species' requirements in terms of mature forest occurrence was estimated on landscape extent that was one level up from its home range scale. The largest scales (1 257 and 7 854 hectares) would be more pertinent in population level considerations, which are beyond the scope of this paper. Only the capercaillie lek is associated to 1 257 ha extent.

3. Results

Since we pooled all the other land cover classes (including water and artifactitious classes), the habitat proportions are given in relation to total landscape area on each scale, not relative to 'forest land' area. The average proportion of mature forest habitat in landscapes was about 15% throughout all examined scales (Table 1). The landscapes around randomly selected points seem to represent average forest and they are congruent with the fact that 65% of the 'forest land' have been regenerated since the 1950s; on 31% of 'forest land' (21% of total area of forestry centre) forests are older than 81 years, and approximately 35% of 'forest land' (24% of total area of forestry centre) belong to developmental classes V (advanced thinning stands), VI (mature forests) and to low-yielding forests (Anon. 1996). This last class includes also the majority of natural old-growth forests in Kainuu area.

Even if the mean proportion of mature forest habitat did not change with scale, the variation in habitat proportion between landscapes decreased rapidly when landscape radius was increased. The ranges of habitat percentage narrowed from 0.3–63.3 on the smallest scale of 20 ha to 4.6–31.4 in the largest landscapes of 7 854 ha (Table 1). The decrease in CV% indicates further that among individual landscapes the values concentrated strongly around the average of 15% as the scale increased (Table 1). This can also be seen in the scale-specific distributions of landscapes in relation to the percentage of mature forest (Fig. 2), where the occurrence of mature forests concentrates on only a few classes on largest scales.

In inspecting the relation of home range requirements and habitat area we disregarded the fact that habitat patches were relatively small and scattered throughout the landscapes, and assessed the landscape potential only with habitat percentage (CA). The total area of examined habitat was comparable to home ranges of flying squirrel (2 ha) and siberian jay/female capercaillie (50 ha) on less than half of 20 ha (48%) and 314 ha (42%) landscapes, respectively. One fourth (25%) of 79 ha landscapes met the requirements of siberian tit

Table 1. Proportion of mature forest (> 100 $m^3 ha^{-1}$; > 80–100 yr.) in relation to area of circular landscapes around random points ($N = 113$) in northeastern Finland.

Radius (m)	Area (ha)	Landscape			% of landscapes with > 30% habitat	% of landscapes with > 60% habitat
		Mean	Range	CV%		
250	20	15.1	0.3–63.3	95.4	15.0	0.8
500	79	14.7	0.6–50.1	77.5	11.5	0
1 000	314	14.2	1.4–39.3	63.4	7.1	0
2 000	1 257	14.4	2.6–39.1	53.4	4.4	0
5 000	7 854	14.5	4.6–31.4	38.6	0.8	0

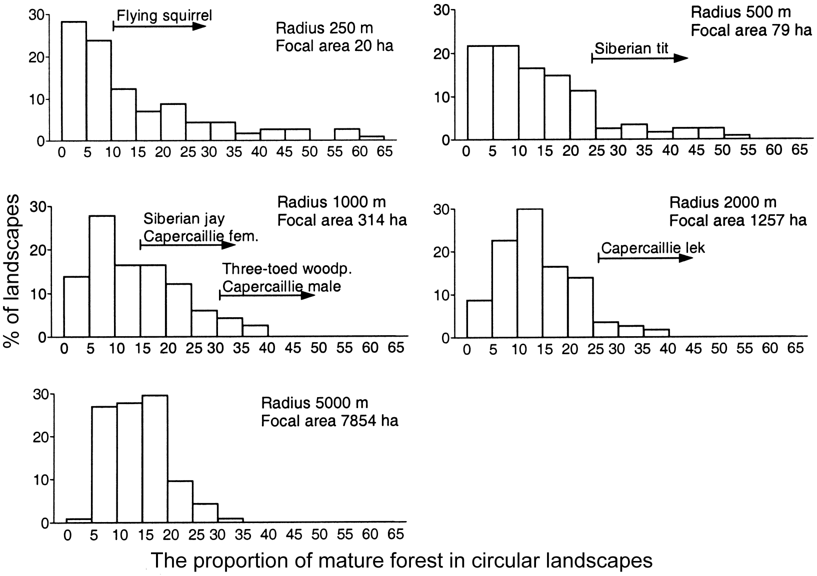

Fig. 2. The distribution of randomly located landscapes in relation to the percentage of mature forest at five different landscape extents. Each species is associated with a 'focal area' that is one level up from its home range scale. The starting point of each arrow indicates the lowest percentage of mature forest that would approximately respond to the home range requirements of species if the habitat occurred as continuous from the species point of view. Thereby, the summed percentages (y-axis) of classes in the right side of the arrow starting point indicate the 'maximum' proportion of suitable landscapes on a given scale.

(20 ha) in this respect, and regarding three-toed woodpecker/capercaillie male home ranges (100 ha) the percentage in 314 ha landscapes was 7%. Habitat area adequate for a viable capercaillie lek (300 ha) was found on 8% of 1 257 ha landscapes. These summed proportions are also illustrated in Fig. 2; arrows on relevant scales (*see* figure text for further explanation) indicate the subset of distribution, where total habitat area/landscape equals or exceeds the area of home ranges.

In terms of comparing our results of landscape metrics' computations and patterns achieved in a randomly generated neutral landscape model (Andrén 1994), the most interesting relations can be seen in 20 ha landscapes (Fig. 3), and their results are presented and discussed in more detail. Number of patches, mean patch size and mean nearest neighbour distance show a clear non-linear relationship with mature forest proportion on the 20 ha scale, and these relationships weaken with diminishing variation as the scale extends, and results of the largest landscapes show as a mere obscuring reflection of those observed on the small scale (Fig. 4).

Even on the smallest spatial level with the greatest variation and highest mature forest percentages the habitat mosaic was very small patterned, or physically fragmented on the great majority of landscapes; in 85% of 20 ha landscapes the proportion of mature forest habitat was less than 30% (Table 1), and among them the mean patch size varied between 0.06 and 2.69 ha (Fig. 4). However, one or two pixel patches were relatively common and they tend to decrease the mean patch size, even though their ecological significance is doubtful, as they do not necessarily deviate from their surroundings otherwise than having a standing volume just a bit over 100 $m^3 ha^{-1}$. Furthermore, in the 20 ha landscapes the mean patch size increased only slightly with the habitat percentage increment remaining under 3 ha until the threshold level of 60% in habitat coverage was reached. On that scale the number of patches first increased with increasing habitat in the landscape and peaked at about 25% (Fig. 3). All computed landscape metrics are interrelated and, therefore, it seems also characteristic that junctures of nonlinearity coincide; increase and turning point of NP was mirrored by MNN, and MPS increase follows the peak in NP (Fig. 4).

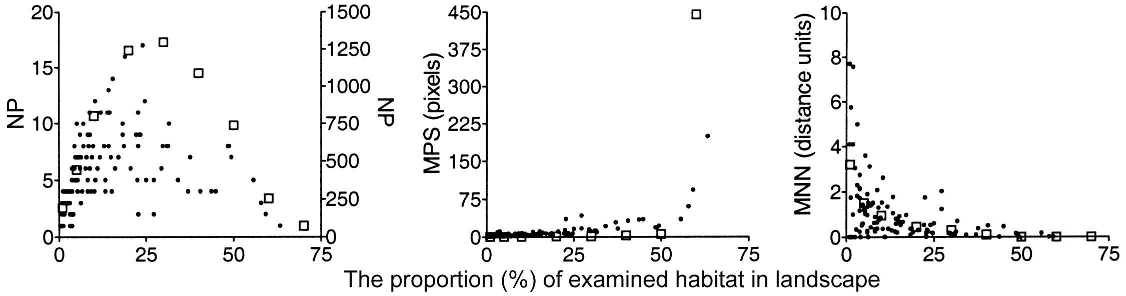

Fig. 3. Comparison of number of patches (NP), mean patch size (MPS) and mean nearest neighbour distance (MNN) between our study and randomly generated model landscapes from Andrén (1994). Black dots describe the data of this study (left-hand side y-axis in NP). Open squares (and right-hand side y-axis in NP) show the results from Andrén (1994). In Andrén's original paper the percentage of examined habitat varied between 0 and 100; due to the smaller variation in our data, only 0%–75% is shown. Contrary to the practice elsewhere in this paper, MPS is measured by the number of pixels and MNN in distance units (one unit = length of a pixel side).

In order to elucidate further the possible randomness/aggregation in the spatial pattern of mature forest, we tested how the distribution of NP deviated from random on different scales. The NP was randomly distributed on 20 ha scale, but not on larger scales (Kolmogorov-Smirnov test with Poisson as a test distribution, on 20 ha scale $Z = 1.182, p = 0.122, n = 115$; on 79 ha scale $Z = 2.717, p < 0.001, n = 115$). Finally, we compared the relationship between LPI and habitat proportion in 20 ha landscapes with results achieved from a neutral model in Andrén (1994) (Fig. 5). In randomly generated neutral landscapes there is a noticeable juncture of non-linearity in LPI between habitat proportions of 50% and 70%, and there was a trace of that also in our data. Compared with a pure random pattern, however, the result suggests certain spatial aggregation of mature forest patches. There is, though, a particular disparity between sampling resolution of the landscape data and the true resolution of environmental heterogeneity (i.e. landscape grain size). Thus, the observed aggregations may in fact be false due to this disparity. This is further discussed in the final section.

4. Discussion

4.1. Environmental heterogeneity

The proportion of the > 100 $m^3 ha^{-1}$ stands is, in general, much higher in natural forest landscapes than in managed ones, but in addition to that, also the scale and resolution of heterogeneity are different. When interpreting these results about the relationship between spatial scale and variance in habitat proportion, we want to emphasise especially that the scale and pattern of environmental heterogeneity, in particular the patch configuration of succesional stages have distinctly altered in the course of forest management in Fennoscandian forests. One could argue that this is more of a supposition since studies on the scale and pattern of heterogeneity in past landscapes of Fennoscandia are lacking. However, information derived from research on forests in Russian Carelia support our view (*see* e.g. Siitonen *et al.* 1994). It is obvious that the decrease of variation in landscape composition and configuration as a function of extending scale is a fundamental feature of every heterogeneous environment. We presume, however, that a corresponding reduction in variance occurred on considerably larger scales in natural landscapes than in present managed forests. This change in heterogeneity is a by-product of small-patterned land ownership, regeneration areas small and uniform in size, and economically optimal even age-distribution of forest stands, which has, according to Pukkala (1994), previously been a common target already at the level of individual forest holdings. Particularly in the case of NE Finland, Reunanen and Nikula (1998) propose that selective cutting applied in the first half of this century had a relatively low impact on forest landscape structure, and that this presently evident structural change is due to the altered methodology of commercial forestry

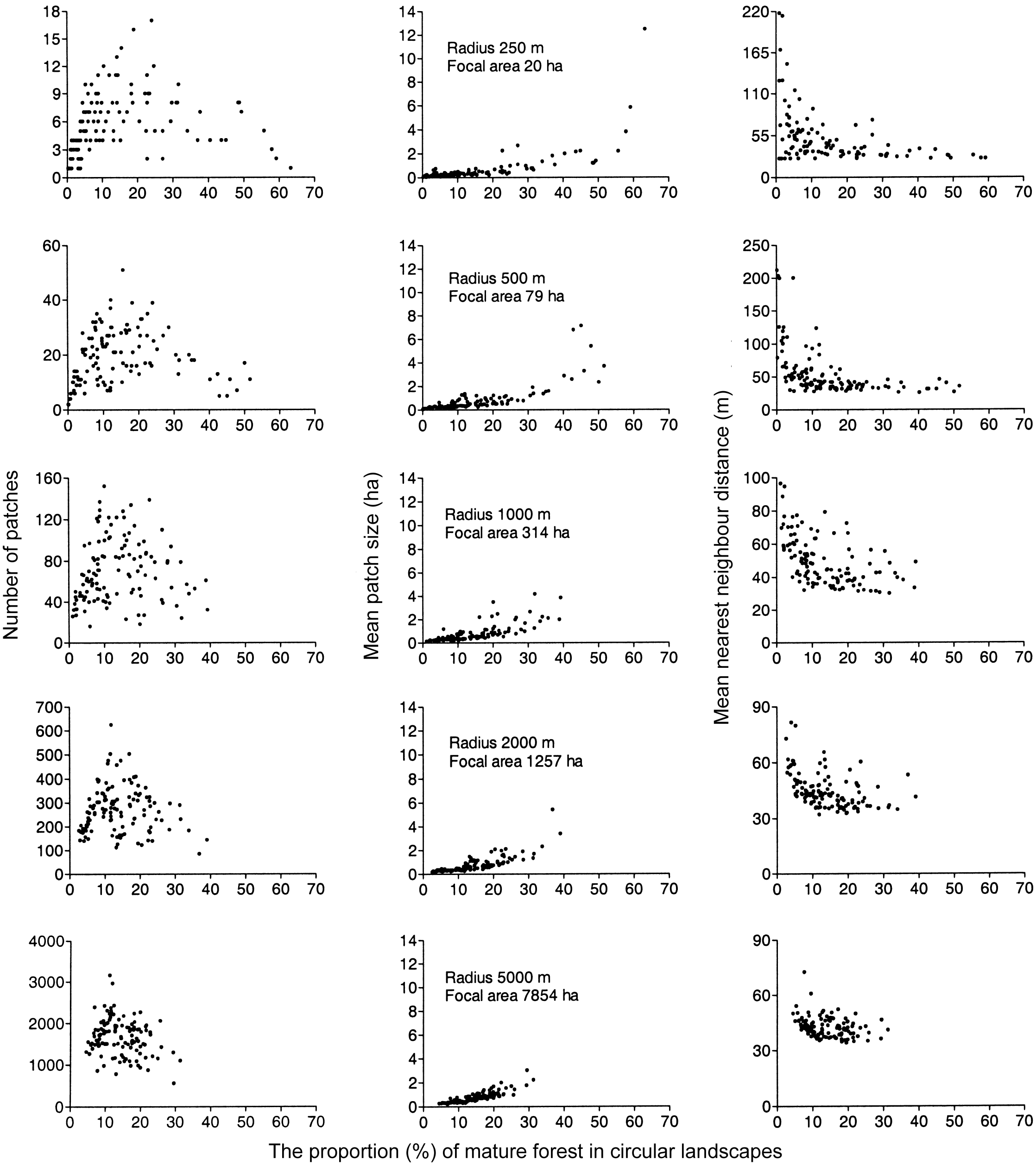

Fig. 4. Number of patches, mean patch size and mean nearest neighbour distance in relation to the proportion of mature forest in circular landscapes with five different radii.

adopted since the 1950s.

In our study area, and at the spatial level relevant to the individuals of the discussed species, the scale and pattern of environmental heterogeneity is of artifactitious origin as the patch mosaic results from commercial forestry. Patchiness is an inherent trait of all environments in nature, but since patch structure is hierarchic and patches themselves are created by a given process with a particular frequency (i.e. single patches last for a particular period of time), an apparent graininess of any habitat mosaic cannot as such be defined as coarse or fine. Thereby, the scale dependencies of an organism must be internalised into the grain concept, and only after that can this definition be made. Furthermore, in the literature there have been different connotations for 'grain' and even debate over the use of the term (Levins 1968, Wiens 1976, Addicott *et al.* 1987, Kotliar & Wiens 1990, Norton & Lord 1990, Wiens 1990). Due to the anthropogenic cause behind patch mosaic in managed forests, we then refer to the 'grain' definition originally presented by Levins (1968) where mosaic is fine grained for an individual if patches are smaller than the home range size and animals encounter several habitat types in their routine activity. The physical — but not necessarily functional — fragmentation of mature forest habitat was evident already in smallest landscape class (Figs. 3 and 5). Thus, as already the smallest of the species have their routine cruising distances in the hundreds-of-metres scale, the average patch mosaic in the examined forest landscapes is fine-grained from the point of view of all discussed species.

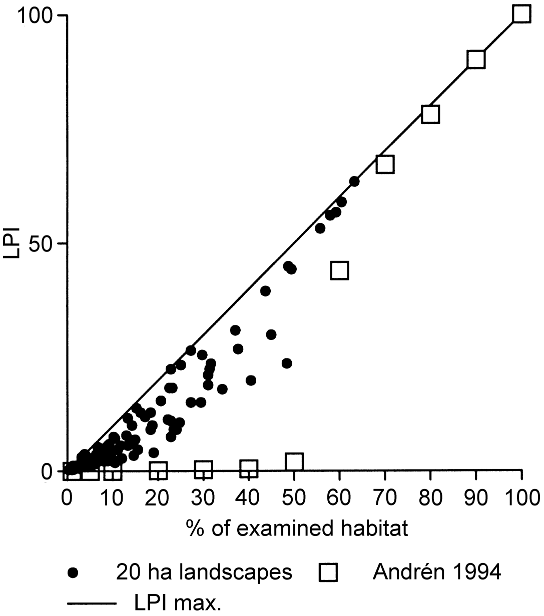

Fig. 5. Comparison of largest patch index (LPI) between this study and randomly generated model landscapes from Andrén (1994). LPI is a percentage of largest patch area from the total area of landscape, and it reaches its maximum value if all of the examined habitat is in one patch.

Although we refer to the forest age in our classification, the well-being of old forest species is only rarely directly associated to the age of trees. Rather are they adapted to some combinations of structural elements, micro-habitats and community structures, which coincide in climax stages. The particular characteristics in habitat classification as well as the important scale (both the resolution and the landscape extent) are different for various species and depend on whether the question is proposed on the scale of an individual or a population (e.g. Haila 1990, Kotliar & Wiens 1990). Therefore, in the goal setting of biodiversity maintenance in a forest planning area, relevant issues are to acknowledge the important forest characteristics and to optimise the scale-dependent variation in their occurrence. Because of our simplified habitat classification relative to species' needs it is obvious that there are suitable habitats for these species in the < 100 m^3 ha^{-1} class as well as large enough but uninhabited areas in the mature forest class. However, irrespective of this artificial 100 m^3 ha^{-1} border, the observed spatial pattern in environmental heterogeneity suggests that the occurrence of individuals in the study area is restricted to large enough patches few in number, or that the individuals perceive the environment in fine-grained manner. The negative implication of coarse-grained response on the population density is apparent if large enough patches are a limiting factor. Similar reduction in density results from the fine-grained response too, if the species is territorial, and individuals must establish their territories in qualitatively variable patch mosaic. A fine-grained habitat mosaic may also decrease the fitness of individuals since substantial proportion of their home range is sub-optimal habitat, although this can be compensated with good moving ability (Tjernberg *et al.* 1993). All of the surveyed species have a good ability to move across forested landscape and, despite the observed habitat pattern, the individuals may in many cases experience the mature forest habitat as continuous at their own operational scales. In spite of this, however, there seems to be a relatively low proportion of landscapes which could respond to the habitat requirements of each species by containing an adequate total amount of mature forest. This applies particularly to siberian tit, three-toed woodpecker and capercaillie.

4.2. Thresholds in non-linear population responses

The importance of critical thresholds in the proportion of suitable habitat has been emphasised in studies modelling the direct effects of habitat fragmentation on populations (Turner & Gardner 1991, Gustafson & Parker 1992, Andrén 1994). Above the threshold, the effects are caused solely by the decrease in habitat area, as predicted by the random sampling hypothesis (Haila 1983b). At the threshold and below, however, population density or community richness may respond dramatically to only minor reduction in habitat area due to abrupt decrease in habitat connectivity and increasing significance of fragmentation effects. Later modelling has suggested further that threshold proportion is sensitive to habitat specificity and dispersal abilities of the target species (With & Crist 1995, Andrén 1996). The knowledge of non-linearities in relations between species viability and environmental gradients (measured, for example, by resource occurrence, habitat area, physical landscape structure etc.), and critical threshold stages in them would be useful in improving the precision of practical guidelines for biodiversity maintenance in managed forests (Mykrä & Kurki 1998). Haila (1995) assessed the practicability of using natural dynamics as a model for management and he also gave a corresponding approach of such threshold values. He emphasised the identification of critical 'qualitative junctures' in natural non-linear processes, i.e. stages in which change is qualitatively important with only a slight change in system parameters, and addressed that an assessment is needed to reveal whether these junctures occur or are lacking in silvicultural forests.

In his review of literature on mammals and birds in mosaic landscapes, Andrén (1994) concluded that for these taxa, critical threshold levels are between 10% and 30% of suitable habitat. In spite of a probable species-specificity in threshold values, the fifteen per cent proportion of mature forest habitat in our study area is so low that habitat spacing can be argued to be important from an ecological standpoint. In terms of NP, MPS and MNN, the relations between landscape metrics and habitat proportion in the landscapes with a 250 m radius resembled the results achieved from randomly generated neutral landscapes (Andrén 1994, With & King 1997) (Fig. 3). This would suggest a random spatial distribution of habitat patches on the smallest examined scale. However, examination of LPI (Fig. 5) reveals that as compared with the random pattern the > 100 m^3 ha^{-1}-pixels are indeed aggregated to a certain degree also on the smallest scale, and the values of single landscapes are closer to the LPI maximum. Maximal LPI (solid line in Fig. 5) is the level of utmost aggregation, because in that case NP is one. Comparison between natural landscapes and the modelled random pattern, however, is complicated with the fact that in real landscapes the grain size is determined 'from the outside' — random landscapes are a result of single pixels emerging or disappearing in a random fashion, but for example in our case the aggregation was partly due to the difference between pixel size (25 m × 25 m) and average area of forest regeneration (1–10 ha). With this resolution a five-hectare patch emerging or disappearing in landscape is innately an 80-pixel aggregation. Comparable to the random spacing pattern of habitat within landscapes was also the fact that NP distributed randomly between circular landscapes on 20 ha scale, but not on larger scales. Furthermore, in the only landscape where the proportion of mature forest habitat exceeded 60%, the habitat formed one percolating, yet continuous patch (NP = 1) (Fig. 3). This is in accordance with the percolation theory (e.g. Gardner & O'Neill 1991), which predicts that when the proportion of habitat in a randomly generated landscape decreases below about 60%, one continuous habitat cluster breaks into discrete patches and size and connectivity of habitat patches can become an important feature of the landscape.

4.3. Conclusions

Since the extraction of natural resources by humans is indispensable in Finnish managed forests, the implementation of biodiversity maintenance must begin with precisely targeted area level and regional level management applications, even if many of the components of biodiversity once occurred prevalently in the forest landscape mosaic.

Instead of applying moderate and standardised improvements extensively in managed forests, it would be more effective to systematically allocate various biodiversity maintenance responsibilities between forest planning areas by aggregating relevant resources spatially (Mykrä & Kurki 1998). Similarly, in a recent discussion on critical thresholds as management guidelines, caution in applying any generalised threshold values was emphasised (Andrén 1999, Mönkkönen & Reunanen 1999), since connectivity is a species-specific characteristic of a landscape, and average threshold values derived from the responses of a suite of species might be far below the habitat area needs of the most demanding ones. Future strategies and their application must be far better tailored according to varying objectives, and this also requires knowledge of local particularities at different scales. Guided by this thinking, we presented here a simple tool for assessing the possibility to maintain sufficient amount of suitable habitat for different forest dwelling mammals and birds.

The spatial scale of our study covered areas from tens of hectares to several thousands of hectares. The planned cut in commercially managed forests is relatively fixed already at those smallest scales due to economical constraints. Even if the most important efforts in conservation biology are to stop habitat loss and to restore degraded habitats (Fahrig 1997), a really significant increase in the proportions of economically inferior but ecologically beneficial features in managed forests seems impossible without a truly profound change from a pure volume based thinking in wood production to strategies that rely more on product quality. Until this kind of change happens, the most important question is: how should this fixed habitat composition of managed forests be spatially configured?

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