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Spatial ecology of breeding birds in forest landscapes: an indicator species approach

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Academic dissertation

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ABSTRACT

Indicator species have been proposed to reveal common status of ecosystems and their biodiversity. In this thesis, forest bird species were studied based on territory and nest site mappings within a forest-dominated landscape in southern Finland. The general aims of the thesis was to find candidates of indicator bird species that would predict general variation in species richness and density of forest bird assemblages, to reveal more exactly species with indicator property at multiple spatial scales, and to study factors that affect occurrence and dynamics of indicator species in forest landscapes.

The potential indicator species were screened by evaluating statistical models. The red-breasted flycatcher (*Ficedula parva* Bechst.), the pygmy owl (*Glaucidium passerinum* L.) and the three-toed woodpecker (*Picoides tridactylus* L.) were found to be the most suitable candidates of multiscale indicators of forest bird species richness. In general, models with small spatial scale and several indicator species were observed to better explain the total variation in species richness. The results show that a carefully selected set of bird indicator species may be useful and efficient method for evaluation of forest bird diversity.

The densities of the above-mentioned three species were also higher in the surroundings of *capercaillie* (*Tetrao urogallus* L.) leks where also the overall species richness of forest birds was higher. The density of capercaillie also coincides with general wildlife richness. Capercaillie can thus be considered a good candidate for an umbrella species for wildlife.

The occurrence of the three-toed woodpecker was influenced by spatial dynamics of the species and the quality of the landscape. Territory quality of three-toed woodpecker may, however, be substantially modified by species interactions and be mediated to its population development. The results suggest the presence of quality threshold values of forest environment, which may determine the occurrence of the three-toed woodpecker and similar species in forest landscapes.

Keywords: capercaillie, forest biodiversity, spatial scales, species richness of forest birds, three-toed woodpecker, umbrella species

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TIIVISTELMÄ

Pesimälinnuston spatiaalinen ekologia metsämaisemissa: indikaattorilajitarkastelu

Indikaattorilajeja on ehdotettu kuvaamaan ekosysteemien yleistä tilaa ja niiden biodiversiteettiä. Tässä työssä tutkittiin eteläsuomalaisen metsämaiseman pesimälinnustoa kartoituslaskennoin. Työn keskeisinä tavoitteina oli löytää sopivia indikaattorilintulajeja, jotka ennustaisivat koko metsälinnuston lajimäärää ja tiheyttä usealla alueellisella mittakaavalla sekä tutkia indikaattorilajien esiintymiseen ja vaihteluun liittyviä tekijöitä metsämaisemissa.

Indikaattorilajiehdokkaita etsittiin tilastollisten mallien avulla. Parhaimmiksi koko metsälinnuston usean mittakaavan indikaattorilajeiksi havaittiin pikkusieppo (*Ficedula parva* Bechst.), varpuspöllö (*Glaucidium passerinum* L.) sekä pohjantikka (*Picoides tridactylus* L.). Koko linnuston lajimäärän vaihtelua selittivät parhaiten pienimittakaavaiset ja usean indikaattorilajin mallit. Tulokset osoittavat sen, että huolellisesti valitun indikaattorilajijoukon avulla on mahdollista tehokkaasti arvioida koko metsälinnuston monimuotoisuutta.

Kolmen edellä mainitun lajin tiheydet olivat suuria metson (*Tetrao urogallus* L.) soidinpaikkojen ympäristöissä, joissa myös koko metsälinnuston lajimäärä oli korkea. Metson tiheys ilmentää myös yleistä riistarikkautta koko Suomen mittakaavassa. Metsoa voidaankin pitää hyvänä ehdokkaana metsäluonnon sateenvarjolajiksi.

Pohjantikan esiintymiseen havaittiin vaikuttavan sekä lajin alueellinen dynamiikka että metsämaiseman laatu. Lajienväliset vuorovaikutukset voivat kuitenkin vaikuttaa pohjantikan reviirin laatuun ja heijastua sen kannan kehitykseen. Työn tulokset viittaavat siihen, että erilaisilla metsäympäristön laadullisilla kynnysarvoilla voi olla merkittäviä vaikutuksia pohjantikan ja muiden lintulajien esiintymiseen metsämaisemissa.

Asiasanat: alueelliset mittakaavat, metsien biodiversiteetti, metso, metsälintujen lajirunsaus, pohjantikka, sateenvarjolaji

ACKNOWLEDGEMENTS

The work included in this thesis is originally influenced by the Finnish tradition of field ornithology and bird census work, and it is a part of a long and winding road to understand at least something about the world of breeding birds in Finnish nature.

I am grateful to my supervisor Jari Kouki for advice, support and co-operation to complete my thesis. I thank my pre-examiners Mikko Mönkkönen and Hannu Pöysä for constructive comments and useful suggestions to this work.

I wish to thank all co-authors of this thesis, Ilkka Hanski, Jari Kouki, Andreas Lindén, Harto Lindén, Jani Pellikka, Juha Tiainen and Erkki Tomppo for considerable input to this work.

My thesis is based on ideas developed in various combinations of bird ecology study groups in the University of Helsinki, the Finnish Game and Fisheries Research Institute and the University of Eastern Finland. These groups have, among other things, concentrated on relevant integration of spatially explicit bird and environmental data and development of efficient mapping census methods of terrestrial breeding birds. I have been privileged to work within these groups both in the office and in the field. I especially thank Juha Tiainen, the key person of these study groups, for long-lasting encourage to study breeding birds and for mental support.

The studies in my thesis cover a time-span of over twenty years. Several people have during this time contributed to the ideas and supported the work of this thesis. Of these people, Ilkka Hanski, Jyrki Holopainen, Jari Kouki, Harto Lindén, Juhani Lokki, Markus Piha, Jarmo Piiroinen, Juha Tiainen, Erkki Tomppo, Kari Vepsäläinen and Ville Vepsäläinen are especially acknowledged.

During the last ten years my interest in forest bird studies has more and more focused on a selected set of species that could serve as indicators of the total forest bird species assemblages. These intensive population studies have widely broadened my view of the spatial ecology of forest birds. I greatly appreciate the work in the three-toed woodpecker study group with Johanna Lakka, Toni Nurmi, Jarmo Piiroinen, Markus Piha and Ville Vepsäläinen in the Evo area.

The Lammi Biological Station always provided excellent facilities during the field season. The work of this thesis has been financially supported by the Ministry of Environment (the Environmental Cluster Programme) and the University of Eastern Finland, School of Forest Sciences.

LIST OF ORIGINAL ARTICLES

The thesis is based on the following articles, which are referred to in the text by their Roman numerals I-IV. The articles II-IV have been reproduced with the kind permission of the publishers while the study I is the author version of the submitted manuscript

I Pakkala, T., Lindén, A., Tiainen, J., Tomppo, E & Kouki J. 2012. Indicators of forest biodiversity: which bird species predict high breeding bird assemblage diversity in boreal forests at multiple spatial scales? Manuscript.

II Pakkala, T., Pellikka, J. & Lindén, H. 2003. Capercaillie *Tetrao urogallus* – a good candidate for an umbrella species in taiga forests. Wildlife Biology 9:309–316.
http://www.wildlifebiology.com/Indices/2003+-+Volume+9/4/426/En/

III Pakkala, T., Hanski, I. & Tomppo, E. 2002. Spatial ecology of the three-toed woodpecker in managed forest landscapes. Silva Fennica 36:279–288.
http://www.metla.fi/silvafennica/full//sf36/sf361279.pdf

IV Pakkala, T., Kouki, J. & Tiainen, J. 2006. Top predator and interference competition modify the existence, abundance and breeding success of a specialist species in a structurally complex forest environment. Annales Zoologici Fennici 43:137–164.
http://www.sekj.org/PDF/anzf43/anzf43-137.pdf

Author's contribution

I. The author planned the study design and performed the field work and data handling, and the author and Andreas Lindén planned and performed the statistical analyses. The author wrote the first draft of the manuscript, and all co-authors contributed to the completion of the manuscript.

II The author and Harto Lindén planned the study design. The author performed the field work and data handling of the Lammi study area, and the respective statistical analyses; the data of the wildlife triangles was collected by volunteers and was analysed by Jani Pellikka. All authors contributed to the writing of the manuscript.

III The author and Ilkka Hanski planned the study design. The author performed the field work. All authors contributed to data handling, statistical analyses, and the writing of the manuscript.

IV The author planned the study design, performed the field work and data handling, and performed and planned the statistical analyses. The author wrote the first draft of the manuscript, and all co-authors contributed to the completion of the manuscript.

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INTRODUCTION

Indicator concept and its various forms

Indicator species have been considered to reveal common status of ecosystems and their biodiversity; information that is urgently needed for e.g. maintaining global biodiversity. Indicator species are generally thought as "species whose characteristics, such as occurrence, density or population development are used as indices of attributes too inconvenient or expensive to measure for other species or environmental conditions of interest" (Landres *et al.* 1988; cf. Stork and Samways 1995, Niemi and McDonald 2004). Indicator species have been considered to indicate overall biodiversity of ecosystems or habitats (e.g. Noss 1990, Ryti 1992, Gaston and Williams 1993, Williams and Gaston 1994). Various studies have tried to find sets of species that would reflect total species richness of other biota or more diverse taxonomic groups (e.g. Kremen 1992, Pearson 1994, Prendergast and Eversham 1997, Jonsson and Jonsell 1999, Gustafsson 2000, Araujo *et al*. 2004, Kati *et al*. 2004, Similä *et al.* 2006, Lewandowski *et al*. 2010). Relevant indicator species or species groups would be applicable in practical management of biodiversity and in conservation planning because inventorying and monitoring all taxa is difficult and laborious (e.g. Meffe and Carroll 1994, Noss 1999, Angelstam *et al.* 2004, Mac Nally and Fleishman 2004, Feld *et al.* 2009, Blasi *et al*. 2010).

In conservation of biodiversity, attention is particularly paid to complementarity and nestedness of various indicator species groups to assure that they are representative and efficient surrogates for total diversity (Margules *et al.* 1988, Prendergast *et al*. 1993, Humphries *et al.* 1995, Faith and Walker 1996, Williams *et al*. 2006, Sætersdal *et al* 2005, Gjerde *et al.* 2007, Juutinen *et al.* 2008, Wiens *et al*. 2008). Indicator species have been selected e.g. by the importance of their sensitivity, applicability and relevance for ecological phenomena studied, feasibility and cost-efficiency of their use, and in situations with simultaneous use of groups of ecologically various species or taxa (Noss 1990, Pearson 1994, Balmford *et al*. 1996a,b, Gaston 1996a,b, McGeoch 1998, Dale and Beyeler 2001, Carignan and Villard 2002, Fleishman *et al*. 2005).

Efforts to highlight the importance of single species have led to various terms and concepts which are also commonly used of suitable indicator species in addition to their indicator status. These include, for example, "umbrella", "flagship" or "keystone" species (Mills *et al.* 1993, Caro and O'Doherty 1998, Simberloff 1998, Andelman and Fagan 2000, Roberge and Angelstam 2004, Caro 2010) that refer to situations where 1) a species has demanding habitat and large area requirements that saving it will automatically save many other species (umbrella species; Schrader-Frechette and McCoy 1993), or 2) a species is well-known and charismatic (often a large vertebrate) that has become a symbol or leading element of campaigns for broader conservation objectives (flagship species; Schrader-Frechette and McCoy 1993), or 3) a species has impacts on many other species, function or structure of the ecosystem that are beyond what might have been expected from a consideration of its biomass or abundance (keystone species; Paine 1969, 1995, Bond 1993, Simberloff 1998). The concept of "focal species" has been used mainly in conservation biology and landscape ecological planning representing those species selected as a focus for specific study, e.g. in identifying potential indicator species (e.g Lambeck 1997, Carroll *et al.* 2001, Bani *et al*. 2002, Niemi and McDonald 2004, Similä *et al*. 2006). Mammals and birds have been common groups as candidate indicator species, e.g. for umbrella species, but more tests of e.g. other vertebrate groups, insects and plants as

umbrella species are needed (Hitt and Frissel 2004, Lawler and White 2008, Roberge et al. 2008b, Branton and Richardson 2010).

The scope in this thesis is limited to birds, and the focus is especially on those bird species that could well explain observed variation of total forest bird species richness. As a biodiversity measure, species richness is generally simple and easily comprehended, and it is also often positively correlated with other, e.g. taxonomic and functional measures of biodiversity (Magurran 1988, Gaston 1996b), but it may still be useful to adopt an integrative approach of taxonomic, phylogenetic and functional diversity measures especially at large spatial scales to get a more comprehensive view of diversity patterns (Wiens and Donoghue 2004, Devictor *et al.* 2010, Meynard *et al.* 2011). In any case, careful standardizations of data sets are needed for appropriate measurements and comparisons of species richness to get reliable estimates (Colwell and Coddington 1994, Gotelli and Colwell 2001).

Northern forest birds: properties and potential indicator species

Many Northern European forest bird species are rather generalists in their habitat use. For these species, their presence and abundance are mainly based on general characteristics, such as forest stand age and tree composition (e.g. v Haartman *et al.* 1963-72, Väisänen *et al.* 1998, Svensson *et al.* 1999). However, some forest bird species are more restricted in their choice of habitat. In particular, the degree of naturalness or lack of human influence, e.g. abundance of large trees, dead wood and multi-layered stands influences the presence of such forest bird species, that often belong to resident and primary or secondary hole-nesting species (Angelstam and Mikusiński 1994, Roberge and Angelstam 2006, Roberge *et al.* 2008a).

In most cases it is possible in general to define a certain habitat patch or forest area as suitable or unsuitable habitat of our forest bird species. If, however, the aim is to explain the total variation of bird species richness in forest environments, also factors like temporal trends, annual fluctuations and spatial variation in population densities of individual species must be taken into account. These patterns are in turn affected by a large range of different factors besides habitat use, e.g. abundance of the species, site-tenacity, species interactions and spatial scale (Wiens 1989, Haila and Järvinen 1990, Haila et al. 1996; see below).

In general, species and forest landscapes are also expected to differ in the extent of empty but suitable habitat depending e.g. on the density of the species, habitat fragmentation and movement capacity of the species (e.g.. Andrén 1994, Hanski 1999). Landscape-level patterns may be important for the occurrence of especially resident species (Jokimäki and Huhta 1996, Kouki and Väänänen 2000, Schmiegelow and Mönkkönen 2002, Brotons *et al.* 2003, Jansson and Andrén 2003, Huhta *et al*. 2004, Sirkiä *et al.* 2011).

The studies of potential and suitable indicator bird species of boreal forests are often based on knowledge about the habitat preferences or possible threshold values of the species in forest landscapes, and comparisons with actual data sets of assemblages of forest bird species are still relatively rare and restricted to few groups of birds.

Angelstam (1992) proposed three species as key or indicator bird species of Fennoscandian boreal forests: the presence of capercaillie (*Tetrao urogallus* L.) indicates a sufficient patch size, hazel grouse (*Bonasa bonasia* L.) that the proportion of deciduous trees is sufficient, and three-toed woodpecker (*Picoides tridactylus* L.) or white-backed

woodpecker (*Dendrocopos leucotos* Bechst.) that there is sufficient amount of dead wood. Forest grouse are in general assumed to be relevant indicators of the status of their ecosystem because of their close tracking of their environment, large spatial requirements of viable populations, specific habitat demands and their vulnerability to predation (Boag and Rolstad 1991, Swenson and Angelstam 1993, Storch 2000). Because of their demanding ecological requirements, responses to the naturalness of forest environment and their for various secondary cavity-nesting bird species, woodpeckers are considered good indicator species of habitat quality and forest biodiversity (Mikusiński and Angelstam 1997, Mikusiński 2006, Drever et al. 2008).

Field studies focusing on species richness and densities of forest species give support to the indicator status of forest grouse and woodpeckers. Positive relations have been observed between capercaillie and species richness and abundance of mountain birds in the Swiss Alps (Suter et al. 2002), and between capercaillie and woodpecker densities in the German Alps (Fischer and Storch 2001). In the above-mentioned studies capercaillie has been proposed as a suitable umbrella species forest bird diversity. The occurrence of hazel grouse has been observed to correlate positively to resident bird species richness in managed boreal forests (Jansson and Andrén 2003).

Mikusiński *et al.* (2001) found significant positive correlations between woodpecker species related to the occurrence of other forest birds at landscape level in Poland. Roberge and Angelstam (2006) estimated middle spotted (*Dendropos medius* Bechst.) and lesser spotted woodpecker (*D. minor* L.) in deciduous forests and three-toed woodpecker in coniferous forests among the best indicators among resident forest birds in a cross-regional evaluation in northern Europe. Drever *et al.* (2008) detected positive correlations between woodpecker species richness and species richness of other forest birds at forest stand level in a study in Canadian forest landscape, and they concluded that woodpecker species richness can serve as a reliable indicator of overall bird richness in most forest stands.

In particular, three-toed woodpecker has considered to be an important keystone species in coniferous-dominated natural forest and a potential umbrella species indicating general habitat quality, including factors like structural complexity and habitat heterogeneity of forest environment (e.g. Imbeau 2001,Angelstam *et al.* 2003, Bütler *et al.* 2004, Pechacek and d'Oleire-Oltmanns 2004, Roberge *et al.* 2008a). Top predators, as hawks or owls, may promote species richness by interspecific interactions or by nesting in structurally complex forest environments and thus their occurrence can indicate potential for high species richness (e.g. Sergio *et al.* 2006, 2008).

Fennoscandian boreal forests are relatively well known ecosystems (e.g. Kouki 1994, Esseen *et al*. 1997, Nilsson *et al.* 2001, Korpilahti and Kuuluvainen 2002, Angelstam and Kuuluvainen 2004, Wallenius *et al.* 2010), and there is a large amount of studies concentrating on the densities and distributions of their breeding bird species (Haila and Järvinen 1990, Esseen *et al*. 1997, Väisänen *et al*. 1998, Svensson *et al*. 1999). However, we still lack quantitative, spatially explicit and systematic landscape level studies of breeding bird assemblages (Roberge and Angelstam 2006). Mostly for logistic reasons, the studies of forest birds have applied line transect or point counts to gather empirical data from large areas. These methods, however, provide only limited information of the exact spatial occurrence of territories. To reliably assess potential indicator species of total bird species richness, to compare territory and species patterns at different spatial scales, and to estimate possible survival of species in various forest landscapes, we need forest bird data within accurate sites from large areas. Such data can be based on intensive and standardised territory or species mapping of breeding bird species which typically requires

4-6 times higher censusing effort. In this study, the efficient, systematic mapping method to define the occurrence of forest bird species was used (see study IV).

AIMS OF THE STUDY

Main aims of the thesis were 1) to find candidates of indicator bird species that would predict observed general variation in species richness and density of forest bird assemblages, 2) to reveal more exactly those species that have indicator property at multiple spatial scales, and 3) to study factors that affect occurrence and dynamics of indicator species in forest landscapes. The studies of the thesis cover various spatial scales from biotope to local landscape level and also include a nationwide approach to get a more comprehensive view of the species and previously mentioned themes.

STUDY AREA

The study area is located in the municipalities of Hämeenlinna (Lammi), Padasjoki and Asikkala in southern Finland (61º 15' N; 25º 00' E). The total area covered is 470 km^2 (I, IV), 465 km^2 (II), and 340 km^2 (III), depending on the respective study. Forest covers 80% of the study area, and spruce-dominated coniferous or mixed mature stands are the most common types of forest. The landscape is a mixture of forests of different ages, agricultural areas, lakes and scattered human settlements with a gradient from a southern agriculture-forest mosaic to northern forest-dominated areas.

In the capercaillie study (II), the wildlife triangle data (see below) covers the whole of Finland.

BREEDING BIRD AND WILDLIFE TRIANGLE DATA

The study area was covered with breeding bird censuses during 1983–2005. Censuses were made by a modification of territory mapping method. This method is based on the method developed by Enemar (1959), on recommendations for an international standard for a mapping method (Anon. 1969), and on improvements of the method suggested by Tomiałojć (1980). Following extensive field tests of the efficiency and reliability of the territory mapping method in the Lammi study area in 1979-1986 (Tiainen *et al.* 1980, T. Pakkala and J. Tiainen, unpublished), a method with 4-5 visits was taken into use by the author to census relatively large areas in forest environments.

All local and regional territory mapping and species occurrence information data on breeding birds in this study were collected by the author and they include a combined set of data from a field effort of totally some 16 000 hours in 1983--2005. These data can be classified to the following three categories, respectively: 1) territory mapping of all bird species; total field effort 4 000 hours; total cover 130 km^2; 2) territory mapping excluding the most abundant bird species of which only species occurrence information was gathered;

total field effort 7 000 hours; total cover 300 km^2; 3) territory mapping of selected bird species and additional information; total field effort 5 000 hours; total cover of mapping 800 km^2 with overlapping areas in different years in these categories. All parts of the study area of 470 km^2 were covered with censuses, but as they were targeted to study forest birds and especially those species typically associated with mature forests, there were relatively more censuses in the northern parts of the study area than in the cultural landscapes of the southern parts of the study area.

As a result of annual breeding bird mappings and species occurrence information, locations of territory centres and nest sites of the species studied and lek centres of capercaillie were defined, and also the numbers of territories or occurrence of the studied forest bird species were estimated. The more detailed descriptions of the bird data sets and procedures used are presented in the respective studies I-IV.

In the capercaillie study (II) the data were based also on the wildlife triangle scheme (see Lindén *et al.* 1996). The data of the years 1989-2001 of the wildlife triangles, census routes of 12 km that are counted both in winter and autumn, and covering representatively whole of Finland, were used.

ENVIRONMENTAL DATA

In studies I, II and IV environmental data based on land cover and forest classification data (Vuorela 1997), digital topographic maps made by the National Land Survey of Finland, aerial photographs and extensive field information on the study area, habitat and landscape types were used. Changes in land use and forestry during the study period were also estimated by these data. The land-use and forestry data were selected to match the bird census years of the particular study areas and spatial scales of the respective study.

In studies I and III numerical thematic maps produced by the Finnish multi-source national inventory were applied as a background information and in measuring the territory and landscape quality. The multi-source inventory method utilises satellite images and digital maps in addition to field measurements (Tomppo 1991, Tomppo *et al.* 2008).

RESULTS

Species richness of forest bird assemblages can be largely predicted by occurrence of a few selected bird species that serve as indicator species

The potential indicator species were screened at various spatial scales by evaluating statistical models that included 1–5 indicator candidate species. In general, models with small scale and several indicator species were observed to better explain the total variation in species richness. As measured by the coefficients of determination, the total variation explained by the occurrence of indicator species increased from an average of 12 % in single-species models to an average of 61 % in five-species models. Already three indicator species explained the variation in species richness reasonably well, on the average 48 % (I).

A few species were found to be good indicators simultaneously at several spatial scales. The red-breasted flycatcher (*Ficedula parva* Bechst.), the pygmy owl (*Glaucidium passerinum* L.) and the three-toed woodpecker were found to be the most suitable candidates of indicators of forest bird species richness (see below). The results show that a carefully selected set of bird indicator species may be useful and quick method for practical evaluation of bird diversity in forest environments (I, Fig. 1)).

Based on comparisons between 41 capercaillie lek sites and 41 control sites (II), the densities of the best three above-mentioned indicator species were also significantly higher in the surroundings of capercaillie leks. The mean densities of red-breasted flycatcher, pygmy owl and three-toed woodpecker were 4.2, 8.5 and 19.3 times higher at the 300-m scale and 1.4, 1.4 and 1.7 times higher at the 1,000 m scale, respectively. The overall species richness of forest birds was also higher around capercaillie leks. Within a 300-m radius, the mean number of breeding forest bird species (excluding capercaillie) at the lek sites was 41.2 and 36.4 at the control sites; the difference is highly significant. Within a 1,000-m radius there was an insignificant difference in favour of lek surroundings (mean 59.6 species) compared with control sites (58.1 species).

On a larger, nationwide scale in Finland, the density of capercaillie is positively correlated with wildlife richness, i.e. the total abundance of 15 other forest-dwelling mammal and bird species with diverse ecology and habitat requirements. Capercaillie can thus be considered a good candidate for an umbrella species for wildlife in taiga forests (II).

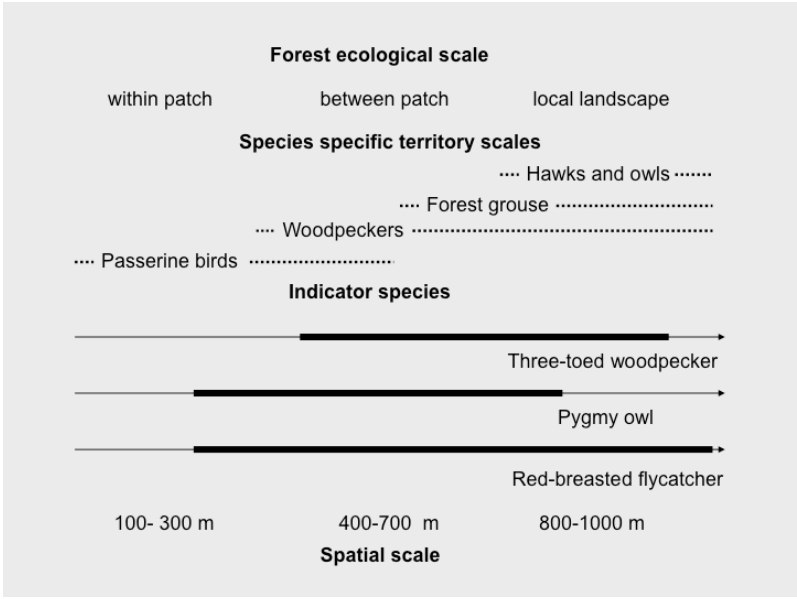

Figure 1. A schematic chart of various spatial scales of boreal forests studied in this thesis. Examples of typical territory scales of some important forest bird groups are shown. The indicator scales of three best forest bird species indicators, three-toed woodpecker, pygmy owl and red-breasted flycatcher are also presented. Bold lines that show the scales where the above-mentioned species are good indicators are seen to overlap with some main species-specific and forest ecological scales, that makes these indicator species important broad-scale indicators of forest environment.

In the goshawk study (IV) densities of sparrowhawk (*Accipiter nisus* L.), ural owl (*Strix uralensis* Pall.), pygmy owl, three-toed woodpecker and great-spotted woodpecker (*Dendrocopos major* L.) were significantly higher around non-occupied goshawk nest sites compared with that at other sites without observed goshawk nests, and goshawk nest sites can thus be considered as potential "hot spots" of various other forest bird species.

Indicator status or property of a forest bird species depends on the spatial scale

The studies of the thesis cover various spatial scales from biotope (ca. 0.1-10 ha) to local landscape (ca. 1 000 – 10 000 ha or 10 – 100 km^2) level. In the screening of indicator species (I), the total number of potential indicator species was rather constant with a range between 24 and 31 at various scales from 1 to 300 ha. There was, however, a turnover of species composition within the class of potential indicator species with increasing scale, as the proportion of common species increased and that of rare species decreased, respectively. The possible indicator property of a species is thus related to the design or scale of the respective study.

There were quite a few species that were indicators at various spatial scales studied (I). The most important species included red-breasted flycatcher that was selected as an indicator species in all scales between 200 and 1000 m and among the five best single species (top-5) in six of these scales, pygmy owl (indicator species in scales of 300–800 m; top-5 in five scales) and three-toed woodpecker (indicator species in scales of 400–900 m; top-5 in five scales). In addition to these top candidates there were some other noteworthy species, namely brambling (*Fringilla montifringilla* L.) (indicator species in five of the scales of 200–1000 m; top-5 in four scales), swift (*Apus apus* L.) (indicator species in six of the scales of 400–1000 m; top-5 in two scales) and Tengmalm's owl (*Aegolius funereus* L.) (indicator species in scales of 400, 600 and 700 m and top-5 in all of these scales). The indicator species at a particular spatial scale is also connected to the respective forest ecological scale. At various spatial scales the indicator property of a species is influenced by scale-dependent environmental factors (see below).

Presence and abundance of the potential indicator bird species is influenced by properties of both the forest landscape and the species interactions

In general, it can be concluded that the presence of indicator species seems to indicate mostly some structural, habitat properties of the forest site in question. In the study of potential indicator species candidates (I), the comparison of changes in total species richness between two successive study years and with the simultaneous change in the presence of an indicator species revealed in general only minor effects of the role of indicator species itself to the variation of total species richness. However, some ecologically relevant interspecific interactions like negative effects of small owls and positive effects of brambling were also found.

In a study of the three-toed woodpecker (III), both territory and landscape quality had significant consequences for the occurrence of the territories of this indicator species. The spatial patterning and permanence of breeding and non-breeding territories were affected by a combination of spatial dynamics of the species and the quality of the landscape, the latter being much influenced by forestry. Species interactions, however, modify the

occurrence of the species (IV). The goshawk, a top predator, had a positive effect and the great spotted woodpecker, a competing species, a negative effect on the existence, abundance and breeding success of three-toed woodpecker.

DISCUSSION

Boreal forests are dynamic ecosystems with several spatiotemporal processes simultaneously affecting occupancies and densities of species and thus the variation in species richness (e.g. Kouki *et al.* 1994, Korpilahti and Kuuluvainen 2002, Angelstam *et al.* 2004, Wallenius *et al*. 2010). The applicability of the results of this study in space and time should be adjusted to relevant forest ecological scales of the studied system (c.f. Wiens 1989 and above). With increasing spatial scale from 100–300 m radius, approximately the ecological scale of the territory size of many forest passerine bird species, to greater scales with 800–1000 m radius corresponding the territories or areas of larger species e.g. hawks, owls and large forest grouse, there is simultaneously a smooth shift from small forest stand scale to local landscape scale with a mosaic of forest patches (Fig. 1). These scales are in turn connected to small-scale elements like possible structural complexity of nest-sites, habitat structure at territory size scale, or large-scale properties of the forest landscape, e.g. the amount of mature forest area.

The occurrence of forest bird species, and thus also potential indicator species are also characterised by various time lags, caused e.g. by their longevity, site-tenacity, and dependence on species-specific elements of changes in forest environments, e.g. habitat loss and fragmentation (c.f. Tilman *et al.* 1994, Wiens 1994, Schmiegelow et al. 1997, Schmiegelow and Mönkkönen 2002, Ewers and Didham 2006). As an example, within the study area of this thesis, several lekking areas of capercaillie in the Northern part of the study area were active already in the early 1960s (Pirkola and Koivisto 1970). The lek network of this area has persisted vital until recent years in spite of intensive forestry in various parts of the area that indicates the quality of this forest environment at a landscape level (c.f. Rolstad and Wegge 1987, Helle *et al.* 1994, Lindén *et al* 2000, Sirkiä *et al.*2010). Also within the study area, individually marked three-toed woodpeckers inhabited the same breeding territories for several years, one female at least during eight successive years (c.f. Pakkala *et al.* 2005), and in one territory site of the species the same nest hole was detected to be used again after 18 years in spite of large changes in the surrounding forest environment (T. Pakkala, unpublished data). The occurrence of any indicator species thus also demonstrates the history of the forest site or landscape in question.

Although the occurrence of forest bird species is closely connected to the properties of forest environment at various spatial scales, it can be, quite difficult to exactly quantify the essential properties of forest sites that make them suitable of each species. In this context the usefulness of indicator species becomes apparent: we can think that the presence of an indicator species at a certain site is, by definition, an indication of the suitability of the respective site for this species and several others *per se*. The indicator species thus "condenses" various properties of forest landscape, habitat structure and small-scale elements for us for e.g. management and conservation scenarios of forest environments.

A critical issue is the applicability of the indicator property of a species in another area, or in general the spatial range within which an indicator is valid (e.g. Storch and Bisonette 2002, Betrus *et al.* 2005, Roberge and Angelstam 2006). For example, as presented in

separate studies of this thesis, the northern and southern parts of my study area differ in the amount and fragmentation of forest environments. This may reflect to occurrence of indicator species even within this area, because in general species and forest landscapes are also expected to differ in the extent of empty but suitable habitat depending e.g. on the density of the species, habitat fragmentation, spatial patterning of habitats, and movement capacity of the species (c.f. Addicott et al 1987, Andrén 1994, Hanski 1999, Ewers and Didham 2005, Guénette and Villard 2005). Landscape-level patterns may be important for the occurrence of especially resident species (Jokimäki and Huhta 1996, Kouki and Väänänen 2000, Schmiegelow and Mönkkönen 2002, Brotons *et al.* 2003, Jansson and Andrén 2003, Huhta *et al*. 2004, Sirkiä *et al.* 2011). Also at a larger scale, within Finland, many forest bird species have great differences in densities and habitat preferences between Southern and Northern Finland (e.g. v. Haartman *et al.* 1963-72, Väisänen *et al.* 1998), which can substantially affect their potential as indicator species simultaneously in both of these areas.

Despite the above-mentioned various limitations in the use of indicator species, the results of the studies in this thesis can be considered very promising. Efficient key-indicator species like three-toed woodpecker, red-brested flycatcher and pygmy owl were found and these species are also known to indicate or have close connection to habitat quality and structure of the forest environment. These species were also good indicators at many spatial scales that are important in forestry, which makes their use logistically applicable. Capercaillie lek areas and goshawk nest sites were also detected to be indicators of high forest bird species richness and density at various spatial scales. The systematic screening of candidate indicator species gave also new information of still rather limited knowledge of potential indictor bird species in boreal forests. However, we need more tests by independent data and to explicitly combine the indicator bird species and changing forest landscapes. After these procedures and validations they hopefully could be applied in practical management and conservation of biodiversity in boreal forests.

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