Specialised woodpeckers and naturalness in hemiboreal forests – Deriving quantitative targets for conservation planning

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ABSTRACT

In many parts of the world's forests, intensive management has resulted in habitat loss for several species. Among these, specialised woodpeckers (Aves: Picidae) have been affected negatively due to their high requirements for resources that are scarce in managed forests. We used the gradient of anthropogenic impact on forests in northern Europe's Baltic Sea region to (1) assess the relationship between the presence of four focal woodpecker species and forest naturalness and (2) quantify their requirements regarding specific resources in four different areas (south-central Sweden, southern Sweden, Lithuania and northeastern Poland). This study focused on specialised woodpecker species of the Dendropicini tribe: the three-toed (Picoides tridactylus), middle spotted (Dendrocopos medius), white-backed (Dendrocopos leucotos) and lesser spotted (Dendrocopos minor) woodpeckers. The occurrence of these species in landscape units of 100 ha was generally related positively to the degree of forest naturalness and to the amounts of resources considered critical for the suitability of their respective habitats. For the middle spotted woodpecker, basal areas $\geqslant 1.0$ m²/ha of large-diameter deciduous trees (DBH $\geqslant 40$ cm) were associated with a high probability of occurrence ($\geqslant 0.9$). For the white-backed woodpecker, the same probability of occurrence was found for basal areas $\geqslant 1.4$ m²/ha of deciduous snags (DBH $\geqslant 10$ cm). Relationships between the occurrence of the three-toed and lesser spotted woodpeckers and snag abundance were more variable among study areas. The results suggest that specialised woodpeckers would benefit from an increase in the area of forest with natural properties. Moreover, they allow defining tentative quantitative targets for sustainable forest management.

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1. Introduction

Habitat loss is recognised as one of the greatest threats to biodiversity worldwide (Wilson, 1988; Pimm and Raven, 2000). Hence, it is crucial to define what constitutes suitable habitat both qualitatively and quantitatively for species that are affected negatively by human land use. In many parts of the world's northern forests, intensive management for sustained-yield wood production has resulted in decreased amounts of key components of forest ecosystems such as dead wood, large trees and multi-layered stands, as well as in the alteration of natural processes (Esseen et al., 1997; Hunter, 1999; Kuuluvainen, 2002). These changes have led to the degradation or loss of habitat for many species. In the intensively managed forests of northern Europe, for example, several forest species have declined or become extirpated during the last decades, in spite of a stable or increasing total area of forest land (Berg et al., 1994; de Jong, 2002; Gärdenfors, 2005; Gregory et al., 2007). Hence, the assessment of forest habitat amount (or loss) cannot be achieved merely through the monitoring of forest cover. Rather, it requires knowledge on the compositional, structural and functional characteristics of forest ecosystems (Noss, 1990).

To assess the extent of habitat loss and to plan for the conservation and restoration of forest ecosystems, benchmarks must be established. One possibility is to use 'naturalness' (sensu Peterken, 1996) as a baseline. Naturalness is best described as a continuous variable, where forest stands and landscapes span a gradient from mainly artificial forests (e.g., intensively managed plantations of exotic tree species on former agricultural land), through semi-natural (low-intensity management), to naturally dynamic forests (Anderson, 1991; Peterken, 1996; Frelich and Puettmann, 1999). The concept of naturalness has been applied in forest conservation science both in North America (Anderson, 1991; Patten, 1991) and Europe (Peterken, 1996; Uotila et al., 2002; Šaudytė et al., 2005). Due to the ubiquity of at least some degree of past or present anthropogenic impact, complete naturalness may not be a desirable or achievable conservation goal. Instead, the aim may be to move the ecosystems sufficiently far towards the natural pole of the gradient (Hunter, 1996; Angermeier, 2000). Defining the natural state (or range of variation) for a given type of forest ecosystem is challenging because it is dependent on the temporal and spatial contexts (Haila, 1997). Yet, historical–ecological knowledge about northern forests allows the identification of attributes which clearly have been affected by anthropogenic land use, and which thereby can be used to describe the relative degree of naturalness. Currently, many policies relating to forest biodiversity conservation make explicit reference to the concept of naturalness. For example, naturalness is one of the official indicators for sustainable forest management adopted by the Ministerial Conference on the Protection of Forests in Europe (Anon., 2003).

The degree of naturalness of the forest influences the population trends and dynamics of a range of species. For example, the status of north-European woodpecker assemblages (Aves: Picidae) has been linked to the degree of natu-ralness of forests at the scale of large regions (Angelstam and Mikusiński, 1994; Mikusiński and Angelstam, 1998). Indeed, through their requirements for breeding and foraging, woodpeckers are dependent on properties (e.g., high abundance of dead and large trees) that often are incompatible with intensive forest management for fibre production (Virkkala et al., 1993; Wesołowski et al., 2005; Garmendia et al., 2006). The dependence of many woodpecker species on large areas of forest with such properties makes them potential candidates as umbrella or focal species for helping the conservation of other species dependent on similar habitats (Martikainen et al., 1998; Wood et al., 2004). Finally, due to their wood-excavation ability, woodpeckers play a keystone role in forests through the provision of cavities for a range of secondary cavity users (Johnsson, 1993; Martin et al., 2004).

Ten species of woodpeckers breed in Europe's hemiboreal forests. Mikusiński and Angelstam (1997, 1998) classified those species into three groups based on their diet and habitat: omnivores, ant-eaters and specialised forest insectivores. This study focuses on the latter group, which includes four species, all of which belong to the Dendropicini tribe (Webb and Moore, 2005): the three-toed (Picoides tridactylus), middle spotted (Dendrocopos medius), white-backed (Dendrocopos leucotos) and lesser spotted (Dendrocopos minor) woodpeckers. All of these species are red-listed in Sweden (Gärdenfors, 2005) and many of them figure on the red lists of other north-European countries (Ingelög et al., 1993). Although the level of knowledge on the life histories of those specialised woodpeckers has increased significantly during the past decades, major knowledge gaps still remain about the quantities of different habitat features that they require. Specifically, although dead wood has been pointed out as the most crucial resource for many specialised forest woodpeckers (Hogstad and Stenberg, 1994; Walankiewicz et al., 2002; Bütler et al., 2004a), quantitative knowledge of dead wood requirements for Palaearctic woodpeckers is still scarce. This may reflect the fact that conducting combined dead wood and woodpecker surveys over a sample of large areas is very time consuming.

To achieve knowledge that is widely applicable to forest and landscape management, studies of habitat requirements should ideally be replicated in several areas (Dunning, 2002; Betts and Villard, in press). Moreover, analysing the response of species to changes in the naturalness of ecosystems requires that one samples a wide enough portion of the gradient of anthropogenic alteration, including benchmark conditions for naturalness. In Europe, some western countries provide examples of forests that have been managed intensively over many centuries, whereas several countries of Eastern Europe belonging to the same ecoregions still harbour large tracts of forests in a near-natural state (Angelstam et al., 1997). In this study, we used the gradient of human impact on forests in the southern Baltic Sea region's West and East to (1) assess the relationship between the presence of specialised woodpeckers and the degree of naturalness of the forest at the landscape scale and (2) quantify the requirements of those species regarding critical resources in different areas belonging to the same broad biogeographic zone.

2. Methods

2.1. Study areas and landscape units

The study was performed in the European hemiboreal vegetation zone, situated between the boreal and lowland temperate forest ecoregions (Mayer, 1984; Laasimer et al., 1993). Hemiboreal forests are characterised by mixtures of boreal and temperate tree species. Among conifers, Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) dominate. Boreal deciduous trees include birches (*Betula* spp.) and aspen (*Populus tremula*), which are particularly abundant in early successional and unmanaged mid-successional phases. Other important deciduous species include alders (*Alnus* spp.) and temperate deciduous species such as pedunculate oak (*Quercus robur*), lime (*Tilia cordata*), ash (*Fraxinus excelsior*), hornbeam (*Carpinus betulus*) and elms (*Ulmus* spp.). The abundance of deciduous trees increases towards the south within the hemiboreal zone (Mayer, 1984), but has declined strongly over time in many areas due to anthropogenic land use (Björse and Bradshaw, 1998).

The study system included four subregions (hereafter 'areas') belonging to the southern Baltic Sea drainage basin: Bergslagen in south-central Sweden (counties of Västmanland, Örebro and Dalarna), eastern Småland in southern Sweden (counties of Kalmar, Kronoberg and Jönköping), south-central Lithuania (mostly in the counties of Kaunas and Marijampolė) and northeastern Poland (eastern part of the Podlasie voivodeship) (Fig. 1). These areas were selected to cover a broad range of anthropogenic impact on forests and to account for the varying relative proportions of different tree species across the hemiboreal zone. Bergslagen, the northernmost of the study areas, is located at the transition

between the hemiboreal and south boreal forest zones (Mayer, 1984). It is characterised by a very long history of intensive forest management, resulting in very small amounts of forest having a near-natural structure and in a strong dominance of conifer-dominated stands (Angelstam, 1997). The study area in Småland also has a long history of land use and forest management (Nordström et al., 1989), but some larger areas of near-natural forest rich in deciduous trees are present in the managed matrix dominated by conifers (Andersson and Löfgren, 2000). In south-central Lithuania, a relatively low intensity of past forest management compared with Sweden has resulted in forests showing large variation in tree species composition and stand structure, including considerable areas of forests with high conservation value (Kurlavičius et al., 2004). The study area in northeastern Poland is located in the transition zone between the hemiboreal and northern temperate forest ecoregions (Mayer, 1984). The forest landscapes of this area show large variation in their degree of naturalness, from the old-growth forests of Białowieża National Park to intensively managed plantations (Angelstam et al., 2002; Angelstam and Dönz-Breuss, 2004).

Woodpeckers and forest stands were surveyed in a total of 111 square landscape units of 100 ha, each covered by ≥80% forest land. Hence, the area of the units was similar to the mean breeding home range size of the most area-demanding woodpecker species included in the study (Angelstam et al., 2004b). For selecting the landscape units, a design based totally on random sampling would have been inappropriate because forests in a near-natural state are so rare in most study areas that they would have been severely underrepresented in the sample. For that reason, we stratified data collection with the aim to encompass a gradient of forest naturalness within each of the four study areas (Table 1). Surveys
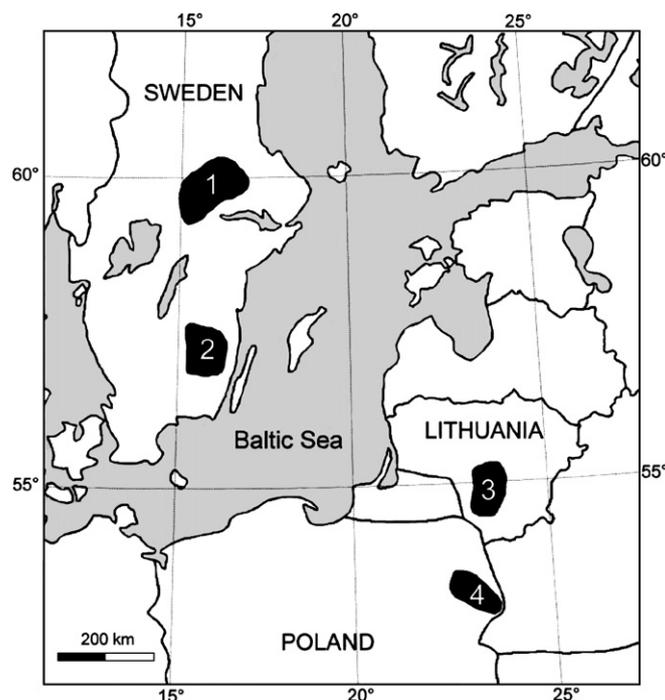

Fig. 1 – The southern Baltic Sea region in northern Europe with the four study areas: 1 – Bergslagen (Sweden), 2 – eastern Småland (Sweden), 3 – south-central Lithuania and 4 – northeastern Poland.

Table 1 – Criteria used to stratify sampling in the four study areas	
Study area (number of landscape units)	Stratification of landscape units according to the level of naturalness (number of landscape units for each stratum)
Bergslagen, Sweden (30)	I. Forests with recent records of an old-forest specialist (three-toed woodpecker[a]) (15) II. Managed forest dominated by conifers (15)
Småland, Sweden (30)	I. Forest with a high proportion of deciduous trees (15) II. Managed forest dominated by conifers (15)
South-central Lithuania (26)	I. Overmature deciduous-dominated forest (9) II. Overmature conifer-dominated forest (4) III. Managed deciduous-dominated forest (9) IV. Managed conifer-dominated forest (4)
NE Poland (25)	I. Old-growth mixed forest (5) II. Managed mixed forest (5) III. Middle-aged to mature conifer-dominated managed forest (5) IV. Young to middle-aged conifer plantations (5) V. Periodically flooded deciduous-dominated forest (5)
a Records were obtained from the Regional Ornithological Society (1998–2000).	

of woodpeckers and forest stands were conducted in 30 landscape units in Bergslagen, 30 in Småland, 26 in Lithuania and 25 in northeastern Poland. Given the typical fine-grained mosaics of forests in the southern Baltic Sea region, each landscape unit generally comprised a large number of forest stands of various ages and tree species compositions. The minimum distance between woodpecker survey transects (see below) belonging to adjacent landscape units was 2.5 km. In northeastern Poland, however, that minimum distance was set to 1 km to account for the limited extent of Białowieża National Park's strict reserve.

2.2. Woodpecker surveys

This study focused on four specialised woodpecker species: the three-toed, lesser spotted, middle spotted and white-backed woodpeckers. All of these species have breeding populations in each of the four study areas or used to be breeding there until they became extirpated in recent times, except the middle spotted woodpecker, whose breeding has never been confirmed in the Bergslagen study area (Gärdenfors, 2005). Moreover, the latter species has been extirpated from Småland (Pettersson, 1984). The white-backed woodpecker used to be widespread in Bergslagen and Småland, but it declined dramatically during the last decades and does not have breeding populations in those areas anymore (Aulén, 1988; Mild and Stighäll, 2005). The three-toed woodpecker used to have a breeding population in the Småland study area but, nowadays, it is not considered an annual breeder there (Svensson et al., 1999; Gärdenfors, 2005). The study areas in Lithuania and northeastern Poland, on the other hand, currently support breeding populations of all four species.

In each landscape unit, woodpeckers were surveyed using a combination of point counts and line transects. Four unlimited-radius point counts of 16 min each, enhanced by the use of playbacks of woodpecker drummings, were performed in the centre of each quadrant of the square landscape unit (i.e., distance of 500 m between adjacent point count stations). The playbacks consisted in a sequence of drummings of three-toed, lesser spotted, white-backed and great spotted (Dendrocopos major) woodpeckers and they were broadcasted during 2 min after 6 and 11 min of listening, respectively. Although no calls of middle spotted woodpecker were included in the sequence, this latter species very often responded to the playbacks (see also Pasinelli, 2003). In addition to the point counts, silent counts were performed along four unlimited-distance line transects joining the point count stations (i.e., running 250 m from the nearest edge of the square). Surveys were conducted between 15 March and 5 May, which corresponds to the period of highest drumming and calling activity for resident woodpeckers. In each landscape unit, surveys were performed once a year in two consecutive years, either 2002–2003 or 2003–2004, except in northeastern Poland where all units were surveyed in 2001 and 2004. Data on the presence–absence of each species in a given unit were obtained by combining observations from the point counts and line transects. A species was considered present if detected on any of the two visits. See Roberge and Angelstam (2006) for details on the bird survey methodology.

2.3. Assessment of forest naturalness

To assess the degree of naturalness, a range of components of natural forest biodiversity were measured in 16 survey plots distributed systematically in a grid fashion (between-plot distance of 250 m) in each square landscape unit (Angelstam and Dönz-Breuss, 2004). At each plot, different variables were assessed within a 30-m radius and the basal areas (m²/ha) of living and dead trees (diameter at breast height (DBH) ⩾ 10 cm) were measured using a relascope. Below, we provide the background for the selection of the naturalness variables and the most important features of data collection. A detailed description of the field measurements is presented in Angelstam and Dönz-Breuss (2004).

No single variable is adequate for describing all deviations from naturalness in forests (Uotila et al., 2002). Instead, a number of variables need to be considered simultaneously. Franklin et al. (1981) recognised three main attributes of forest ecosystems: composition, structure and function. This framework has been adopted in several indicator systems for forest biodiversity and naturalness (e.g., Noss, 1990; Larsson, 2001; Angelstam and Dönz-Breuss, 2004). To assess the degree of naturalness of the forest, we used three variables for each of those three attributes (Table 2).

Compositional variables should represent the types of elements that are characteristic of forests with a high degree of naturalness. Intensive forestry in hemiboreal forests has generally resulted in lower tree species richness within stands, mostly due to the planting of single species after felling and to homogenization of stand composition through silviculture (Nilsson, 1997). We used the mean number of native tree species per relascope point as a measure of within-stand tree

Table 2 – Mean values of the nine forest variables used to describe naturalness (standard deviation in brackets) for the landscape units surveyed in each of the four study areas in the Baltic Sea region, and factor loadings from a principal components analysis (see Section 2 for explanations of the variables)

Forest variables describing naturalness	Bergslagen ($n = 30$)	Småland ($n = 30$)	Lithuania ($n = 26$)	NE Poland ($n = 25$)	PC1[a]
Composition					
Mean number of native tree species (number/ relascope point)	2.00 (0.37)	2.32 (0.62)	3.16 (0.75)	3.15 (1.61)	**0.871**
Proportion of plots with $\geqslant 10\%$ of basal area deciduous	0.28 (0.20)	0.56 (0.24)	0.91 (0.15)	0.69 (0.40)	**0.688**
Mean number of CWD types (number/ relascope point)	1.09 (0.51)	1.26 (0.64)	1.37 (0.65)	1.62 (1.45)	**0.877**
Structure					
Proportion of plots with uneven-aged structure	0.28 (0.28)	0.16 (0.15)	0.17 (0.19)	0.68 (0.36)	**0.578**
Mean basal area of old living trees (DBH $\geqslant 40$ cm) (m²/ha)	0.54 (0.70)	0.89 (0.81)	1.87 (2.18)	4.63 (5.11)	**0.782**
Mean number of special trees providing micro-habitats (number/plot)	0.73 (0.38)	1.14 (0.39)	1.53 (0.45)	1.08 (1.02)	**0.796**
Function					
Proportion of plots with uprooting	0.41 (0.22)	0.58 (0.14)	0.54 (0.21)	0.51 (0.31)	**0.712**
Proportion of plots with periodic flooding	0.13 (0.11)	0.18 (0.17)	0.24 (0.18)	0.33 (0.38)	0.240
Mean harvesting intensity index	1.44 (0.55)	1.93 (0.47)	1.63 (0.36)	1.62 (1.02)	−**0.525**

a Values in bold depict significant associations with the first axis (PC1) of the principal components analysis.

species richness. Moreover, anthropogenic forest use has resulted in a decrease in the deciduous component at the landscape scale (Esseen et al., 1997; Björse and Bradshaw, 1998; Lindbladh and Bradshaw, 1998). We used the proportion of plots with $\geqslant 10\%$ of living basal area composed of deciduous trees as a measure of the importance of the deciduous component at the scale of the landscape unit. Additionally, timber extraction has led to decreases in the amounts of dead wood and in the variety of forms in which it occurs (Linder and Östlund, 1992; Kohv and Liira, 2005). To assess dead wood diversity, we used a modified version of Stokland's (2001) coarse woody debris (CWD) profile. We distinguished two diameter classes (DBH 10–39 cm or $\geqslant 40$ cm) and four decay classes (standing snag, hard log, soft log and decayed log), yielding a total of eight types of CWD. We used the mean number of CWD types represented per relascope point as a measure of dead wood diversity in each landscape unit.

Structural variables refer to the spatial configuration of the elements, to their quantities and to habitats found in natural forests. Intensive forest management has generally resulted in a simplification of the age structure within the stands, leading to decreased vertical diversity (Brokaw and Lent, 1999; Esseen et al., 1997; Östlund et al., 1997). We counted the number of broad age classes out of six (regeneration, young, middle-aged, mature, ageing and old-growth; cf. Angelstam and Dönz-Breuss, 2004) represented within each survey plot. We used the proportion of plots with an uneven-aged structure ($\geqslant 3$ age classes present) per landscape unit as the age structure variable. Sustained timber extraction has also often resulted in a lower abundance of large-diameter trees at the landscape scale (Linder and Östlund, 1992; Kohv and Liira, 2005). We used the mean basal area of living trees $\geqslant 40$ cm DBH to estimate large tree abundance. Finally, forests with a high degree of naturalness often contain types of trees that are uncommon in intensively managed forests

and that provide habitat for many species, such as hollow, lichen- or moss-covered, bent, forked and giant (DBH $\geqslant 80$ cm) trees (Esseen et al., 1997; Angelstam and Dönz-Breuss, 2004). We used the mean number of special tree types present per plot as an index of the occurrence of those special micro-habitats.

Functional variables concern the processes that are characteristic for naturally dynamic forests as well as the anthropogenic processes that tend to move the ecosystems away from naturalness. Processes such as windthrow and flooding are typical of naturally dynamic hemiboreal forests (Faliński, 1986; Nilsson, 1997; Šaudytė et al., 2005). Thus, we used the proportion of plots with uprooted trees and signs of periodic flooding, respectively, as two natural process variables. We also computed a harvesting intensity index based on the abundance and age of cut stumps within each survey plot: 0 = no stumps, 1 = old stumps only, 2 = single or few ($\leqslant 5$) fresh stumps and 3 = several (> 5) fresh stumps. The mean index value for all plots within each landscape unit was used as a measure of harvesting intensity.

2.4.   *Critical forest resources*

After assessing the response of woodpeckers to the composite measure of forest characteristics expressed by forest naturalness, we quantified their requirements regarding specific resources. We reviewed the literature from Scandinavia and the Baltic Sea region to identify the structural habitat feature considered most critical at the scale of a home range for each species. Dead and dying trees were found to be the most important resource for the three-toed woodpecker (Amcoff and Eriksson, 1996; Walankiewicz et al., 2002; Bütler et al., 2004a,b; Wesołowski et al., 2005) and the white-backed woodpecker (Hogstad and Stenberg, 1994; Wesołowski, 1995; Walankiewicz et al., 2002). We assessed the response of those

two species to the basal area of dead trees (DBH $\geqslant$ 10 cm). The lesser spotted woodpecker is also dependent on dead wood, but in addition to dead trees it may also forage to a large extent on (often thin) dead branches in the crowns of living trees (Nilsson et al., 1993; Olsson, 1998). However, since we did not estimate the amount of dead branches in living trees, we restricted the analyses to dead trees for this species as well. Previous studies have shown that dead trees constitute a crucial variable for explaining the occurrence of the lesser spotted woodpecker (Olsson et al., 1992; Pettersson, 1993) and have pointed to their importance as foraging and nesting substrates for this species (Hogstad, 1978; Nilsson and Pettersson, 1990; Stenberg, 1996; Svensson et al., 1999). The three-toed woodpecker is generally considered a specialist of conifer forests, but a number of studies have shown that it also uses deciduous trees and stands to a considerable extent in parts of its range (Hogstad, 1977, 1978; Wesołowski and Tomiałojć, 1986; Bergmanis and Strazds, 1993; Amcoff and Eriksson, 1996; Angelstam et al., 2004b). Therefore, we examined its response both to the basal area of dead coniferous trees and to that of all dead trees including deciduous species. White-backed and lesser spotted woodpeckers, by contrast, are usually considered as deciduous forest specialists, although they can utilise coniferous trees to some extent (Nilsson et al., 1993; Czeszczewik and Walankiewicz, 2006). Consequently, we assessed their response specifically to the basal area of dead deciduous trees and then also to the basal area of all dead trees including coniferous species. In addition to standing dead trees (hereafter 'snags'), we also examined the response of those three species to the total amount of hard dead wood, that is, the sum of snags and hard (relatively undecayed) lying dead trees (hereafter 'logs'). In the case of the middle spotted woodpecker, large-diameter deciduous trees – often characterised by the presence of large branches in the crown and a rough bark texture – were identified as the most critical resource (Pettersson, 1984; Wesołowski and Tomiałojć, 1986). We assessed the response of that species to the basal area of living deciduous trees $\geqslant$40 cm DBH, as trees over this size usually develop fissured bark and large branches.

2.5. Statistical analyses

Considering the multivariate nature of the forest naturalness data, we used a principal components analysis (PCA) based on the nine variables presented above to obtain a gradient in naturalness for the southern Baltic Sea region. Transformations were applied to the data prior to the analysis whenever appropriate (Zar, 1999). We interpreted the number of significant axes and their association with the original variables using the broken-stick criterion (Jackson, 1993; Peres-Neto et al., 2003). The PCA on the set of naturalness variables identified only one major axis, explaining 49% of the variance in the data (PC1). Additional axes were not significant and only explained a minor portion of the variance (e.g., 14% for PC2 and 11% for PC3). Seven of the nine original naturalness variables were positively associated with PC1 (Table 2). In addition, the variable 'periodic flooding' showed a weak, non-significant positive association with that axis. Finally, the harvesting intensity index showed a negative association with

PC1. Therefore, the first axis was interpreted as representing a gradient in forest naturalness and the scores on that axis were used as the 'naturalness variable' in subsequent analyses.

We used univariate logistic regression models to examine the relationship between the occurrence of each woodpecker species and, respectively, the degree of naturalness of the forest and the amounts of specific resources deemed critical for each species. The significance of the models was determined using the likelihood ratio test. Model fit was assessed using the area under the curve (AUC) of a receiver operating characteristic (ROC) plot, which ranges from 0.5 for random performance to 1.0 for perfect fit (Hosmer and Lemeshow, 2000). For Lithuania and northeastern Poland (i.e., the two study areas where all four species were found), we assessed the relationship between forest naturalness and the number of specialised woodpecker species per landscape unit using ordinal logistic regression, checking the proportional odds assumption with likelihood ratio tests (Hosmer and Lemeshow, 2000).

Ecological data are often characterised by positive spatial autocorrelation, whereby the values observed in nearby units are more similar to each other than expected for random pairs of such units (Legendre, 1993). In regression analysis based on spatial data, positive spatial autocorrelation may increase the risk for type I error due to a lack of independence among survey units. We assessed spatial autocorrelation in woodpecker distribution that was unexplained by forest characteristics by calculating Moran's I coefficients for the residuals of the logistic regression models (Diniz-Filho et al., 2003). The number of distance classes was set at 10 following Sturge's rule (Legendre and Legendre, 1998) and class limits were selected to maximise the similarity in sample size among classes (Diniz-Filho et al., 2003).
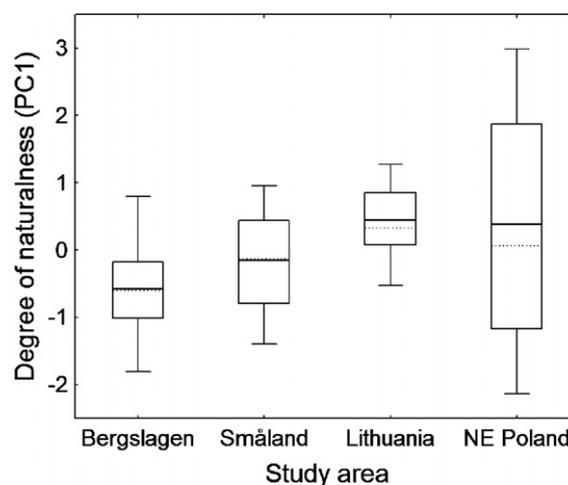

Fig. 2 – Degree of naturalness of the forests in the surveyed landscape units of the four study areas as measured by scores on the first axis of a PCA (*n* = 30 in Bergslagen, *n* = 30 in Småland, *n* = 26 in south-central Lithuania, *n* = 25 in northeastern Poland). The box-plots present the mean (plain line), median (dotted line), 25 and 75 percentiles (box), and range (whiskers).

3. Results

3.1. Forest naturalness

The four study areas differed markedly in the range of naturalness of the surveyed forests (Fig. 2, Table 2). The landscape units in northeastern Poland covered the widest span of forest naturalness, including the most and least natural units of all study areas. On the other hand, the landscape units in Lithuania were restricted to a narrow range of intermediate to relatively high naturalness. The lowest mean degree of forest naturalness was found in Bergslagen, while landscape units in Småland showed intermediate to low naturalness values (Fig. 2).

The occurrence of the specialised woodpeckers was positively linked to forest naturalness for all species in Bergslagen, Småland and northeastern Poland, and for one species – the three-toed woodpecker – in Lithuania (Table 3). The latter species responded significantly to forest naturalness in all three areas where it occurred. The AUC was over 0.75 in each of those areas, indicating a high discrimination power. Middle spotted and white-backed woodpeckers showed a significant positive response to the degree of naturalness in northeastern Poland, again with a high discrimination power (AUC > 0.8). In Lithuania, the effect of naturalness on those two species was positive but not statistically significant. The occurrence of the lesser spotted woodpecker was significantly related to forest naturalness both in Småland and northeastern Poland (with AUCs of 0.87 and 0.77, respectively), but not significantly so in Lithuania (Table 3).

Of the 10 combinations of species and study areas (Table 3), only the lesser spotted woodpecker in northeastern Poland showed a significant autocorrelation in the residuals of logistic regression against naturalness ($P < 0.05$; Bonferroni adjusted). The pattern was one of positive autocorrelation for nearby (~10–20 km) landscape units, gradually turning into negative autocorrelation for units located farther apart (~40–70 km). This suggests that factors not accounted for in the model probably were responsible for autocorrelation in the spatial distribution of that species. Therefore, the observed response of that species to the level of forest naturalness in northeastern Poland should be interpreted cautiously.

The number of specialised woodpecker species present in a given landscape unit was significantly related to the degree
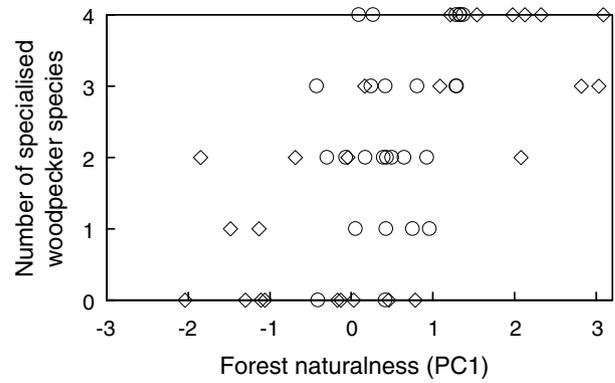

Fig. 3 – Relationship between the degree of naturalness of the forest and the number of specialised forest-insectivorous woodpecker species for landscape units of 100 ha in south-central Lithuania (*n* = 26; circles) and northeastern Poland (*n* = 25; diamonds).

of naturalness of the forest in both areas considered (Lithuania, $P = 0.023$; northeastern Poland, $P = 0.0002$; Fig. 3). To account for the spatial autocorrelation in lesser spotted woodpecker data in the latter area, we performed a second analysis excluding that species. The model was still significant ($P < 0.0001$) and its residuals showed no significant autocorrelation.

3.2. Amounts of critical resources

The occurrence of the different woodpecker species was generally related positively to the amounts of forest components deemed critical for the suitability of their respective habitats. The presence of the three-toed woodpecker was positively linked to the basal area of coniferous snags both in Bergslagen and northeastern Poland, but the effect was not significant in Lithuania (Table 4a; Fig. 4a). A probability of occurrence of 0.9 corresponded to basal areas of coniferous snags of 1.0 m^2/ha in Bergslagen and 2.9 m^2/ha in northeastern Poland. In Lithuania, the occurrence of the three-toed woodpecker was positively related the total basal area of hard dead wood (Table 4a). Similarly, in Bergslagen and northeastern Poland, models based on the total amount of hard dead

Table 3 – Logistic regression models describing the relationship between forest naturalness and the occurrence of specialised woodpeckers

Study area	Three-toed woodpecker			Middle spotted woodpecker			White-backed woodpecker			Lesser spotted woodpecker		
	β_1 [a]	β_0 [b]	AUC [c]	β_1	β_0	AUC	β_1	β_0	AUC	β_1	β_0	AUC
Bergslagen	2.695**	1.101	0.851**	Outside distribution range			Regionally extinct			Insufficient data		
Småland	Regionally extinct			Regionally extinct			Regionally extinct			3.007**	−0.097	0.873**
Lithuania	2.271*	−1.860	0.771*	0.812[ns]	0.894	0.600[ns]	0.643[ns]	0.368	0.575[ns]	1.054[ns]	0.037	0.638[ns]
NE Poland	1.200**	−2.357	0.886**	3.581***	−2.002	0.987***	0.894**	−0.187	0.821**	0.794*[d]	0.492	0.771*

[ns] $P > 0.10$ (non-significant), * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.
a Parameter estimate.
b Constant.
c Area under the ROC curve. *P*-value refers to the null hypothesis of AUC = 0.5.
d Significant spatial autocorrelation of model residuals.

Table 4a – Relationship between the amount of dead wood and the occurrence of the three-toed woodpecker						
	Three-toed woodpecker		Univariate logistic regression model			
	Present	Absent				
	Mean (range)	Mean (range)	β_1[a]	β_0[b]	AUC[c]	$x_{0.9}$[d]
Bergslagen, central Sweden	$n = 13$	$n = 17$				
Snags, coniferous (m²/ha)	0.72 (0.06–2.44)	0.25 (0.00–1.00)	4.18**	−1.95	0.81**	1.0
Snags, all spp. (m²/ha)	0.96 (0.25–2.94)	0.26 (0.00–1.00)	6.63***	−3.55	0.93***	0.9
Dead wood[e], coniferous (m²/ha)	1.60 (0.50–3.13)	0.71 (0.00–1.94)	2.60***	−2.96	0.85**	2.0
Dead wood, all spp. (m²/ha)	2.00 (0.69–4.38)	0.76 (0.06–2.06)	3.55***	−4.46	0.91***	1.9
Småland, southern Sweden	$n = 0$	$n = 30$	Regionally extinct			
South-central Lithuania	$n = 9$	$n = 17$				
Snags, coniferous (m²/ha)	0.43 (0.00–1.56)	0.36 (0.00–1.69)	0.33ns	−0.77	0.57ns	–
Snags, all spp. (m²/ha)	1.24 (0.44–2.63)	0.76 (0.06–1.88)	0.31+	−1.91	0.69ns	–
Dead wood, coniferous (m²/ha)	0.89 (0.00–3.31)	0.72 (0.00–3.69)	0.21ns	−0.80	0.58ns	–
Dead wood, all spp. (m²/ha)	2.35 (0.69–4.75)	1.38 (0.13–4.00)	0.89*	−2.23	0.76*	5.0
Northeastern Poland	$n = 6$	$n = 19$				
Snags, coniferous (m²/ha)	1.64 (0.06–4.13)	0.17 (0.00–1.50)	1.43**	−2.01	0.85*	2.9
Snags, all spp. (m²/ha)	3.26 (0.75–6.94)	0.65 (0.00–3.00)	1.20**	−3.06	0.90**	4.4
Dead wood, coniferous (m²/ha)	2.91 (0.44–6.63)	0.47 (0.00–2.44)	1.00**	−2.33	0.87**	4.6
Dead wood, all spp. (m²/ha)	5.74 (2.13–10.69)	1.42 (0.00–5.31)	0.73**	−3.46	0.92**	7.8

ns$P > 0.10$ (non-significant), +$P < 0.10$, *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.
a Parameter estimate.
b Constant.
c Area under the ROC curve. P-value refers to the null hypothesis of AUC = 0.5.
d Value of the predictor variable corresponding to a probability of occurrence of 0.9.
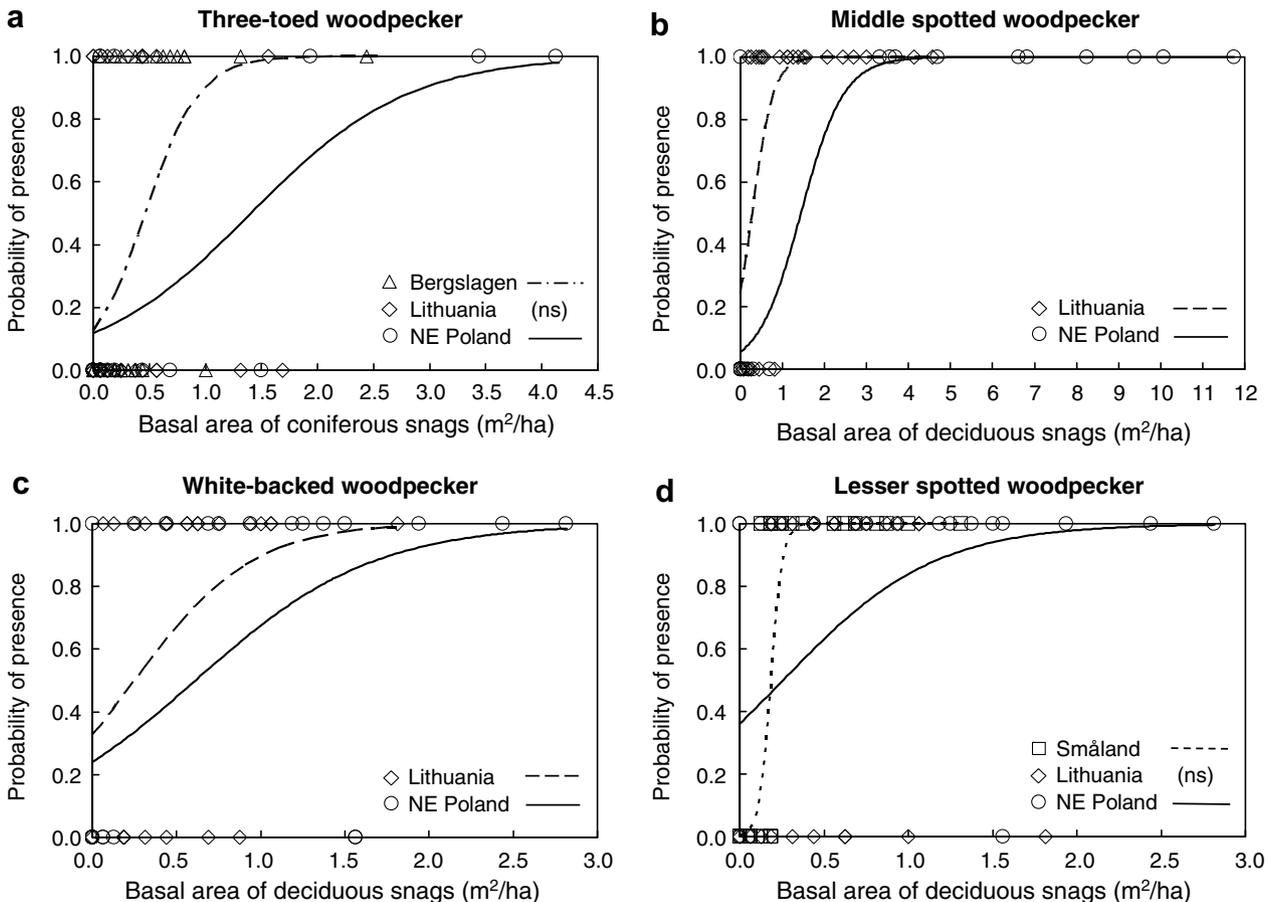e 'Dead wood' refers to the sum of snags and hard (relatively undecayed) logs.

Fig. 4 – Relationship between the occurrence of four forest insectivorous woodpecker species and the amounts of species-specific critical resources. The symbols present the observed amounts for presence and absence and the curves depict fitted logistic regression models (cf. Tables 4a–d).

wood had lower P-values and better fits than those including only coniferous snags.

For the middle spotted woodpecker, probability of presence rose abruptly with an increasing basal area of large (DBH $\geqslant$ 40 cm) deciduous trees both in Lithuania and northeastern Poland (Table 4b; Fig. 4b). This species exhibited a type II threshold in its response (sensu Guénette and Villard, 2004), whereby it occurred consistently above a basal area of ~0.8 m²/ha of large-diameter deciduous trees. A probability of occurrence of 0.9 corresponded to 0.8 m²/ha in Lithuania and 2.6 m²/ha in northeastern Poland. However, the higher value in northeastern Poland could be an artefact of the lack of data for basal areas in the range 1–3 m²/ha in that area. For this reason, and considering that the curves from those two neighbouring areas had similar shapes, we pooled the data from Lithuania and northeastern Poland. The combined model was highly significant (P < 0.001) and had an excellent fit (AUC = 0.94). There was no interaction between the factor 'study area' and the variable 'large-diameter deciduous trees' (P = 0.46), suggesting a similar response in those two neighbouring areas. For the combined model, the basal area of large-diameter deciduous trees yielding a probability of occurrence of 0.9 was 1.0 m²/ha (95% confidence interval [0.7–2.4]).

The presence of the white-backed woodpecker was positively linked to the amount of dead wood in both areas where it has breeding populations today (Table 4c; Fig. 4c). The basal areas of deciduous snags and hard deciduous dead wood were significant predictors both in Lithuania and northeastern Poland. The response of this species to the amount of deciduous snags was similar in the two areas (Fig. 4c). The basal areas of deciduous snags corresponding to a probability of occurrence of 0.9 were 1.0 m²/ha in Lithuania and 1.8 m²/ha in northeastern Poland. Combining the data from the two areas yielded a highly significant model (P < 0.001) with a good fit (AUC = 0.82) and without interaction between the factor 'study area' and the variable 'deciduous snags' (P = 0.57). Based on the combined data set, the basal area of deciduous snags yielding a probability of occurrence of 0.9 was 1.4 m²/ha (95% confidence interval [0.9–3.8]).

The occurrence of the lesser spotted woodpecker was positively related to the amounts of deciduous snags and other types of hard dead wood in Småland and northeastern Poland (Table 4d; Fig. 4d). In Lithuania, however, none of the considered dead wood variables was significant. In Småland, there was a sharp response similar to a type I threshold (sensu Guénette and Villard, 2004): the curve rose in a nearly vertical manner at 0.2 m²/ha (Fig. 4d). In northeastern Poland, the curve rose more gradually, but this was mostly due to the absence of the woodpecker from one unit with a large basal area of snags. The basal areas of deciduous snags yielding a

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Table 4b – Relationship between the basal area of large-diameter deciduous trees and the occurrence of the middle spotted woodpecker (see Table 4a for details)

	Middle spotted woodpecker					
	Present	Absent	Univariate logistic regression model			
	Mean (range)	Mean (range)	β_1	β_0	AUC	$x_{0.9}$
Bergslagen, central Sweden	$n = 0$	$n = 30$	Outside distribution range			
Småland, southern Sweden	$n = 0$	$n = 30$	Regionally extinct			
South-central Lithuania	$n = 20$	$n = 6$				
Large[a] deciduous trees (m²/ha)	1.53 (0.19–4.56)	0.29 (0.00–0.81)	3.96[**]	−1.13	0.90[**]	0.8
Northeastern Poland	$n = 11$	$n = 14$				
Large deciduous trees (m²/ha)	6.19 (0.00–11.75)	0.10 (0.00–0.69)	1.97[***]	−2.83	0.94[***]	2.6

a DBH $\geqslant$ 40 cm.

Table 4c – Relationship between the amount of dead wood and the occurrence of the white-backed woodpecker (see Table 4a for details)

	White-backed woodpecker					
	Present	Absent	Univariate logistic regression model			
	Mean (range)	Mean (range)	β_1	β_0	AUC	$x_{0.9}$
Bergslagen, central Sweden	$n = 0$	$n = 30$	Regionally extinct			
Småland, southern Sweden	$n = 0$	$n = 30$	Regionally extinct			
South-central Lithuania	$n = 17$	$n = 9$				
Snags, deciduous (m²/ha)	0.65 (0.06–1.81)	0.34 (0.00–0.88)	2.87[*]	−0.72	0.74[*]	1.0
Snags, all spp. (m²/ha)	0.92 (0.06–2.63)	0.94 (0.06–1.88)	−0.07[ns]	0.70	0.53[ns]	–
Dead wood, deciduous (m²/ha)	1.13 (0.13–3.25)	0.58 (0.00–1.38)	1.99[*]	−0.98	0.75[*]	1.6
Dead wood, all spp. (m²/ha)	1.68 (0.13–4.75)	1.77 (0.25–4.00)	−0.07[ns]	0.76	0.56[ns]	–
Northeastern Poland	$n = 13$	$n = 12$				
Snags, deciduous (m²/ha)	1.20 (0.00–2.81)	0.28 (0.00–1.56)	1.88[**]	−1.15	0.83[**]	1.8
Snags, all spp. (m²/ha)	2.13 (0.06–6.94)	0.35 (0.00–1.75)	1.44[**]	−1.20	0.87[**]	2.4
Dead wood, deciduous (m²/ha)	2.12 (0.00–4.06)	0.62 (0.00–3.75)	0.94[**]	−1.11	0.83[**]	3.5
Dead wood, all spp. (m²/ha)	3.82 (0.13–10.69)	0.98 (0.00–4.13)	0.65[**]	−1.21	0.82[**]	5.2

Table 4d – Relationship between the amount of dead wood and the occurrence of the lesser spotted woodpecker (see Table 4a for details)						
	Lesser spotted woodpecker		Univariate logistic regression model			
	Present	Absent				
	Mean (range)	Mean (range)	β_1	β_0	AUC	$x_{0.9}$
Bergslagen, central Sweden	$n = 1$	$n = 30$	Insufficient data			
Småland, southern Sweden	$n = 13$	$n = 17$				
Snags, deciduous (m²/ha)	0.56 (0.13–1.31)	0.07 (0.00–0.19)	29.35[***]	−5.47	0.97[***]	0.3
Snags, all spp. (m²/ha)	0.98 (0.25–1.75)	0.31 (0.06–1.00)	6.22[***]	−3.94	0.93[***]	1.0
Dead wood, deciduous (m²/ha)	1.07 (0.25–2.19)	0.17 (0.00–0.75)	6.32[***]	−2.96	0.96[***]	0.8
Dead wood, all spp. (m²/ha)	2.35 (0.44–3.69)	0.90 (0.25–2.38)	2.89[***]	−4.54	0.90[***]	2.3
South-central Lithuania	$n = 16$	$n = 10$				
Snags, deciduous (m²/ha)	0.56 (0.19–1.06)	0.52 (0.00–1.81)	0.26[ns]	0.33	0.61[ns]	–
Snags, all spp. (m²/ha)	1.01 (0.31–2.63)	0.79 (0.06–2.25)	0.61[ns]	−0.08	0.61[ns]	–
Dead wood, deciduous (m²/ha)	0.96 (0.25–1.81)	0.90 (0.00–3.25)	0.14[ns]	0.34	0.62[ns]	–
Dead wood, all spp. (m²/ha)	1.92 (0.69–4.75)	1.38 (0.13–3.88)	0.52[ns]	−0.38	0.66[ns]	–
Northeastern Poland	$n = 16$	$n = 9$				
Snags, deciduous (m²/ha)	1.08 (0.00–2.81)	0.19 (0.00–1.56)	2.22[**]	−0.57	0.84[**]	1.2
Snags, all spp. (m²/ha)	1.84 (0.00–6.94)	0.28 (0.00–1.75)	1.53[**a]	−0.53	0.84[**]	1.8
Dead wood, deciduous (m²/ha)	1.98 (0.00–4.06)	0.38 (0.00–2.31)	1.29[**a]	−0.69	0.87[**]	2.2
Dead wood, all spp. (m²/ha)	3.39 (0.13–10.69)	0.79 (0.00–2.75)	0.74[**a]	−0.64	0.78[*]	3.8
a Significant ($P < 0.05$) spatial autocorrelation of model residuals.						

probability of occurrence of 0.9 were 0.3 m²/ha in Småland and 1.2 m²/ha in northeastern Poland. The species was absent from several landscape units with large basal areas of deciduous snags in Lithuania.

Similarly to the analyses regarding forest naturalness, significant spatial autocorrelation of model residuals was only found for the lesser spotted woodpecker in northeastern Poland ($P < 0.05$; Bonferroni adjusted), although not for the residuals of the model based on the amount of deciduous snags (Table 4d).

4. Discussion

4.1. Forest naturalness and woodpeckers

To our knowledge, this study is the first to relate empirically the occurrence of woodpecker species to a quantitative and general measure of forest naturalness at the scale of local landscapes for several different areas. In floodplain forests of southwestern Germany, Spitznagel (1990) found a positive relationship between woodpecker species richness and the proportion of old natural forest within 25 ha grid cells. That study included two of the species covered in the present investigation: the middle and lesser spotted woodpeckers. Both occurred most frequently in areas with large extents of old and closed woods. At the scale of countries in Europe, Mikusiński and Angelstam (1997, 1998) related the status of woodpecker assemblages to the degree of socio-economic development. Woodpecker diversity was negatively related to the degree of urbanization and other socio-economic variables affecting land use intensity. In the present study, the occurrence of four woodpeckers classified as specialised forest insectivores was generally associated with a high degree of naturalness. Moreover, the number of woodpecker species observed per landscape unit increased with forest naturalness. The three-toed woodpecker was positively linked to nat-

uralness in all three study areas where breeding populations are still present. For the middle, white-backed and lesser spotted woodpeckers, the effect of forest naturalness was positive everywhere, although not statistically significant in Lithuania.

In the Lithuanian study area, forest landscapes with a long history of intensive forest management were absent. Consequently, the sampled landscape units in that area showed the narrowest range of naturalness of all study areas, most of them being concentrated in the upper-central portion of the gradient (Fig. 2). Hence, the limited range of values for the predictor variable in the Lithuanian material may have precluded the detection of patterns that would become apparent at lower or higher degrees of naturalness. To explore that possibility, we pooled the data from Lithuania with those from northeastern Poland (i.e., the nearest study area), added 'study area' as a factor in the model and examined the effect of the interaction 'study area × naturalness' on the incidence of the three woodpecker species for which the naturalness model was not statistically significant in Lithuania. The interaction term was non-significant for all three species ($P = 0.08$, 0.77 and 0.74 for middle spotted, white-backed and lesser spotted woodpecker, respectively). Therefore, the results from Lithuania do not seem to contradict the patterns observed in the other areas. More generally, this stresses the importance of covering a wide enough range of values for the explanatory variable in this kind of ecological dose–response studies (Angelstam et al., 2004a).

There were four cases of recent regional extirpations in our study system: the middle spotted and three-toed woodpeckers in Småland, as well as the white-backed woodpecker in Bergslagen and Småland. In south-central and southern Sweden, a long history of intensive forest management has resulted in a lower degree of naturalness of the forests. In countries east of the Baltic, by contrast, large extents of forests with high naturalness can still be found due to a

historically lower intensity of land use in many areas (Angelstam et al., 1997). Thus, these regional extinction events provide additional evidence for the dependence of those specialised woodpeckers on properties typical of forests with a high degree of naturalness.

4.2. Towards conservation targets?

Because naturalness, as assessed here, is time-consuming to measure and difficult to manage without quantitative performance targets, we wanted to determine whether the occurrence of specialised woodpecker species was related to the amounts of specific forest resources considered critical to the quality of their respective habitats. The models linking the occurrence of the middle spotted and white-backed woodpeckers to, respectively, large-diameter deciduous trees and deciduous snags were fairly consistent for the two study areas where those species are still found today. This allowed the identification of tentative targets for these habitat features corresponding to high probabilities of occurrence for those two woodpecker species.

For the middle spotted woodpecker, the target identified regarding large-diameter deciduous trees ($\geqslant 1.0$ m^2/ha) corresponds to a minimum density of eight deciduous trees of 40 cm DBH per ha, or five trees of 50 cm DBH. It should be kept in mind that this result was obtained in closed-canopy forest, where large-diameter deciduous trees were interspersed with smaller trees that may also have contributed, to some degree, to habitat quality for the woodpecker. Thus, this target may not be directly applicable to other types of middle spotted woodpecker habitats such as wooded grasslands typical of pre-industrial agricultural landscapes. In Swiss forests, Pasinelli (2000) observed densities of ~12–132 large oaks (DBH $\geqslant 36$ cm) per hectare in middle spotted woodpecker territories. In a German study, a mean basal area of 12 m^2/ha was recorded in breeding territories, corresponding to a minimum of 15 oaks > 60 cm DBH per ha (Coch, 1997; in Pasinelli, 2003). In northeastern Switzerland and Austria, respectively, estimates of oak densities required to support one breeding pair per 10 ha were 26 oaks of 50–90 cm DBH per ha and ~80 oaks with mean DBH of 43 cm (Bühlmann and Pasinelli, 1996 and Michalek et al., 2001; both in Pasinelli, 2003). In Spain, Robles et al. (2007) found that the densities of large oaks (DBH $\geqslant 37$ cm) per hectare were 1 ± 1 (mean ± S.E.) in young forest tracts where the woodpecker was absent, and 57 ± 8 in mature forest tracts where it occurred. The generally higher basal areas and densities of large trees observed in studies performed at the scale of a territory suggest that the target of $\geqslant 1$ m^2/ha identified in the present study for a scale of 100 ha may not be directly applicable to the smaller scale of individual breeding territories for this species (usually < 25 ha; Pasinelli, 2003). Therefore, we recommend that the target large-tree abundance value from the present study be used only for management at the landscape scale, and that the higher values obtained in the previous studies performed at smaller spatial scales be used to derive targets for patches corresponding to the woodpecker's territory (or home range) size within those landscapes.

In addition to old oak-dominated forest, we also observed middle spotted woodpecker in large tracts of riverine alder-dominated forest without oaks or very large trees. This provides additional evidence that older oak-dominated forests are not the only forest type fulfilling the requirements of that species (see also Wesołowski and Tomiałojć, 1986; Hertel, 2003; Pasinelli, 2003; Weiß, 2003). Finally, although we have emphasised the importance of large-diameter deciduous trees, mostly for foraging, an additional factor that needs to be considered when planning for middle spotted woodpecker habitat is the presence of decaying trees or branches suitable for nest excavation (Pettersson, 1984; Pasinelli, 2000; Kosiński et al., 2006; Robles et al., 2007).

Regarding the white-backed woodpecker, the results suggest that basal areas of deciduous snags $\geqslant 1.4$ m^2/ha (DBH $\geqslant 10$ cm) over an area of 100 ha correspond to resource levels highly suitable for the species (probability of presence $\geqslant 0.9$) and may represent a reasonable target. In western Norway, Gjerde et al. (2005) obtained a mean snag (DBH $\geqslant 5$ cm) basal area of ~1 m^2/ha in study plots of 100 ha with presence of the white-backed woodpecker. In Białowieża Forest (northeastern Poland), Czeszczewik and Walankiewicz (2006) obtained a mean density of 17 snags/ha (all species) with DBH $\geqslant 20$ cm (i.e. $\geqslant 0.5$ m^2/ha) in stands with occurrence of white-backed woodpecker, and suggested that value as a minimum management target. The basal area of dead trees yielding a high probability of white-backed woodpecker occurrence in the present study can be converted into wood volume using the following function: Volume = basal area × tree height × shape index (Anon., 1986; Bütler et al., 2004a). Due to the variation in tree species and height of individual snags, it is difficult to obtain a precise figure. Still, a rough estimate can be calculated by assuming that the mean height of dead trees ranged between 15 and 20 m (the mean dominant height in forests occupied by the white-backed woodpecker was 22.3 m for living trees) and that the shape index may have ranged from 0.4 to 0.6 (Anon., 1986). Using these values, the volume of standing deciduous dead stems yielding a probability of occurrence of 0.9 for the white-backed woodpecker would be approximately 8–17 m^3/ha over a 100-ha landscape unit. This is much more than the mean volumes observed in managed forests. In hemiboreal Sweden, for example, Fridman and Walheim (2000) estimated that the mean snag volume was 1.5 m^3/ha on managed forest land, only a fraction of which represented deciduous species.

For the lesser spotted and three-toed woodpeckers, results varied among areas, including increasing functions with diverging slopes and non-significant relationships. This precluded the definition of general management targets. In old deciduous forests, a substantial proportion of the dead wood is present as dead branches on living trees, which may be used to a considerable extent by the lesser spotted woodpecker (Nilsson et al., 1993; Olsson, 1998). Variations in the availability and use of this unmeasured dead wood component may have contributed to the observed discrepancies among areas for that species. Moreover, differences among landscape units and areas regarding the quality of the deciduous snags as foraging substrates (species, degree of decay, bark condition) may have had some importance. With regards to the three-toed woodpecker, Bütler et al. (2004a) compared that species' requirements for snags between Sweden and Switzerland and found sharp occurrence thresholds in both

countries. Note that the 30 landscape units in Bergslagen in the present study include Bütler et al.'s (2004a) 20 Swedish units, although woodpecker occurrence data are from independent surveys. Based on empirical data (Bütler et al., 2004a) and a bioenergetic model (Bütler et al., 2004b), these authors recommended target values of 1.3–1.6 m^2/ha of snags in an area of 100 ha. Although the three-toed woodpecker is generally considered a conifer-forest species feeding preferentially on snags, the good performance of the models based on total amounts of dead wood including that from deciduous species in all areas in the present study (including Lithuania) suggests that deciduous trees and lying dead wood may contribute to habitat quality for that species. This is supported by a number of studies showing that the three-toed woodpecker also utilises deciduous trees for foraging and nesting (Hogstad, 1977; Bergmanis and Strazds, 1993; Amcoff and Eriksson, 1996; Angelstam et al., 2004b), and that it may occasionally forage on fallen dead trees and branches (Cramp, 1985; own observations).

More generally, our results point to the fact that surveys performed using the same methodology may lead to different quantitative estimates of the species' requirements in different areas. A number of studies have shown that presence–absence models developed for single species in one area may have a limited predictive ability in other areas within the same region (e.g., Reunanen et al., 2002; Betts et al., 2006). Such variation can be due, among other things, to geographical differences in local population dynamics of the species or in the characteristics of vegetation and other structures contributing to habitat suitability. In the present study, the amounts of dead wood corresponding to a given probability of occurrence were generally higher in areas where this critical resource was more abundant. Specifically, the basal areas of snags yielding a high probability of occurrence for the three-toed and lesser spotted woodpeckers were higher in northeastern Poland than in Sweden. These differences were mostly due to the absence of the woodpeckers in a few landscape units with large basal areas of snags in the former area. Our data do not allow identifying the causes of those absences, but factors linked to unmeasured habitat variables, the influence of the larger landscape context, metapopulation dynamics, predation or interspecific competition may be involved.

The proposed targets should be seen as working hypotheses for active adaptive landscape-scale management and for further research rather than as strict guidelines. Indeed, the analyses present a number of limitations. First, in spite of a relatively high sampling intensity, it is possible that some individuals remained undetected, leading to 'false absences'. This could have contributed to the observed differences among areas, including the lack of statistical significance of some of the models. However, the vast majority of the woodpecker individuals were detected acoustically, meaning that variations in visibility among forests with varying structure and composition probably did not bias our results. Although theoretically possible, we do not believe that acoustic detectability would have been systematically correlated with the measured forest variables in such a strong way as to create the observed patterns. Generally, there were many data points in the region of low resource abundances and fewer data points for high resource abundances (Fig. 4). Thus, we would expect that individual cases of false absences in the range of low values on the resource axis would only have a limited impact on the shapes of the relationships, whereas potential false absences in the range of high resource values may have a greater impact. In the latter case, false absences would have yielded shallower logistic curves, resulting in an overestimation of the resource amounts corresponding to a given probability of presence (e.g., 0.9). The corresponding targets would thus have been conservative from a habitat management perspective.

A second limitation is that data on presence–absence during the breeding season provide more limited information about habitat suitability than measures focusing on the reproductive success and survival of individuals. Yet, because collecting comprehensive fitness data at large spatial scales is very time-consuming, models based on presence–absence data are likely to remain a major source of information for defining management targets while more cost-efficient methods to estimate fitness are being developed. Still, further studies emphasising the relationship between fitness of the studied species and the amounts of dead wood and large-diameter trees would be desirable in order to refine the quantitative knowledge of the species' requirements. Another limitation of the analyses is that the landscape units surveyed may have overlapped only partly with the birds' home ranges, which could lead to a dilution effect due to the averaging of the values over larger areas, and thereby to an underestimation of the birds' requirements. This effect would be stronger in areas where the matrix outside the limits of the home ranges provides low amounts of critical resources. This could be expected in the Swedish study areas, where most forest landscapes are intensively managed. Finally, although conserving or restoring the amounts of a critical resource is expected to increase habitat quality, management focusing solely on a single habitat variable may not ensure persistence at the local and regional scales. Additional variables to be considered may include, for example, those affecting the continuous supply of high-quality feeding and nesting substrates in time, interspecific interactions such as predation and competition (Pakkala et al., 2006), and habitat connectivity at the scale of larger landscapes and regions (Carlson, 2000; Pakkala et al., 2002).

5.   Conclusions

The results of this study performed at the scale of local landscapes, together with previous work at the scale of regions and countries (Mikusiński and Angelstam (1997, 1998)), suggest that specialised woodpeckers are linked to properties characteristic of natural forests at multiple spatial scales. Thus, both general recommendations to increase the amounts of critical resources and conservation planning aiming to increase the area of forest and cultural woodland with natural properties are expected to be beneficial to the populations of those species. More specifically, the results point to the importance of dead wood and large-diameter trees for the occurrence of those woodpeckers. Quantitative, ecologically-based targets for the amounts of dead wood and other critical

structures are urgently needed to guide forest management and conservation (Guénette and Villard, 2005; Ranius and Fahrig, 2006; Poulin et al., 2008). Because it would be an overwhelming task to quantify the necessary amounts of dead wood and large-diameter trees with different qualities for the persistence of all species dependent on those resources, there is a need for some prioritisation in the work toward the development of such targets. Focusing on demanding indicator or umbrella species may offer a good starting point in that respect (Angelstam et al., 2003; de Jong and Almstedt, 2005; Ranius and Fahrig, 2006). The four woodpecker species considered in this study have been shown to be reliable indicators of species-rich bird communities (Jansson, 1998; Mikusiński et al., 2001; Roberge and Angelstam, 2006). There is also evidence that the white-backed woodpecker could function as an umbrella or focal species (Martikainen et al., 1998; Mild and Stighäll, 2005; Roberge et al., submitted for publication). Thus, conservation management aiming to provide suitable habitat for those woodpecker species may also benefit a large number of sympatric species dependent on the same habitats or resources. The results of this study have allowed defining tentative management targets for the middle spotted and white-backed woodpeckers. Moreover, they have highlighted the variability existing in the ecological requirements of some species among areas. Further studies are needed that focus on quantifying the requirements of demanding species for other resources that have become scarce as a result of anthropogenic land use in various ecosystem types. When communicated effectively to decision-makers, such performance targets may constitute a major contribution to active adaptive management programmes.

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