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Indicators of forest biodiversity: which bird species predict high breeding bird assemblage diversity in boreal forests at multiple spatial scales?

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Indicator species have been proposed to be used for revealing common status of ecosystems and their biodiversity. We studied breeding forest birds in southern Finland. Our aim was to find bird species combinations that would predict species richness of forest bird assemblages at several spatial scales. We evaluated statistical models that included 1–5 indicator candidate species, and ranked them according to the Bayesian information criterion. The red-breasted flycatcher *Ficedula parva*, the pygmy owl *Glaucidium passerinum* and the three-toed woodpecker *Picoides tridactylus* were found to be the best multiscale indicators. Models at smaller spatial scales, including several indicator species better explained the total variation in species richness. The indicators mostly revealed properties of the forest site rather than variation in species richness caused by species interactions. Our results show that a suitable set of indicator species may be a useful and quick method for the evaluation of bird diversity in forest environments.

Introduction

Indicators are species whose characteristics, such as occurrence, density or reproductive success are used as indices of attributes too difficult, inconvenient or expensive to measure for other species or environmental conditions of interest (e.g. Landres *et al*. 1988, Stork & Samways 1995, McGeoch 1998, Niemi & McDonald 2004). Indicator species may indicate overall status of the environment (e.g. Hellawell 1986, Spellerberg 1991, Dallinger *et al*. 1992, Paoletti & Bressan 1996, Hilty & Merenlender 2000) or the biodiversity of ecosystems or habitats (e.g. Noss 1990, Ryti 1992, Gaston & Williams 1993, Williams & Gaston 1994). Several studies have tried to find a set of species that would reflect total species richness of other biota or more diverse taxonomic groups (e.g. Kremen 1992, Pearson 1994, Prendergast & Eversham

1997, Jonsson & Jonsell 1999, Gustafsson 2000, Araujo *et al*. 2004, Kati *et al*. 2004, Similä *et al*. 2006, Brin *et al*. 2009, Lewandowski *et al*. 2010). Such indicator species or species groups would naturally be very applicable in the practical management of biodiversity and in conservation planning because inventorying and monitoring all taxa is impossible in practical applications (e.g. Verner 1984, Martikainen *et al* 1998, Noss 1999, Lindenmayer *et al*. 2000, Angelstam *et al*. 2004, Williams *et al*. 2006, Hurme *et al*. 2008, Feld *et al*. 2009, Blasi *et al*. 2010).

Many Fennoscandian forest bird species are rather generalists in their choice of habitat. For these species, differences in assemblage structures are based on general characteristics, such as forest stand age and tree composition (cf. Väisänen *et al*. 1998, Svensson *et al*. 1999). However, some species are much more demanding in their choice of habitat. In particular, the degree of naturalness, e.g. abundance of large trees, dead wood and multi-layered stands influences the presence of resident and primary or secondary hole-nesting forest bird species (Angelstam & Mikusiński 1994, Pakkala *et al*. 2006, Roberge & Angelstam 2006, Roberge *et al*. 2008, Jokimäki & Solonen 2011). Features of the landscape may also be important for the occurrence of especially resident species (Jokimäki & Huhta 1996, Kouki & Väänänen 2000, Schmiegelow & Mönkkönen 2002, Brotons *et al*. 2003, Jansson & Andrén 2003, Huhta *et al*. 2004, Sirkiä *et al*. 2011).

Our aim was to seek candidate species to serve as indicators of high bird diversity in boreal forests. We set the following two criteria to identify good indicator species: (1) species should explain observed variation in total bird species richness; and (2) explanatory power of the species should be detectable at multiple spatial scales. We did not measure the direct relation between the presence of a potential indicator species and e.g. habitat quality or structure of the forest landscape.

We used presence–absence data of forest bird species from complete mappings of these species. As both spatial and temporal scales affect the occurrence and species richness of birds (Wiens 1989), and thus the assemblages of potential indicators (e.g. Noss 1990, Hammond 1994, Weaver 1995, Rykken *et al*. 1997, McGeoch 1998, Feld *et al*. 2009), we ranked and compared indicator candidates at various scales, studied their ecological properties, and analyzed separately the effects of site and species on the constancy of the indicator property.

A suitable forest indicator species is expected to explain the variance in total bird species richness at multiple scales, as well as indicate the structure of the forest environment. To explore the indicator value of breeding birds, we evaluated the following hypotheses:

1. Species richness of forest bird assemblages can largely be explained by the occurrence of a few selected bird species that serve as indicators. We explore the best single species and combinations of several (2–5) species in order to explain variation in total species richness of forest bird species.
2. If some species are indicators at several spatial scales they may be considered broad-scale key indicator species. We explore potential indicator species at multiple spatial scales. Species that have indicator status at several spatial scales are considered valuable indicator species.
3. Presence of the indicator species can reflect properties of both the habitat and species interactions. While indicator species of high species richness indicate the structure of forest environments, they might also affect species richness directly through positive or negative species interactions. To test the presence of the latter mechanism in the indicator properties of various species, we compare total species richness between replicates of study plots and control for changes in the forest landscape.

Material and methods

Study area

The study area is located in the municipalities of Hämeenlinna (Lammi), Padasjoki and Asikkala in southern Finland (61°15´N, 25°00´E; Fig. 1). Its total area is 470 km^2, 80% of which consist of forests. 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 agricultural-forest mosaic to northern forest-dominated areas.

Bird data and census methods

All data on breeding birds in this study were collected by the author TP and include a combined set of data from a total field effort of approximately 16 000 hours in 1983–2005, when the study area was covered by breeding-bird censuses. Censuses were conducted using a modified territory and species mapping method usually consisting of 4–5 visits made between late April and late June. Using this highly standardized and efficient method, we gained accurate and comparable measures of total species richness of forest birds within study sites (*see* Pakkala *et al*. 2006 for a detailed description of the bird data and census methods).

Study design

The occurrence of 81 forest bird species (Appendix) was studied by census mapping at 180 study sites (*see* below) situated on the corners of 1 × 1 km^2 grid units of the Finnish national coordinate system with zone 27, called KKJ 3 here, within the study area (Fig. 1). Presences or absences were determined within 10 different radii (100, 200, 300, 400, 500, 600, 700, 800, 900 and 1000 m) from the corners of the 1 × 1 km^2 grid, and the determination of presences was based on the locations of territory centres or nest sites of each species. Study sites were selected from the total data set (*see* Pakkala *et al*. 2006) to (1) contain complete species information at all study scales (*see* above), (2) include dominantly forested landscapes so that the proportion of the area of forest land at each of these study scales was at least 50% per site, (3) cover two successive years of each study site, and without any major changes in the forest environment of the surroundings of these sites that could affect numbers and territory locations of the studied bird species.

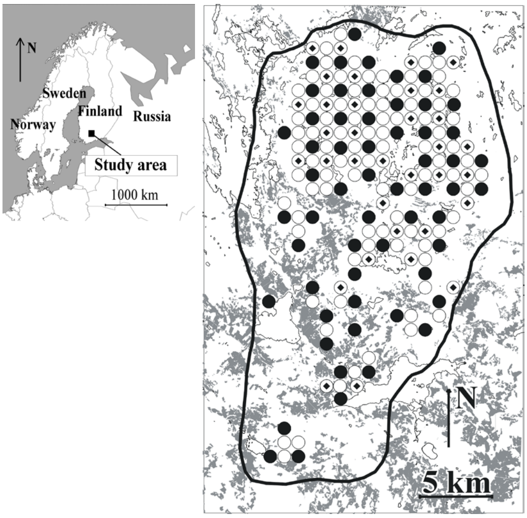

Fig. 1. Location of the Lammi study area (delineated) with positions of all 180 study sites shown with different symbols as follows: ● = 59 sites located at least 2 km from each other (used in analyses of all scales), ⦿ = 34 sites located at least 1.5 km from each other and from previously mentioned sites (used in analyses of 100–700 m scales), and ○ = 87 sites located at least 1 km from each other and from previously mentioned sites (used in analyses of 100–500 m scales). Lakes are delimited by thin black lines and agricultural areas by grey shading. Other areas consist mostly of forests.

During the study period, intensive forest management (including clear-cutting) was the main cause for forest changes. A threshold value of 10% of the total land area of clear-cuts between two successive study years was used to select the above-mentioned sites for this study (forest environment data are explained in the next section). Within a single study site, these two successive study years were the same for all study scales. To avoid overlap and decrease dependencies (statistical or ecological) at larger scales, 93 study sites located at least 1.4 km apart were selected from the previously mentioned 180 study sites, and were used in analyses of the 600 and 700 m radii. Respectively, 59 study sites located at least 2 km apart were used in analyses of the 800–1000 m radii (Fig. 1).

Forest and landscape data

We quantified habitat and landscape types for

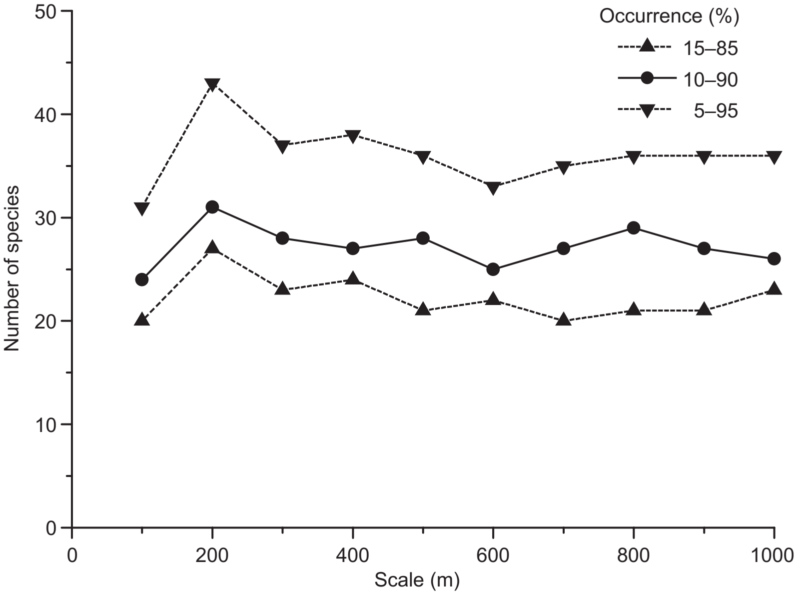

Fig. 2. Numbers of potential indicator species at different ranges of occurrence at various spatial scales. A range of 10%–90% was chosen to be most suitable in this study (*see* text for details).

the 180 study plots. Quantification was based on numerical thematic maps produced by the Finnish multi-source national forest inventory (Tomppo *et al*. 1998, 2008, 2009, 2012), 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 from the study area. The following land classes and their areas were computed within all radii (100–1000 m): water, agricultural land, open mires, young forests (< 20 years old, including clear-cuts) and middle-aged and old forests (> 20 years old; including forests both on mineral and peat soil). Changes in land use and forestry during the study period were also estimated from these data. The land-use and forestry data were selected to match the bird census years of the particular study plots.

Model selection and indicator species ranking

Our goal was to identify those forest bird species whose occurrence best explains total variation in species richness of all the remaining forest bird species. All species occurring at 10% to 90% of the study sites were regarded as potential indicator species at a given scale. At each scale (= radius of the circular study sites) and for all species, the proportion of occurrence of all study sites, p_{occ} were divided into four different classes: common: $p_{occ} > 0.9$; potential indicator: $0.1 \leq p_{occ} \leq 0.9$; rare: $0 < p_{occ} < 0.1$; missing: $p_{occ} = 0$ (Appendix). Occurrences were defined by the presence–absence information of the pooled data of two successive study years (*see* section ‘Study design’ above). We compared three different occurrence limits a priori (5%–95%, 10%–90%, 15%–85%; Fig. 2), with the selected 10% to 90% guaranteeing adequate numbers of both potential indicator species at all scales (Fig. 2) and in different classes of regression models used in the model selection procedure (Appendix, *see* below).

At each of the ten spatial scales, we evaluated all possible combinations of models with observed presences of 1–5 potential indicator species as explanatory variables in ordinary multiple regression models. The response variable was observed species richness, excluding the species occurring as predictors in that particular model. The response was normalized to zero mean and unit variance to make the residual variance directly proportional to the amount of explained variance, and hence the models comparable. All possible models were then ranked by their parsimony, measured as the Bayesian information criterion (BIC, also known as the Schwarz criterion; Schwarz 1978; cf. Mac Nally 2000, Mac Nally & Fleishman 2002). BIC is calculated as BIC = $-2\ln L(\theta_p|y) + P\ln N$; where N is sample size; P is the number of independently estimated parameters; $L(\theta_p|y)$ is the maximized value of the Likelihood for the estimated model given the data y. For a model with homoscedastic normally distributed residuals, the expression $\ln L(\theta_p|y)$ can be calculated as $-0.5 \times N \times \ln(\mathrm{RSS}/N)$, where RSS is the residual sum of squares (Schwarz 1978, Johnson & Omland 2004).

Model ranking was based on the differences (Δ_i) in BIC values compared to the best model — the one which has the lowest BIC — calculated for model i as $\Delta_i = \mathrm{BIC}_i - \mathrm{BIC}_{\min}$. By this method we ranked the 20 best models for all scales and numbers of indicator species used as explanatory variables. Of these 20 models, relative weights of evidence for each model, W_i; $i = 1,\ldots, 20$, can be calculated as $W_i = \exp\left(-\Delta t/2\right)/\sum_{j=1}^{20}\exp\left(-\Delta_j/2\right)$. These weights, analogous to Akaike weights (Akaike 1978, Johnson & Omland 2004) can be interpreted as an approximate probability that model i is the most parsimonious one for explaining the observed data, given the candidate set of 20 models. We calculated species-specific scores (Table 1) for each indicator bird species present in any of the twenty best models. These scores, the relative importance of each indicator species,

Table 1. Indicator species that were selected to models explaining most of the total variation in species richness of forest birds. Species ranking was based on scores that represent the relative support of the species in question being present in the best model. The scores were calculated as summed BIC-weights for those top 20 models (from all possible subsets; ranked according to BIC) that included the species as a predictor. At each scale, the five best indicator species with their scores in models with 1, 2, 3, 4 or 5 indicator species are shown. If there were even scores, the species were then ranked by their order of appearance in the best 20 models. Values of BIC and the coefficient of determination r^2 are shown for the five best single species at each scale. sp = species.

Scale	Species	BIC 1 sp	r^2 1 sp	Score				
				1 sp	2 sp	3 sp	4 sp	5 sp
100 m	Blackbird *Turdus merula*	–27.9	0.210	0.611				
	Pied flycatcher *Ficedula hypoleuca*	–26.7	0.205	0.337	0.188			
	Spotted flycatcher *Muscicapa striata*	–22.2	0.185	0.035	0.166	1	0.999	0.997
	Siskin *Carduelis spinus*	–19.5	0.173	0.009	0.740	1	0.982	0.934
	Wood warbler *Phylloscopus sibilatrix*	–18.6	0.168	0.006			0.512	
	Redwing *Turdus iliacus*				0.554	0.997	0.997	0.930
	Songthrush *Turdus philomelos*				0.131			
	Garden warbler *Sylvia borin*					0.002		
	Blue tit *Parus caeruleus*					0.001	0.380	0.567
	Treecreeper *Certhia familiaris*							0.683
200 m	Blackbird *Turdus merula*	–51.5	0.307	0.492	0.817	0.382		
	Pied flycatcher *Ficedula hypoleuca*	–51.0	0.305	0.385	0.997	0.988	0.716	0.902
	Treecreeper *Certhia familiaris*	–48.4	0.295	0.108	0.051	0.558		
	Hazel grouse *Bonasa bonasia*	–44.5	0.280	0.015	0.124		0.314	0.583
	Willow tit *Parus montanus*	–34.5	0.239	0				
	Wood warbler *Phylloscopus sibilatrix*				0.005	0.342		
	Blue tit *Parus caeruleus*					0.250	0.901	0.910
	Common crossbill *Loxia curvirostra*						0.600	0.957
	Greenish warbler *Phylloscopus trochiloides*						0.469	0.837
300 m	Woodpigeon *Columba palumbus*	–18.3	0.167	0.265	0.996	0.984	0.979	0.923
	Pygmy owl *Glaucidium passerinum*	–18.1	0.166	0.239		0.590		
	Coal tit *Parus ater*	–16.8	0.160	0.125				0.573
	Red-breasted flycatcher *Ficedula parva*	–16.8	0.160	0.120	0.003	0.381	0.973	0.971
	Brambling *Fringilla montifringilla*	–16.7	0.160	0.119	0.991	0.968	0.976	0.633
	Blue tit *Parus caeruleus*				0.004	0.016		
	Greenish warbler *Phylloscopus trochiloides*				0.003		0.022	
	Redstart *Phoenicurus phoenicurus*						0.977	0.923

continued

Table 1. Continued.

Scale	Species	BIC 1 sp	r^2 1 sp	Score				
				1 sp	2 sp	3 sp	4 sp	5 sp
400 m	Three-toed woodpecker *Picoides tridactylus*	–34.8	0.240	0.441	0.001			
	Green sandpiper *Tringa ochropus*	–34.4	0.238	0.360	1	1	1	1
	Red-breasted flycatcher *Ficedula parva*	–32.7	0.231	0.149	0.962	0.817	0.996	0.997
	Pygmy owl *Glaucidium passerinum*	–30.5	0.221	0.05	0.037	0.181	0.004	
	Tengmalm's owl *Aegolius funereus*	–19.5	0.172	0				
	Coal tit *Parus ater*				0	0.948	0.999	0.962
	Swift *Apus apus*					0.047	0.999	1
	Fieldfare *Turdus pilaris*							0.522
500 m	Red-breasted flycatcher *Ficedula parva*	–52.0	0.309	1	1	1	1	1
	Three-toed woodpecker *Picoides tridactylus*	–33.7	0.235	0				
	Pygmy owl *Glaucidium passerinum*	–22.8	0.188	0				
	Green sandpiper *Tringa ochropus*	–21.3	0.181	0	0.994	0.971	0.916	0.668
	Brambling *Fringilla montifringilla*	–16.3	0.158	0				
	Black grouse *Tetrao tetrix*				0.004	0.038		
	Rustic bunting *Emberiza rustica*				0.001			
	Swift *Apus apus*				0	0.884	0.916	0.854
	Wryneck *Jynx torquilla*					0.007		
	Hooded crow *Corvus corone*						0.751	0.551
	Blackcap *Sylvia atricapilla*						0.217	0.736
600 m	Red-breasted flycatcher *Ficedula parva*	–17.5	0.277	0.737	0.834			
	Three-toed woodpecker *Picoides tridactylus*	–15.0	0.256	0.204	0.067	0.534	0.840	0.985
	Pygmy owl *Glaucidium passerinum*	–12.3	0.235	0.055				
	Tengmalm's owl *Aegolius funereus*	–6.4	0.185	0.003				
	Swift *Apus apus*	–3.0	0.154	0.001	0.125	0.510	0.164	
	Brambling *Fringilla montifringilla*				0.779	0.485	0.963	0.998
	Blackcap *Sylvia atricapilla*				0.063	0.502		
	Fieldfare *Turdus pilaris*					0.481	0.941	0.976
	Wryneck *Jynx torquilla*						0.805	0.981
	Lesser spotted woodpecker *Dendrocopos minor*							0.763
700 m	Red-breasted flycatcher *Ficedula parva*	–6.8	0.188	0.546	0.979	0.993	0.988	0.987
	Pygmy owl *Glaucidium passerinum*	–6.4	0.185	0.440				0.603
	Tengmalm's owl *Aegolius funereus*	3.5	0.093	0.003				
	Three-toed woodpecker *Picoides tridactylus*	4.1	0.087	0.002				
	Grey-headed woodpecker *Picus canus*	4.3	0.086	0.002				
	Rustic bunting *Emberiza rustica*				0.832	0.243		
	Black grouse *Tetrao tetrix*				0.077	0.754	0.735	0.738
	Parrot crossbill *Loxia pytyopsittacus*				0.034			
	Swift *Apus apus*				0.033			
	Two-barred crossbill *Loxia leucoptera*					0.759	0.826	0.778
	Sparrowhawk *Accipiter nisus*					0.162	0.342	0.375
	Ural owl *Strix uralensis*						0.289	
800 m	Black grouse *Tetrao tetrix*	–7.3	0.270	0.954	0.991	1	1	1
	Rustic bunting *Emberiza rustica*	1.5	0.152	0.012				
	Wryneck *Jynx torquilla*	2.3	0.140	0.008				
	Capercaillie *Tetrao urogallus*	3.4	0.125	0.005				
	Parrot crossbill *Loxia pytyopsittacus*	3.6	0.121	0.004			0.510	0.916
	Red-breasted flycatcher *Ficedula parva*				0.726	0.160		
	Pygmy owl *Glaucidium passerinum*				0.186	0.055		
	Three-toed woodpecker *Picoides tridactylus*				0.033	0.786	0.952	0.951
	Golden oriole *Oriolus oriolus*				0.014	0.825	0.961	0.951
	Two-barred crossbill *Loxia leucoptera*						0.068	
	Hooded crow *Corvus corone*							0.383

continued

Table 1. Continued.

Scale	Species	BIC 1 sp	r^2 1 sp	Score				
				1 sp	2 sp	3 sp	4 sp	5 sp
900 m	Red-breasted flycatcher *Ficedula parva*	2.4	0.140	0.360	0.928	0.801	0.846	0.976
	Capercaillie *Tetrao urogallus*	5.4	0.095	0.081				
	Brambling *Fringilla montifringilla*	5.5	0.092	0.074	0.141			0.601
	Three-toed woodpecker *Picoides tridactylus*	5.6	0.091	0.072				
	Buzzard *Buteo buteo*	5.7	0.089	0.068			0.334	0.916
	Parrot crossbill *Loxia pytyopsittacus*				0.423	0.586	0.368	
	Rustic bunting *Emberiza rustica*				0.107			
	Swift *Apus apus*				0.074			
	Golden oriole *Oriolus oriolus*					0.255		
	Long-eared owl *Asio otus*					0.024		
	Fieldfare *Turdus pilaris*						0.560	0.601
	Goshawk *Accipiter gentilis*						0.486	0.947
1000 m	Two-barred crossbill *Loxia leucoptera*	1.0	0.159	0.221	0.251			
	Buzzard *Buteo buteo*	1.7	0.149	0.156				
	Goshawk *Accipiter gentilis*	2.5	0.137	0.104				
	Brambling *Fringilla montifringilla*	2.7	0.135	0.095	0.190	0.267	0.533	0.702
	Swift *Apus apus*	3.2	0.128	0.075	0.290	0.477	0.619	0.714
	Red-breasted flycatcher *Ficedula parva*				0.316	0.435	0.242	
	Lesser spotted woodpecker *Dendrocopos minor*				0.276	0.477	0.637	0.718
	Honey buzzard *Pernis apivorus*					0.308	0.535	0.715
	Nutcracker *Nucifraga caryocatactes*							0.370

were calculated as the sum of the above-mentioned weights over all of the 20 models in which the species in question appeared (Burnham & Anderson 2002, Johnson & Omland 2004). We then ranked all indicator species present in the 20 best models (as predictor variables) by their scores in each category of 1–5 indicator species, and selected the five best indicator species in each category and at each scale (Table 1) for closer investigation.

All statistical analyses were performed with MATLAB (MathWorks Inc., Natick, MA).

Interspecific interactions as a mechanism for indicator property

Although the best indicator species may explain a relatively large part of the variation in species richness, other environmental factors than the presence of the indicator species itself (e.g. habitat quality) are likely to be of high importance. To study the role of the indicator species presence, i.e. possible effects of interspecific interactions, we selected the five best indicator species (among the models of one indicator species) at all spatial scales and compared the differences in changes of species richness between two successive study years. We restricted the comparisons to sites where the indicator species was present at least during one study year and made comparisons using three different conditions: (1) the indicator species is present in the first period but absent in the second; (2) the indicator species is present in both periods; and (3) the indicator species is absent in the first period but present in the second. If the indicator species as such (by species' interactions) is important, changes in total species richness between the previously mentioned three classes should differ: in class 1 we should, in general, expect a decrease and in class 3, respectively, an increase in species richness. Class 2 acts as a control group without change in the effect of the indicator species. These different situations were thought of as random treatments and the differences in response, i.e. change in species richness, were studied by one-way analysis of variance (separately for all scales). The

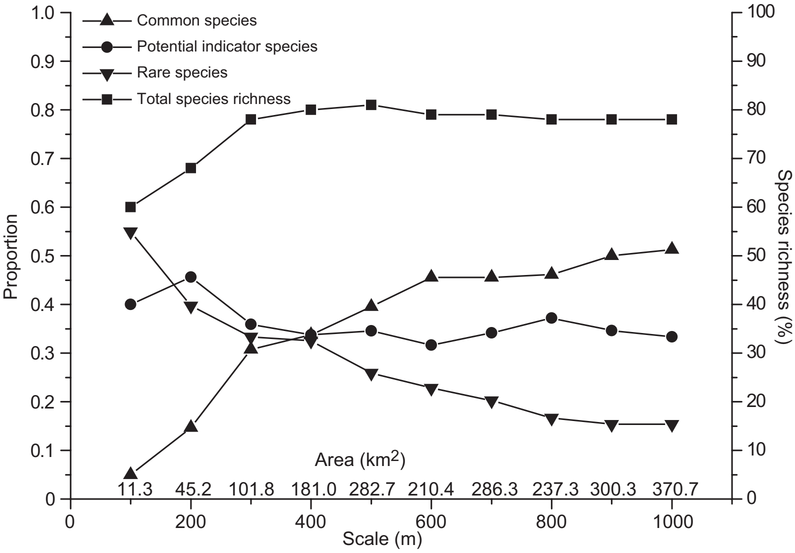

Fig. 3. Proportions of potential indicator ($0.1 \leq p_{occ} \leq 0.9$), rare ($0 < p_{occ} < 0.1$) and common ($p_{occ} > 0.9$) forest bird species of all forest bird species at various spatial scales and total species richness of all study sites at respective scales. Data of two successive years of each study site were pooled. The total area studied at each scale is also shown. Note that the number of study sites varies with scale (cf. Appendix) and because of pooling the data, areas of two study years are summed together. At scales from 300 m upwards, total species richness and the proportion of potential indicator species remains relatively stable. There is, however, a turnover of species composition within the class of potential indicator species with increasing scale, as the proportion of common species increases and that of rare species decreases, respectively.

null hypothesis — equal average change in species richness for all treatments — implies that possible indicator properties are because of habitat characteristics alone. Imperfect detection of species presence will weaken the power of this test (increase the risk of type II errors).

Results

Numbers of potential indicator species at various spatial scales

The total number of potential indicator species was rather constant and ranged between 24 and 31 at various scales (Fig. 3). At scales from 300 m upwards, total species richness and the proportion of potential indicator species remained relatively stable (Fig. 4). 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 (Fig. 4). With increasing scale and reasonably large areas covered, the proportions of common, indicator, and rare species tend to reach, in general, proportions 50%, 35%, and 15% of the total species number, respectively (Fig. 4).

The best set of indicator species

We found several suitable indicator species that depended both on the spatial scale and on the number of indicator species in the respective model (Table 1 and Appendix). By selecting the five best indicator species of the 20 best models in each model category of 1–5 indicator species, the total number of selected indicator species varied between 8 and 12 between different spatial scales (Table 1). It is not, however, straightforward to rank these forest bird species by their overall indicator value. Based on the scores, i.e. the relative importance of selected indicator species, it can be observed that most models at various scales contain typically only 2–3 “important” species (Table 1). Also, in models with

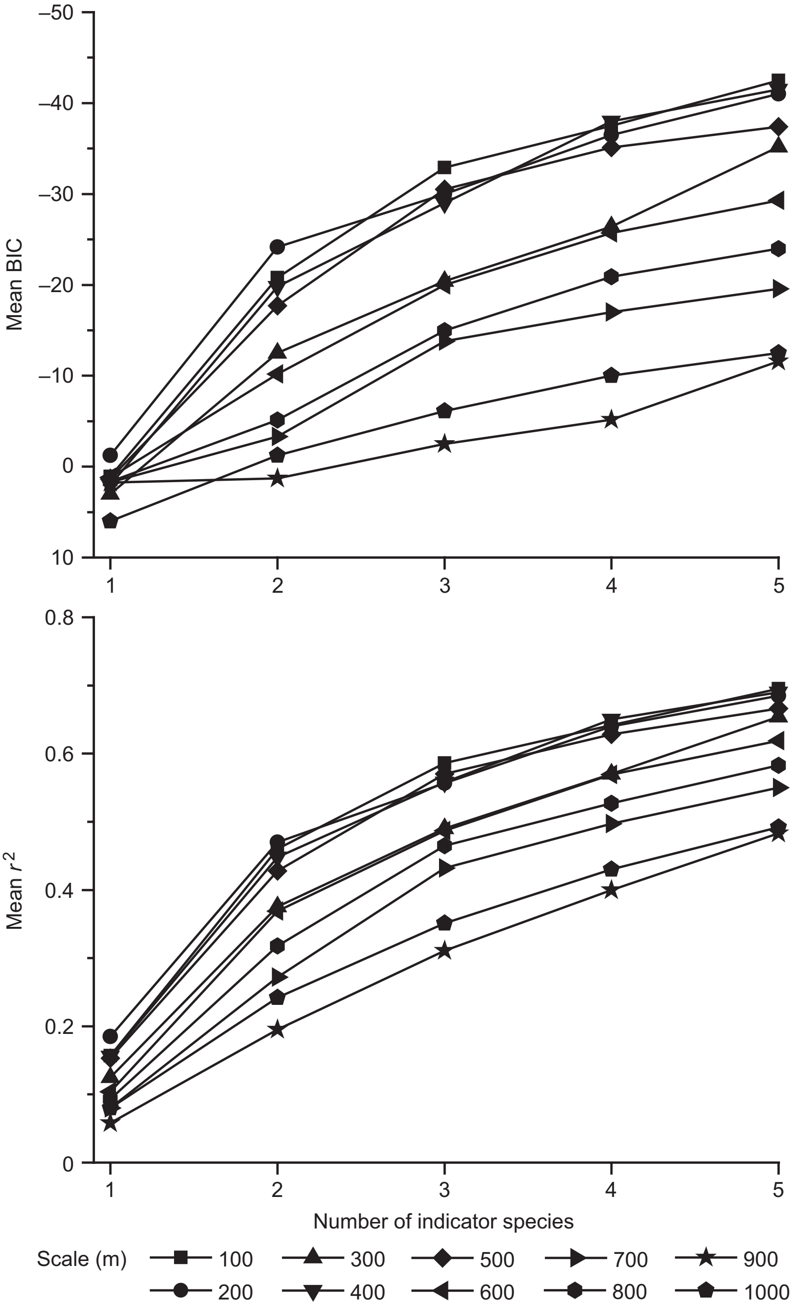

Fig. 4. Mean Bayesian Information Criterion (BIC; upper panel) and mean coefficients of determination (r^2; lower panel) of the 20 best models that were searched to explain total variation in species richness of forest birds (cf. Table 1). Pooled data of two successive study years and the same 59 study sites (cf. Fig. 1) at all scales were used. Both BIC and r^2 depended highly significantly on scale and on the number of indicator species in the model. In general, models at smaller scales and with several indicator species better explained total variation in species richness. However, species richness is lower at smaller scales, and the potential indicator species change with increasing scale (cf. Appendix), which affects the results. Note that the direction of vertical axes in the upper panel ("Mean BIC") is reverse to ensure better comparability between the two panels.

several species it may be difficult for a single species, even a potential indicator, to enter the model if another species with a very similar spatial occupancy pattern has already been selected to the same model. However, there were some species that were selected to several of the best-indicator models and these species were also among the best single-indicator species at various scales. We can, thus, consider these species strong candidates for broad-scale key indicators of forest bird species richness.

The most important species included the red-breasted flycatcher, which was selected as an indicator species at all scales between 300 and 1000 m and among the five best single species (top-5) at six of these scales, the pygmy owl (indicator species at scales 300–800 m; top-5 at five scales) and the three-toed woodpecker (indicator species at scales 400–900 m; top-5 at five scales). In addition to these top candidates, there were other noteworthy species, namely the brambling (*Fringilla montifringilla*) (indicator species at five of the scales of 200–1000 m; top-5 at four scales), the swift (*Apus apus*) (indicator species at six of the scales of 400–1000 m; top-5 at two scales) and Tengmalm's owl (indicator species at scales 400, 600 and 700 m; top-5 at all of these scales).

Besides the above-mentioned indicator species, there were noticeable single indicator species at smaller scales (100–300 m), including the hazel grouse, the woodpigeon *Columba palumbus*, the blackbird *Turdus merula*, the wood warbler *Phylloscopus sibilatrix*, the spotted flycatcher *Muscicapa striata*, the pied flycatcher *Ficedula hypoleuca*, the coal tit *Parus ater*, the treecreeper *Certhia familiaris* and the siskin *Carduelis spinus*. The blue tit *Parus caeruleus* was also selected to indicator models at all scales where it was a candidate species (100–300 m). At the mid-scales (400–600 m), the green sandpiper *Tringa ochropus* was an important single indicator species (at 400 and 500 m), and at large scales (700–1000 m) the goshawk, the buzzard *Buteo buteo*, the black grouse, the capercaillie, the wryneck *Jynx torquilla*, the grey-headed woodpecker *Picus canus*, the parrot crossbill *Loxia pytyopsittacus*, the two-barred crossbill *Loxia leucoptera* and the rustic bunting *Emberiza rustica* were selected among the five best single species indicator models (*see* Appendix).

There were also some species that were not selected to the five best single-species indicator models at any scale, but were important in respective models with several species. These species include the redwing *Turdus iliacus* (at 100 m), the redstart *Phoenicurus phoenicurus* (at 300 m), the hooded crow *Corvus corone* (at 500 m), the fieldfare *Turdus pilaris* (at 600 and 900 m), the golden oriole *Oriolus oriolus* (at 800 m), the lesser spotted woodpecker (at 1000 m) and the honey buzzard *Pernis apivorus* (at 1000 m).

Because the occurrence of potential indicator species was restricted between 10% and 90%, rare species such as some hawks and owls, the white-backed woodpecker, the Siberian jay *Perisoreus infaustus* or the red-flanked bluetail *Tarsiger cyanurus* did not have the possibility to be potential indicator species in this study. Likewise, some relatively common species were potential indicator species only at a restricted number of scales (*see* Appendix).

Variation in species richness: interspecific interactions and the indicator property

When we compared mean changes in species richness between groups with variations in the presence of an indicator species (five best indicator species candidates at all scales were selected; *see* above and Table 1), we found only 8 of 43 statistically significant differences between treatments ($p < 0.05$; Table 2). After adjusting for multiple comparisons using the Bonferroni correction ($\alpha = 0.05/43 = 0.0012$), there were four significant differences. A more detailed analysis of the eight significant cases showed that the observed significant differences between the above-mentioned three classes did not form a homogenous pattern. There were two obviously negative impacts of small owls (pygmy owl: 300 m scale and Tengmalm's owl: 400 m) and six positive impacts of passerine birds (red-breasted flycatcher: 600 m; brambling: 500, 900 and 1000 m; parrot crossbill: 800 m). In addition, the woodpigeon had a positive impact on species richness at the 300 m scale. However, of the four significant cases related to Bonferroni-adjusted p value, three concerned positive effects of the brambling on species richness, and one negative effect of the pygmy owl.

Capturing variation in species richness: effects of scale and the number of indicator species

We calculated mean BIC and coefficients of determination (r^2) for the 20 models that, in relation to their complexity, best explained the total variation in species richness of forest birds. To exclude the effects of sample size, the same 59 study sites (Fig. 1) at all scales were used and

Table 2. Tests for explicit effects of the best single indicator species' presence (species are listed in Table 1). Differences in changes of species richness between two successive study years were compared using three different conditions: (1) the indicator species is present in the first period but absent in the second ("10"); (2) the indicator species is present in both periods ("11"); and (3) the indicator species is absent in the first period but present in the second ("01"). If the indicator species is having a positive effect there should be a decrease in species richness in condition 1, and an increase in condition 3 compared with condition 2 that acts as a control group. The opposite pattern should be found in the case of a negative effect. Differences between changes in species richness (in one year) were studied by one-way AOV at all scales. N_{10}, N_{11} and N_{01} show the sample sizes in each of the three classes. Of the 43 cases with adequate sample sizes tested, only eight were statistically significant ($p < 0.05$) and compared with the respective adjusted p value after the Bonferroni correction, $p = 0.0012$ ($\alpha = 0.05$; the number of multiple comparisons = 43) there were only four significant differences, which indicates that forest sites are often more important in explaining species richness than species interactions. The direction (impact: positive or negative) of the eight above-mentioned significant differences is also shown.

Species	N_{10}, N_{11}, N_{01}	F	p	Impact
Scale 100 m, N = 180				
Blackbird *Turdus merula*	15, 10, 13	0.214	0.808	
Pied flycatcher *Ficedula hypoleuca*	6, 12, 8	1.453	0.255	
Spotted flycatcher *Muscicapa striata*	22, 18, 21	0.228	0.797	
Siskin *Carduelis spinus*	27, 67, 20	1.443	0.241	
Wood warbler *Phylloscopus sibilatrix*	14, 9, 11	1.604	0.217	
Scale 200 m, N = 180				
Blackbird *Turdus merula*	14, 79, 16	0.286	0.752	
Pied flycatcher *Ficedula hypoleuca*	25, 49, 23	1.012	0.367	
Treecreeper *Certhia familiaris*	8, 80, 10	1.561	0.215	
Hazel grouse *Bonasa bonasia*	13, 91, 13	0.545	0.581	
Willow tit *Parus montanus*	12, 127, 14	1.053	0.352	
Scale 300 m, N = 180				
Woodpigeon *Columba palumbus*	21, 101, 25	3.849	0.024	positive
Pygmy owl *Glaucidium passerinum*	4, 15, 6	11.488	< 0.001	negative
Coal tit *Parus ater*	38, 34, 33	1.858	0.161	
Red-breasted flycatcher *Ficedula parva*	9, 10, 10	0.318	0.731	
Brambling *Fringilla montifringilla*	29, 3, 23	0.728	0.488	
Scale 400 m, N = 180				
Three-toed woodpecker *Picoides tridactylus*	10, 19, 9	0.033	0.968	
Green sandpiper *Tringa ochropus*	20, 71, 21	0.194	0.824	
Red-breasted flycatcher *Ficedula parva*	16, 15, 14	2.004	0.148	
Pygmy owl *Glaucidium passerinum*	5, 29, 4	2.502	0.097	
Tengmalm's owl *Aegolius funereus*	17, 4, 21	4.135	0.024	negative
Scale 500 m, N = 180				
Red-breasted flycatcher *Ficedula parva*	29, 23, 27	0.962	0.387	
Three-toed woodpecker *Picoides tridactylus*	12, 29, 11	1.462	0.242	
Pygmy owl *Glaucidium passerinum*	5, 41, 6	1.263	0.292	
Green sandpiper *Tringa ochropus*	20, 109, 22	0.944	0.392	
Brambling *Fringilla montifringilla*	47, 14, 43	9.018	< 0.001	positive
Scale 600 m, N = 93				
Red-breasted flycatcher *Ficedula parva*	14, 22, 17	4.725	0.013	positive
Three-toed woodpecker *Picoides tridactylus*	3, 21, 8	0.005	0.995	
Pygmy owl *Glaucidium passerinum*	1, 25, 2	not tested	–	
Tengmalm's owl *Aegolius funereus*	16, 4, 12	0.307	0.738	
Swift *Apus apus*	0, 51, 0	not tested	–	
Scale 700 m, N = 93				
Red-breasted flycatcher *Ficedula parva*	17, 35, 18	0.194	0.824	
Pygmy owl *Glaucidium passerinum*	3, 31, 5	0.564	0.574	
Tengmalm's owl *Aegolius funereus*	23, 5, 16	0.225	0.800	
Three-toed woodpecker *Picoides tridactylus*	5, 28, 7	2.447	0.101	
Grey-headed woodpecker *Picus canus*	4, 21, 6	0.152	0.860	

continued

Table 2. Continued.

Scale 800 m, *N* = 59				
Black grouse *Tetrao tetrix*	0, 52, 0	not tested	–	
Rustic bunting *Emberiza rustica*	3, 44, 2	0.714	0.495	
Wryneck *Jynx torquilla*	15, 27, 11	1.055	0.356	
Capercaillie *Tetrao urogallus*	0, 23, 0	not tested	–	
Parrot crossbill *Loxia pytyopsittacus*	12, 9, 11	5.542	0.009	positive
Scale 900 m, *N* = 59				
Red-breasted flycatcher *Ficedula parva*	9, 34, 8	0.860	0.430	
Capercaillie *Tetrao urogallus*	0, 26, 0	not tested	–	
Brambling *Fringilla montifringilla*	17, 17, 18	24.287	< 0.001	positive
Three-toed woodpecker *Picoides tridactylus*	2, 21, 4	0.976	0.391	
Buzzard *Buteo buteo*	3, 6, 2	1.691	0.244	
Scale 1000 m, *N* = 59				
Two-barred crossbill *Loxia leucoptera*	3, 9, 2	0.347	0.714	
Buzzard *Buteo buteo*	4, 6, 4	1.018	0.393	
Goshawk *Accipiter gentilis*	2, 8, 0	not tested	–	
Brambling *Fringilla montifringilla*	18, 19, 16	16.997	< 0.001	positive
Swift *Apus apus*	0, 44, 0	not tested	–	

the response was normalized. Both BIC and r^2 depended highly significantly on scale (two-way AOV; BIC: $F_{9,36} = 25.0$, $p < 0.001$; r^2: $F_{9,36} = 39.7$, $p < 0.001$) and on the number of indicator species in the model (two-way AOV; BIC: $F_{4,36} = 106.4$, $p < 0.001$; r^2: $F_{4,36} = 489.6$, $p < 0.001$). In general, models at a smaller scale and several indicator species better explained total variation in species richness than models at larger scales with one or two indicator species (Fig. 4). As measured by r^2, 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 variation in species richness reasonably well, on average 48%. The scales of 100, 200, 400 and 500 m had the highest coefficients of determination. However, species richness was lower at smaller scales and the potential indicator species changed with increasing scale (Table 1 and Appendix), which affected the results and makes direct comparisons more complicated.

Discussion

Key indicators of forest bird species richness

In this study, top indicator species candidates were the red-breasted flycatcher, the pygmy owl, and the three-toed woodpecker. These species are all hole-nesters and prefer structurally complex mature or old-growth forest environments (von Haartman *et al*. 1963–1972, Dementev & Gladkov 1966, 1968, Glutz von Blotzheim & Bauer 1980, 1993, Mikkola 1983, Väisänen *et al*. 1998, Winkler & Christie 2002, Taylor 2006). Earlier studies within the same study area also stress the similarities in spatial patterning and habitat use of these three species: the densities of all three species were observed to be significantly higher at capercaillie lek sites and their surroundings compared to non-lek control areas (Pakkala *et al*. 2003). Densities of three-toed woodpeckers and pygmy owls were significantly higher also at goshawk nesting areas compared to non-goshawk control areas (Pakkala *et al*. 2006). The territory distribution of the three-toed woodpecker within the total study area was found to be uneven and aggregated in large mature forest areas with highest densities in old-growth forest patches (Pakkala *et al*. 2002), mainly similar to the respective patterns of the pygmy owl and red-breasted flycatcher (T. Pakkala unpubl. data).

The three-toed woodpecker is considered an important indicator species of forest landscapes (e.g. Angelstam 1992, Imbeau 2001, Bütler *et al*. 2004, Roberge *et al*. 2008a). The pygmy owl is intimately associated with three-toed woodpeckers in forest environments (e.g. Pakkala *et al*. 2006), and as seen above, all of the six top indicator candidate species mentioned above show aggregated distribution patterns and also have their highest densities approximately in the same parts of our study area that indicates also the potential "true" indicator value of all these species.

The second best set of three broad-scale indicator species includes the brambling, the swift, and Tengmalm's owl. Tengmalm's owl and the swift are both hole-nesters, Tengmalm's owl prefers structurally complex mature forests (e.g. Mikkola 1983, Korpimäki 1988), whereas the Finnish forest population of the swift usually breeds in large and old trees near borders of mature forests or in clear-cut areas (von Haartman *et al*. 1963–1972, Väisänen *et al*. 1998).

Overall, quite a few species were selected in the best indicator species models, with some turnover at changing spatial scales. However, as several technical aspects affect the selection procedure simultaneously in a complicated manner, we prefer to interpret the results as an overall view and introduce the most suitable indicator species candidates rather than strictly rank these species by their indicator property. It is noteworthy that with increasing spatial scales from 100–300 m radius, approximately the ecological scale of the territory size of many forest passerines, to larger scales (800–1000 m radius) corresponding to the territories or areas of larger species e.g. hawks, owls and large forest grouse, there is simultaneously a smooth shift from the smaller forest stand scale to the local landscape scale with a mosaic of forest patches. We could reason that apart from being indicators of total variation of species richness, the selected indicator species reflect the species-specific ecological scales of the forest environment. These scales are respectively connected to small-scale elements like possible structural complexity of nest-sites, habitat structure of the territory, or large-scale properties of the forest landscape, e.g. the amount of mature forest area. The observed spatial patterns of the above-mentioned indicator species are in turn closely connected to the biotope and landscape structure of the study area, but these relations are not analysed in this study. In practical situations, e.g. when assessing forest bird diversity and its development using indicator species, habitat structure and information about the ecological scales of patterns and dynamics of forest landscapes in question are of importance.

Scale-dependency of the indicator property

Although variation in the total number of potential indicator species is relatively restricted at various study scales, and their proportion, as well as total species richness tends to stabilize with increasing scale, there is considerable turnover of indicator species candidates at different spatial scales. This scale-dependent variation in the composition of possible indicator candidate species is a combined effect of the definition and selection procedure of suitable indicator species, sample size, and the scale itself (connected to the structure of the forest environment of the study area), which in turn affects the probabilities of the species to be selected as an indicator.

The definition of the occurrence levels of the potential indicator species, in combination with our study design of multiple spatial scales, leads to a situation where the number of potential indicator species peaks at intermediate scales. At small spatial scales with smaller total areas covered, some potentially relevant species may be missing or are too rare to be selected as indicator candidates; and correspondingly, at larger spatial scales, many candidate species occupy most or all study sites and are therefore not considered as potential indicators in this study. There are, however, complementary approaches by which rare or common species could be considered as indicator species.

Rare species are, in general, problematic because standard systematic, random, or even stratified random sampling methods can be highly inefficient whereas nonrandom methods can lead to statistical problems (e.g. Gaston 1994, Thompson & Seber 1996, Thompson 2004, Guisan *et al*. 2006). Rare species can, however, be interesting potential indicator species, and various more efficient sampling techniques including e.g. adaptive cluster sampling, spatial predictions based on niche-based distribution models or subjective sampling based on information about the species and study areas can be applied (e.g. Ståhl *et al*. 2000, Ferrier 2002, Thompson 2004, Guisan *et al*. 2006, Hedgren & Weslien 2008). Within our study area with explicit information about the locations of territories or nest sites of forest bird species, we could e.g. focus also on these respective sites of the rare species, apply our screening procedure, and then estimate the potential indicator species.

Indicators in forest environments: site or species?

Overall variation in bird species richness in forest environments is a function of temporal trends, annual fluctuations and spatial variation in population densities of individual species. These patterns are affected by a large range of different factors, such as habitat use, site-tenacity and species interactions (cf. Wiens 1989, Haila & Järvinen 1990, Haila *et al*. 1996). A good indicator species by definition "explains" or "predicts" well the observed variation in species richness, but is this explanatory power connected to the presence of the indicator species *per se* or some other factors related to the biotic or abiotic environment? We assumed that habitat changes between the two successive study years are minor, as only pairs of observations without major anthropogenic alteration of the habitat (forestry) were included in our analyses. There are still, however, mechanisms through which total species richness can be changed between years without a noticeable change in the structure of the forest environment of the study site, e.g.: (1) simultaneous population dynamics of several breeding bird species caused by external effects, e.g. food availability or weather conditions, (2) changes in the forest landscape at broader spatial scales around the study area that reflect the occupancy of several species within the study area, (3) positive and negative interspecific effects that affect several breeding bird species.

Of the previously mentioned mechanisms, we consider 1 and 2 as generally plausible, but in practice probably causing minor effects on variation in total species richness between two successive years, because the study period covers a long, 23-year time interval with study sites censused asynchronously in space and time. Explanation 3 mainly concerns predation, competition or heterospecific attraction that can modify annual species composition and territory locations of local forest bird assemblages (e.g. Wiens 1989, Hakkarainen & Korpimäki 1996, Forsman *et al*. 2001, Mönkkönen & Forsman 2002, Hakkarainen *et al*. 2004, Pakkala *et al*. 2006). Possible positive effects of the indicator species itself is a special case of explanation 3.

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. Apart from a few, seemingly occasional positive impacts, we found only two negative impacts namely those of pygmy and Tengmalm's owls and three positive impacts of the brambling that can be of ecological relevance. The negative effects were observed at the smallest spatial scales (pygmy owl 300 m radius; Tengmalm's owl 400 m radius) where these species were indicator candidates, corresponding to the territory sizes of the species' passerine prey. Corresponding negative effects were not detected at larger scales (pygmy owl: 400, 500, 700 m; Tengmalm's owl: 600, 700 m radius) where comparisons were made (Appendix). Pygmy and Tengmalm's owls are hole-nesting species preferring mature and structurally diverse forest environments (*see* above), and they can have negative effects on species among the hole-nesting forest bird guild and affect spatial distributions of their prey, above all passerines (e.g. Forsman *et al*. 2001, Mönkkönen & Forsman 2002, Pakkala *et al*. 2006).

The brambling, also one of the top indicator species candidates, was the only species analyzed that showed broad-scale positive effects by "itself". It does not show site-fidelity (Mikkonen 1983, 1985) and can select suitable areas that could be suitable also for other species, and the observed positive effects of brambling could be connected to spatially synchronous dynamics of several species (which is not explicitly studied here). It is possible that besides independent, spatially synchronous dynamics some heterospecific attractions could be involved, i.e. other, already present bird species provide cues to other species to settle in good breeding habitats (cf. Mönkkönen & Forsman 2002).

We conclude that the indicator species in our study seem to indicate mostly the site in question rather than the respective species assemblage. We believe that the above-mentioned results also provide support for using pooled data. By combining data from successive years (and without changes in the forest environment, as in our case) more reliable results are obtained, e.g. by increasing the efficiency of bird censuses to decrease biases in the results due to present, but undetected species (e.g. Kodric-Brown & Brown 1993, Remsen 1994, Blackburn & Gaston 1998, de Silva & Medellin 2001, Thomson *et al*. 2005, Urban *et al*. 2012).

Conclusions

In general, our results are very promising. We identified efficient key-indicator species like the three-toed woodpecker, the red-breasted flycatcher and the pygmy owl that are also known to indicate or have close connections to habitat quality and structure of the forest environment. These key-indicator species were also good indicators at many spatial scales that are important in forestry, which makes their use logistically applicable.

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Appendix. The occurrence of 81 forest bird species with a permanent territory within the study sites of the study area. At each scale (= radius of the circular study sites) and for all species, the proportion of occurrence of all study sites, p_{occ} were divided into four different classes: C (= common): $p_{occ} > 0.9$; I (= potential indicator): $0.1 \leq p_{occ} \leq 0.9$; R (= rare): $0 < p_{occ} < 0.1$; M (= missing): $p_{occ} = 0$. Those species that were selected to the best models as indicator species at the respective scale are marked with "**I**" and those to the five best single species models with "**I***" (cf. Table 1). Occurrences were calculated by pooled data of two successive years of each study site. At each scale, the number of study sites, areas of study units and mean number of species/study unit, total number of species and numbers of species in each occupancy class are also shown. All numbers of species are calculated from the pooled data. Species of forest landscapes that occur mainly in clear-cutting and other open areas or in young stands as well as species of predominantly cultural areas were not included (e.g. nightjar *Caprimulgus europaeus*, woodlark *Lullula arborea*, white wagtail *Motacilla alba*, icterine warbler *Hippolais icterina*, jackdaw *Corvus monedula*, red-backed shrike *Lanius collurio*, scarlet rosefinch *Carpodacus erythrinus*, greenfinch *Carduelis chloris* and yellowhammer *Emberiza citrinella*). Only the forest population of the swift *Apus apus* was included (i.e. subpopulations breeding in villages and farmsteads was excluded). Occurrences of black grouse *Tetrao tetrix* and capercaillie *T. urogallus* were defined by the locations of lek centres.

	Occurrence at spatial scales (radius, m)									
	100	200	300	400	500	600	700	800	900	1000
Black kite *Milvus migrans*	M	M	M	M	R	R	R	R	R	R
Honey buzzard *Pernis apivorus*	R	R	R	R	I	I	I	I	I	**I**
Goshawk *Accipiter gentilis*	M	R	R	R	I	I	I	I	**I**	**I***
Sparrowhawk *A. nisus*	R	R	I	I	I	I	**I**	I	I	I
Buzzard *Buteo buteo*	R	R	R	R	I	I	I	I	**I***	**I***
Osprey *Pandion haliaetus*	M	M	R	R	R	R	R	R	R	R
Kestrel *Falco tinnunculus*	M	M	M	R	R	R	R	R	R	R
Hobby *F. subbuteo*	R	R	R	R	R	R	R	R	I	I
Merlin *F. columbarius*	M	R	R	R	R	R	R	R	R	R
Hazel grouse *Bonasa bonasia*	I	**I***	C	C	C	C	C	C	C	C
Black grouse *Tetrao tetrix*	R	I	I	I	**I**	I	**I**	**I***	C	C
Capercaillie *T. urogallus*	R	R	R	I	I	I	I	**I***	**I***	I
Woodcock *Scolopax rusticola*	R	I	I	I	C	C	C	C	C	C
Green sandpiper *Tringa ochropus*	R	I	I	**I***	**I***	C	C	C	C	C
Stock dove *Columba oenas*	M	M	R	R	R	R	R	R	R	R
Woodpigeon *C. palumbus*	I	I	**I***	C	C	C	C	C	C	C
Cuckoo *Cuculus canorus*	R	I	I	I	I	C	C	C	C	C
Eagle owl *Bubo bubo*	M	R	R	R	R	R	R	I	I	I

continued

Appendix. Continued.

	Occurrence at spatial scales (radius, m)									
	100	200	300	400	500	600	700	800	900	1000
Hawk owl *Surnia ulula*	M	M	R	R	R	M	M	M	M	M
Tawny owl *Strix aluco*	R	R	R	R	R	R	R	R	R	R
Ural owl *S. uralensis*	R	R	R	R	I	I	**I**	I	I	I
Great grey owl *S. nebulosa*	M	M	R	R	R	M	M	M	M	M
Long-eared owl *Asio otus*	M	R	R	R	R	R	I	I	**I**	I
Tengmalm's owl *Aegolius funereus*	R	R	I	**I***	I	**I***	**I***	I	I	I
Pygmy owl *Glaucidium passerinum*	R	R	**I***	**I***	**I***	**I***	**I***	**I**	I	I
Swift *Apus apus*	R	R	I	**I**	**I**	**I***	**I**	I	**I**	**I***
Wryneck *Jynx torquilla*	R	R	I	I	**I**	**I**	I	**I***	C	C
Grey-headed woodpecker *Picus canus*	M	R	R	I	I	I	**I***	I	I	I
Black woodpecker *Dryocopus martius*	R	R	I	I	I	I	I	I	I	I
Great spotted woodpecker *Dendrocopos major*	I	I	C	C	C	C	C	C	C	C
Lesser spotted woodpecker *D. minor*	R	R	R	R	I	**I**	I	I	I	**I**
White-backed woodpecker *D. leucotos*	M	M	M	R	R	R	R	R	R	R
Three-toed woodpecker *Picoides tridactylus*	R	R	I	**I***	**I***	**I***	**I***	**I**	**I***	I
Tree pipit *Anthus trivialis*	I	C	C	C	C	C	C	C	C	C
Waxwing *Bombycilla garrulus*	M	R	R	R	R	R	R	R	R	R
Wren *Troglodytes troglodytes*	I	I	C	C	C	C	C	C	C	C
Dunnock *Prunella modularis*	I	C	C	C	C	C	C	C	C	C
Robin *Erithacus rubecula*	C	C	C	C	C	C	C	C	C	C
Red-flanked bluetail *Tarsiger cyanurus*	M	M	R	R	R	R	R	R	R	R
Redstart *Phoenicurus phoenicurus*	R	I	**I**	I	C	C	C	C	C	C
Blackbird *Turdus merula*	**I***	**I***	C	C	C	C	C	C	C	C
Fieldfare *T. pilaris*	R	R	I	**I**	I	**I**	I	I	**I**	C
Songthrush *T. philomelos*	**I**	C	C	C	C	C	C	C	C	C
Redwing *T. iliacus*	**I**	C	C	C	C	C	C	C	C	C
Mistle thrush *T. viscivorus*	R	I	I	I	I	I	I	I	I	I
Lesser whitethroat *Sylvia curruca*	I	I	C	C	C	C	C	C	C	C
Garden warbler *S. borin*	**I**	I	C	C	C	C	C	C	C	C
Blackcap *S. atricapilla*	R	I	I	I	**I**	**I**	I	I	C	C
Wood warbler *Phylloscopus sibilatrix*	**I***	**I**	C	C	C	C	C	C	C	C
Chiffchaff *P. collybita*	I	I	C	C	C	C	C	C	C	C
Willow warbler *P. trochilus*	C	C	C	C	C	C	C	C	C	C
Greenish warbler *P. trochiloides*	R	**I**	**I**	I	I	C	C	C	C	C
Arctic warbler *P. borealis*	M	M	R	R	R	R	R	R	R	R
Goldcrest *Regulus regulus*	I	C	C	C	C	C	C	C	C	C
Spotted flycatcher *Muscicapa striata*	**I***	C	C	C	C	C	C	C	C	C
Pied flycatcher *Ficedula hypoleuca*	**I***	**I***	C	C	C	C	C	C	C	C
Red-breasted flycatcher *F. parva*	R	I	**I***	**I***	**I***	**I***	**I***	**I**	**I***	**I**
Long-tailed tit *Aegithalos caudatus*	R	I	I	C	C	C	C	C	C	C
Nuthatch *Sitta europaea*	M	M	R	R	R	R	R	M	M	M
Willow tit *Parus montanus*	I	**I***	C	C	C	C	C	C	C	C
Crested tit *P. cristatus*	I	I	C	C	C	C	C	C	C	C
Coal tit *P. ater*	R	I	**I***	**I**	C	C	C	C	C	C
Blue tit *P. caeruleus*	**I**	**I**	**I**	C	C	C	C	C	C	C
Great tit *P. major*	I	I	C	C	C	C	C	C	C	C
Treecreeper *Certhia familiaris*	**I**	**I***	C	C	C	C	C	C	C	C
Golden oriole *Oriolus oriolus*	M	R	R	R	R	R	I	**I**	**I**	I
Jay *Garrulus glandarius*	R	I	I	I	C	C	C	C	C	C
Siberian jay *Perisoreus infaustus*	M	M	R	R	R	R	R	R	R	R

continued

Appendix. Continued.

	Occurrence at spatial scales (radius, m)									
	100	200	300	400	500	600	700	800	900	1000
Hooded crow *Corvus corone*	R	R	I	I	**I**	I	I	**I**	I	I
Raven *C. corax*	R	R	R	R	I	I	I	I	I	I
Nutcracker *Nucifraga caryocatactes*	M	R	R	R	R	R	R	I	I	**I**
Chaffinch *Fringilla coelebs*	C	C	C	C	C	C	C	C	C	C
Brambling *F. montifringilla*	R	I	**I***	I	**I***	**I**	I	I	**I***	**I***
Siskin *Carduelis spinus*	**I***	C	C	C	C	C	C	C	C	C
Redpoll *C. flammea*	R	I	I	I	I	C	C	C	C	C
Common crossbill *Loxia curvirostra*	I	**I**	I	I	C	C	C	C	C	C
Parrot crossbill *L. pytyopsittacus*	R	R	I	I	I	I	**I**	**I***	**I**	I
Two-barred crossbill *L. leucoptera*	M	M	R	R	R	I	**I**	**I**	I	**I***
Hawfinch *Coccothraustes coccothraustes*	M	M	R	R	R	R	R	R	R	R
Bullfinch *Pyrrhula pyrrhula*	I	I	C	C	C	C	C	C	C	C
Rustic bunting *Emberiza rustica*	R	R	I	I	**I**	I	**I**	**I***	**I**	I
Number of study sites	180	180	180	180	180	93	93	59	59	59
Area of study unit (ha)	3.14	12.6	28.3	50.3	78.5	113	154	201	254	314
Mean number of species/study unit	12.0	24.6	34.6	39.6	44.0	46.4	49.2	50.9	52.3	53.2
Number of all species	60	68	78	80	81	79	79	78	78	78
Number of potential indicator species	24	31	28	27	28	25	27	29	27	26
Number of rare species	33	27	26	26	21	18	16	13	12	12
Number of common species	3	10	24	27	32	36	36	36	39	40