Divergent responses of flagship, keystone and resource-limited bio-indicators to forest structure

Amalia Segura*, Javier Castaño-Santamaría, Paola Laiolo* and José Ramón Obeso

Research Unit of Biodiversity (UO/CSIC/PA). University of Oviedo, Campus de Mieres, Edificio de Investigación V Planta, 33600 Mieres, Spain.

*Corresponding authors

E-mail addresses:

amaliasegura@gmail.com (A. Segura)

paola.laiolo@csic.es (P. Laiolo)

Phone: +34 985 10 81 30

Fax: +34 985 10 47 77

Abstract

Bio-indicators are often proposed to set conservation priorities in forest habitat owing to the difficulties of determining forest intrinsic ecological value. Here, we tested the efficacy of a number of potential bird indicator groups in monitoring beech *Fagus sylvatica* forest status by analyzing their associations with the spatial and structural variables of forest vegetation that indicate key ecological patterns and processes. The density of cavity nesting birds, indicating the presence of limited forest resources ("resource-limited indicators"), was influenced by tree species diversity, vertical species mingling and diameter, parameters reflecting maturity, gap-dynamic processes, as well as resource and shelter availability. Heterogeneity in shrub species composition, another parameter depending on forest dynamics, was positively associated with the occurrence of Capercaillie, a "flagship" species for forest conservation. The presence of woodpeckers, a "keystone" group that provides shelter and foraging substrate to other organisms, was positively affected by the basal area of standing dead trees that is indirectly associated with natural nutrient availability. These findings suggest that single indicators fail to provide a complete assessment of forest status, and their use in monitoring or managing forest ecosystem need to be contextualized to specific ecological patterns. The combined use of several indicators, representing various taxa, functions and life histories, appears to be preferable, and is logistically feasible if these can be surveyed together. Several indicators would likely display a wider range of sensitivities to the modification of natural processes and permit more comprehensive tracking of forest dynamics than single flagship, keystone or resource-limited indicators.

Key-words*: birds, bioindicators, Capercaillie, woodpeckers, tits, forest structure.

Introduction

Biological indicators, or bioindicators, are organisms or groups of organisms whose characteristics, such as presence, density or reproductive performance, are used to monitor environmental changes when the complexity of a habitat prevents the appraisal of all its ecological attributes (Landres et al. 1988). Bioindicators have multiple applications in conservation biology and environmental policy. Some, the so called "keystone species", serve to track community-wide processes, for instance when they create the conditions for the presence of other species, others are associated with aspects of habitat quality and diversity (biodiversity indicators, or "umbrella species"). Species that do not meet these criteria, but have a "charismatic appeal", may contribute to attracting public interest and funds for conservation, or serve in educational programs ("flagship species"; Caro 2010), although their efficacy has been questioned in both instances (Andelman and Fagan, 2000; Genovart et al. 2013).

Among terrestrial habitats, forests have an exceptional intrinsic ecological value, as a reservoir of biodiversity, for playing a key role in nutrient cycling and gas emission reduction, and for protecting soil and water (Vitousek 1984; Waring and Schlesinger 1985). Forests are also one of the most endangered and complex habitat on the earth (Bowles et al. 1998) and, unsurprisingly, the creation and restoration of natural woodland has become a major objective of sustainable forestry throughout the world and especially Europe, where the declining trend is reverting (Schröter al. 2005). A wealth of indicators has been proposed to measure forest specific ecological conditions and has been used in management for decades. The conservation and ecological value of these indicators is however still debated (Noss 1999), owing to the complexity of the processes underlying the actual conservation status of forests, which is hardly

characterized by single bio-indicators (Carignan and Villard 2002). Moreover, although several studies have tested for the congruence and associations of different indicators across taxa (e.g. by comparing bird, insect or mammal indicators), few have analyzed the association of different indicators with aspects of ecosystem status (Lawton et al. 1998; Tremblay et al. 2007; Carrascal et al. 2012).

Among the most popular habitat quality indicators are forest birds (Bani et al. 2006; Moning and Muller 2008). Birds, apart from exhibiting diverse ecological functions, are sensitive to some structural and spatial characteristics of forests that indicate pivotal ecological process, such as canopy-gap dynamics, plant–animal interactions, and forest carbon storage (Laurance et al. 2006; Sekercioglu 2006). For instance, the abundance of specific guilds, such as those of frugivorous, nectarivorous or hole-nesting birds is determined by the spatial and temporal availability of critical resources and by the structure of forest food webs (Levey 1988). The overall diversity of forest birds may depend on micro-climatic stability, tree replacement and demography (Attiwill 1994; Brawn et al. 2001; Pretzsch 2009). The density of certain forest specialists, such as woodpeckers and scavengers, is strictly tied to biomass decomposition dynamics and responds to changes in the relative density of live and dead tree biomass (Petty and Avery 1990; Virkkala et al. 1994; Nair 2007). Eventually, forest specialists may sometimes serve as flagship species, facilitating conservation publicity (Veríssimo et al. 2009).

Despite this evidence however, at the local scale birds are the preferred target for forest monitoring and environmental assessment because they are widespread and easy to survey with standard methodology, rather than solely because of ecological aspects (Pearson 1995). In this study, we aimed to compare the efficacy of several bird indicator groups in monitoring forest status and conservation by analyzing their associations with

the spatial and structural variables of forest vegetation, which indicate forest integrity, ecological patterns and processes. For instance, tree size and distribution, which indirectly indicate forest maturity, are important features determining the resistance of forest ecosystems to physical perturbations (Castedo-Dorado et al. 2009), resilience to pest outbreaks (Jactel et al. 2005), disease (Pautasso et al. 2005), fire (Wirth 2005), or extreme weather events (Dhôte 2005). As a further example, tree species composition is a key driver of forest biodiversity and ecosystem processes, such as nutrient cycling, and may reflect forest gap-dynamics (Oxbrough et al. 2012). Eventually, the amount of fallen or standing dead wood is associated with nutrient reservoir and recycling within forest ecosystems (Ranius and Fahrig 2006).

To serve as forest bird indicators, we centered this study on (1) cavity nesting birds, in their role of resource-limited species, i.e. species requiring specific resources that are in critically short supply (Noss 1999), (2) woodpeckers, specialized cavity-excavating birds that are known to disproportionately impact the community given their abundance (keystone species) (Mikusiński et al. 2001; Drever et al. 2008; Drever and Marin 2010; Remm and Lohmus 2011), and (3) Capercaillie *Tetrao urogallus*, a flagship species that promotes public support for conservation efforts (Obeso and Bañuelos 2003) and which, in specific spatial contexts, becomes an umbrella species associated with high diversity values (Suter et al. 2002; Pakkala et al. 2003; Laiolo et al. 2011) (Table 1). We studied the habitat requirements of the three different indicators, expecting that they will respond differently to different forest structural predictors, given their diverse ecology. Woodpeckers and cavity nesting birds may be more common in plots with high tree biomass and abundant snags, while the capercaillie may favor heterogeneous forests (Swenson and Angelstam 1993; Martin et al. 2004; Sánchez et al. 2007; Laiolo et al. 2011). We test whether some indicator (resource-limited, flagship or keystone) is better

than others in capturing variation in forest characteristics and can, ultimately, serve to predict ecological changes in forest ecosystems.

Materials and methods

The montane forests of Cantabrian Mountains in Asturias (NW Spain) have a broadleaf canopy dominated by the beech *Fagus sylvatica*, with the white birch *Betula alba* and oaks *Quercus* spp. covering the upper and lower fringes, respectively. The scarce underwood of these forests is composed by the hazelnut *Corylus avellana*, the holly *Ilex aquifolium*, the rowan *Sorbus aucuparia*, and medium - to small size shrubs of the genus *Vaccinium, Erica, Rubus, Cytisus* (more details in Vegetation Structure section). These forests have been heavily logged in the past centuries, but since the 1960-70s wood extraction declined and they are now included in a wide network of regional and national protected areas (García et al. 2005; Robles et al. 2007).

This study was conducted across the entire latitudinal and altitudinal range (434 to 1558 m a.s.l.) of mature beech forests (i.e. unlogged for at least 50 years and composed of > 80% beech trees) (Appendix 1). These forests present strong structural gradients and host threatened and diverse fauna, thus are well suited to analyzing the relationships between bioindicators and forest structure and composition.

Indicator survey: woodpeckers and cavity nesting birds

In April-June 2010-2011 we surveyed the entire bird community in 185 circular plots of 100 m radius, separated by > 200 m from each other. These plots were arranged along 34 daily transects, 1.5 – 2.5 km long, each including from 5 to 8 plots. Plots were surveyed from sunrise until 12 noon, the period of maximum bird activity, in good

weather conditions (Bibby et al. 2000). We followed a standard point count method, well suited to survey small passerines and forest birds in general (Blondel et al. 1970; Järvinen and Lokki 1978; Caprio et al. 2008), in which we recorded all birds seen or heard in 10 min periods in the circular bands of 50 and 100 m (a laser telemeter was used, Nikon 550 AS and Leica Rangemaster 1200). Each plot was visited only once during early spring (Shiu and Lee 2003). Geographical coordinates and elevation of the centre of each plot were established by means of a GPS.

From the whole bird data-set, we extracted density values of cavity nesting birds (8 species, listed in Table 1) in the circular band of 50 m radius only, since these species can be accurately surveyed in 0.78 ha areas (Laiolo et al. 2011). The presence/absence of woodpeckers, represented by three species in the study area (Table 1), was estimated in the widest survey band (100 m, surveyed area = 3.14 ha), in order to take into account the largest home range size of these species. Since woodpeckers can move large distances during breeding (Rolstad et al. 1995), we were careful not to record the same individual in successive plots along the same transect.

Indicator survey: Capercaillie

Because of its special protection in Asturias, spatial requirements and daily routine, the Capercaillie cannot be surveyed by point counts as other bird indicators can. We therefore considered the surveys performed by the Asturian Environmental Agency to obtain data on the presence/absence of this grouse in the study plots in the period 2005 and 2007, plus updated information obtained in 2010 (Laiolo et al. 2011). Local environmental wardens surveyed 47 sexual display areas (here called leks for simplicity), that were known to be occupied since the 1980s, when the species surveys

were first performed. Each Capercaillie lek was surveyed at least twice by 2-3 wardens between April and May, period when both cocks and hens center their activities (foraging, displaying and breeding) in the lek area (Martínez 1993). Each lek area was reached during the night to record Capercaillie dawn activities without altering bird behavior, and it was left well after the end of displaying. When no activity was recorded the observers searched for Capercaillie signs (feathers, fresh droppings, footprints in snow, etc.) in an area of up to 1 km^2 to confirm lek abandonment (Quevedo et al. 2006a and b). The same procedure was used by Laiolo et al. (2011) to record Capercaillie occurrence and to study its association with bird diversity at increasing distance from the lek center. The entire survey procedure of wardens in the Cantabrian range is described in Quevedo et al. (2006a) and Blanco-Fontao et al. (2011 and 2012).

Vegetation structure

We assessed vegetation parameters in woodlots that ranged in size from 400 to 3600 m^2, depending on stand density, in order to achieve a minimum of 35 trees to measure structural variables; vegetation diversity was instead estimated in the smallest surface (20 × 20 m) (see below, Castaño-Santamaría et al. 2013). We first measured dasometric variables including diameter, total height, and base canopy height of 35 trees, which were used to estimate the number of trees per hectare, and the basal area (i. e. the area of a given section of land covered by the cross-section of tree trunks and stems at their base; measured in m^2 of wood divided by the plot surface). By focusing on the four trees with the largest diameter, we measured their height and diameter and averaged them. These field measurements were used to calculate a series of indexes that describe the spatial and structural patterns of vegetation in woodlands, in keeping with Motz et

al. (2010). Briefly, forest spatial structure can be characterized by three aspects: aggregation, "species mingling" and size differentiation (Gadow et al. 2011). Aggregation is expressed by an index of regularity of tree positions (Clark and Evans Index, R – regularity); "species mingling" reflects the degree of spatial segregation of the tree species in a forest and is measured by two indexes of segregation, in the vertical (Simpson vertical Index, D_v – vertical species mingling) and horizontal layers (Simpson stratified Index, D_{st} – horizontal species mingling) (Appendix 2). The above indexes were always estimated taking into account the edge-correction proposed by Pommerening and Stoyan (2006). Size differentiation was measured by two different indexes: the coefficient of variation of tree diameter ($CV_{dbh)}$ and the coefficient of variation of tree height (CV_h) (Pommerening 2002). Within woodlots we also measured the total basal area of standing dead trees (or snags; BA_d) (Ranius and Fahrig 2006) (Appendix 2). Eventually, in the 20 × 20 m lots we measured tree species diversity (Simpson Diversity Index, D) to account for the occurrence of tree species other than beech (*Quercus petraea, Betula pubescens, Sorbus aria, S. aucuparia, Ilex aquifolium, Taxus baccata* and *Acer pseudoplatanus*) and shrub species richness (S), to account for forest strata other than the canopy (*Vaccinium myrtillus, Erica arborea, E. vagans, E. australis, Ilex aquifolium* and *Crataegus monogyna*). Orientation and slope were measured in the field, using a hypsometer to determine slope and an optic compass to determine orientation.

Due to large number of vegetation parameters estimated per each lot in the field (see below), we placed 1-2 woodlot within each bird transect (so that the distance of lot center from point-count plots in that transect was 0 - 490 m), and one in each Capercaillie lek area (i.e. at < 900 m from Capercaillie lek centers), for a total of 57 lots. Home ranges of the Capercaillie are large enough (several hundred hectares) to include

the lots inside, while in the case of cavity nesting birds (the species with the smallest territories) some lots indeed bordered the survey areas without falling within. Lots were however located where vegetation structure was representative of the forest patch (transect or lek area): dissimilarity in vegetation structural parameters changed with distance only when considering distances > 1 km from the lot, and even at longer distances did not display a clear decreasing or increasing pattern (Mantel test, -0.134 < R < 0.121, all P < 0.011 for the three indicator data sets). On the basis of this evidence, we consider that our estimates of forest structure adequately represent the habitat characteristics of the bird survey areas (transects or leks).

Statistical analysis

To test for the relationships between bird indicators and between indicators and the vegetation structure variables, we performed Generalized Linear Models (GLMs) and Generalized Linear Mixed Models (GLMMs) respectively. Type III models were run, testing each main effect after controlling for the other determinants. In GLMMs, apart from vegetation variables as fixed effects, we entered the identity of the woodlot as a random effect (more than one point-count could be associated with a woodlot within a transect), and bird plot geographic coordinates and elevation as covariates, to take into account (and control for) the potential non independence of data from areas close by. The time of day and day number (month) were originally accounted for in the analysis as covariates, in order to control for changes in bird detectability; however none of these temporal variables did affect our dependent variables, worsening model performances. A Poisson distribution of errors was used in the case of density data (cavity nesting birds) and a Binomial distribution of errors was used in the case of occurrence data

(woodpeckers, Capercaillie). We tested those models that included the variables that were biologically and ecologically relevant on the basis of literature on deciduous forest avifauna (Laiolo et al. 2004; Laiolo et al. 2011) (20 models per indicator group, listed in Appendix 3). The Akaike's Information Criterion (AIC) was used to identify the best parsimonious models to explain woodpecker occurrence, cavity nesting bird density and Capercaillie occurrence; we considered similar strength evidence those models separated by ΔAIC < 2 (Anderson 2008).

All statistical analyses were performed with the software R 1.21, with the package *lme4* (R DevelopmentCore Team 2006).

Results

Relationships between indicators

In the 47 Capercaillie survey plots, no significant association was found between the occurrence of this grouse and the abundance of cavity nesting birds or the occurrence of woodpeckers as estimated by point-counts (GLMMs, all $Z < 0.037$, $P > 0.93$). On the contrary, the occurrence of woodpeckers and the density of cavity-nesting birds were positively associated (GLM: $Z = 3.879$, $P < 0.001$, N = 185 plots).

Relationship between indicators and habitat characteristics

Cavity nesting birds occurred in almost all plots (148), with abundances of between 1 and 12 individuals. The highest elevation, northernmost and westernmost plots hosted the lowest density of cavity nesting species (GLM: elevation: $Z = -4.89$, $P < 0.001$, N =

185, latitude: $Z = 3.79$, $P < 0.001$, $N = 185$, and longitude: $Z = -2.390$, $P < 0.005$, $N = 185$). When all vegetation variables were entered however, geographic variables did not affect abundances further and models entering them had the highest AIC values (see Appendix 3). In the two best models we found a negative relationship between bird abundances and tree height variation, which suggests that cavity nesting species were more abundant in woodlots with scarce vertical heterogeneity. A positive relationship was found with tree species diversity, vertical species mingling and tree diameter variation, (Table 2, Figure 1A).

Woodpeckers were present in 27 plots and occurred at low abundances (one or two individuals per plot). We found a positive relationship between this indicator group and the basal area of snags, suggesting that woodpeckers were more abundant in plots with abundant dead wood (Table 2, Figure 1B).

The Capercaillie was found to occur in only 14 of the 47 lek areas surveyed. This grouse was positively associated with shrub species richness and occurred in the highest elevation plots of the study forests (Table 2, Figure 1C; Appendix 3).

In summary, the three indicators exhibited clear differences in their habitat preferences (Table 3).

Discussion

We found that each indicator was associated with different forest characteristics, with snag biomass being important for woodpeckers, heterogeneity in the canopy layer for cavity nesting birds and heterogeneity in the understory for the Capercaillie. Presence and abundance of indicators were likely controlled by distinct patterns and processes within forest stands and, as a consequence, these species were not always spatially

associated between themselves, making all of them necessary to determine the complexity of processes occurring in forest habitats. Indeed, the density of cavity nesting birds was positively associated with the occurrence of woodpeckers, suggesting that common structural elements attract both groups of indicators. Large mature trees with decaying portions present both crevices that shelter a diverse insect fauna and large canopy surfaces, thus benefitting both insectivorous birds that feed on foliage and those that feed on stems (Fan et al. 2003; Laiolo et al. 2004). Heterogeneity in forest structure or composition favored both the Capercaillie and cavity nesting birds, although, due to their trophic requirements and habits, the former occurred in stands in which the diversity of the shrub layer peaked and the latter where the diversity of the canopy layer (tree species diversity, vertical species mingling and diameter variability) was the highest (Laiolo 2002; Laiolo et al. 2004; Bañuelos et al. 2008).

Habitat associations of cavity nesting birds

The density of cavity nesting birds was influenced by canopy height structure and tree species diversity, peaking in stands with the highest tree species composition and vertical species mingling. These parameters, which reflect gap-dynamic processes in mature undisturbed forests (Kohyama 1993), are positively associated with resource availability for birds (Sabo and Holmes 1983), and are good indicators of the diversity and stability of interactions in a forest ecosystem (Levey 1988; Laiolo and Rolando 2005). The density of cavity nesting species also increased in plots with large trees, which were heterogeneous in size, a characteristic that allows the coexistence of a more diverse and abundant assemblage of foliage, twig, and stem bird feeders (Laiolo 2004). This diversity turns out to be important for the maintenance of the forest itself, since

these birds improve forest resilience in the face of severe disturbance events and they also control insect outbreaks (Martin and Eadie 1999; Mols and Visser 2002), thus they help retain the integrity of trophic processes and indirectly defend canopy trees from insect damage (Van Bael et al. 2003).

Habitat associations of woodpeckers

The association between woodpeckers and the basal area of snags can be explained by selection for nesting and as rich foraging habitats, since the abundance of crevices and large xilophagous insects increases in old-growth stands with dead trees, especially when these trees are large (Tyrrell and Crow 1994; Hagan et al. 1997). In our study area, the basal area of snags was more important than their number (woodpeckers occurred when snag basal area > 0.2 m^2 ha^{-1}), and a similar relationship has been observed in woodpeckers from other montane forests of Europe (Bütler et al. 2004). This critical dead wood threshold could become a practical management target, to preserve the various ecological functions provided by this group of species. Woodpeckers, by removing the bark of dead or partially dead wood when foraging, expose the underlying substrate, and its hidden arthropod communities, to other insectivorous animals that benefit from this behavior (Bull and Jackson 1995). Moreover, they accelerate the process of wood decomposition and nutrient redistribution by exposing trees to the action of wood-decomposing organisms, as well as contributing to the dispersal of fungi that participate in the process of decay (Farris et al. 2004). This ecosystem service contributes/adds to the other important role of woodpeckers, that of providing nesting habitats for cavity nesting species (birds, mammals, amphibians, reptiles and insects; Thomas et al. 1979; Welsh 1990), which is

often constrained by hole availability more than by food (Newton 1994; Martin and Eadie 1999; Sánchez et al. 2007). *Dryocopus martius* digs large cavities suitable for nocturnal raptors (Sonerud 1985; Johnsson et al. 1993), while *Dendrocopos major* provides small-medium size cavities for passerines (Martin et al. 2004), thus both species may exert a strong control on the density of secondary cavity nesting species (Martin and Eadie 1999; Camprodon et al. 2008), as also highlighted by the positive association between these indicators found in this study.

Habitat associations of the Capercaillie

The wide home ranges and large scale habitat requirements, together with the pronounced decline in recent decades, likely override the importance of local vegetation structure in determining the actual distribution of the Capercaillie in the Cantabrian Mountains (Obeso and Bañuelos 2003; Quevedo et al. 2006a; Laiolo et al. 2011). In this study, the only vegetation variable that was associated with Capercaillie occurrence was the diversity of the shrub belt. The growth of a complex understory is facilitated by irregularities in the canopy that permit light to reach the lower belt, which is often shaded by a dense canopy in young or managed beech woods but may be exposed in undisturbed, old beech stands (Laiolo et al. 2004). Shrubs in lek areas likely provide shelter or foraging habitat for the Capercaillie, which feeds on bilberry leaves and fruits (Storch 1995; Blanco-Fontao et al. 2012). The preference of this grouse for upland forests may be related either to the overall higher availability of less-disturbed forest at higher elevations (García et al. 2005), or to an increase in bilberry quality, an important food source, with elevation (Obeso and Fernández-Calvo 2002).

Although a flagship species needs to be popular, not necessarily ecologically significant (Caro and O'Doherti 1999), it must be acknowledged that large areas of the study montane forests have been protected in the last decades thanks to the threatened Cantabrian Capercaillie (García et al. 2005). The occurrence of this grouse has therefore served to conserve the habitat of less charismatic taxa and reasonably preserve forest structure from major anthropogenic disturbance, all factors that in the long run may promote the maintenance (or natural evolution) of forest ecological functions.

Conclusions

We found close relationships between bird indicators and the characteristics of the forest stands where they live, but each indicator was associated with different patterns and processes within forest stands. Although single bird indicators fail to provide a complete assessment of forest status, we believe that they may still provide insight into whether specific ecological processes are increasing or decreasing in extent. For instance, gap-dynamics may be tracked by monitoring cavity nesting birds and the Capercaillie, since they likely create suitable habitats for both indicators, although through different mechanisms (via an effect on tree composition and structure in the former, and on shrub species richness in the latter). The state and level of natural wood decay processes may determine woodpecker presence (via the amount of dead wood) and, indirectly, that of cavity nesting birds (via the influence of woodpeckers in providing new foraging or nesting substrates in decaying wood).

Therefore, although monitoring forest dynamics and modification may require a wide range of taxa to be studied (Carignan and Villard 2002), this study shows that the bird taxon includes assemblages that can be surveyed within the same survey framework

with relatively limited effort (Laiolo et al. 2011), and which possess life histories divergent enough to display a wide range of sensitivities to the modification of natural processes within forest habitats.

Acknowledgements

References

Andelman SJ, Fagan WF (2000) Umbrellas and flagships: efficient conservation surrogates or expensive mistakes? Proc Natl Acad Sci 97: 5954-5959.

Anderson DR (2008) Model Based Inference in the Life Sciences: a Primer on Evidence. Springer, New York.

Attiwill PM (1994) The disturbance of forest ecosystems - the ecological basis for conservative management. For Ecol Manage 63: 247-300.

Bani L, Massimino D, Bottoni L, Massa R (2006) A multiscale method for selecting indicator species and priority conservation areas: A case study for broadleaved forests in Lombardy, Italy. Conserv Biol 20: 512-526.

Bibby CJ, Burgess ND, Hill D A (2000) Bird Census Techniques. Elsevier Academic Press, London.

Bañuelos MJ, Quevedo M, Obeso JR (2008) Habitat partitioning in endangered Cantabrian capercaillie *Tetrao urogallus cantabricus*. J Ornithol 149: 245-252.

Blanco-Fontao B, Quevedo M, Obeso J R (2011) Abandonment of traditional uses in mountain areas: typological thinking versus hard data in the Cantabrian Mountains (NW Spain). Biodivers Conserv 20: 1133-1140.

Blanco-Fontao B, Obeso JR, Bañuelos MJ, Quevedo M (2012) Habitat partitioning and molting site fidelity in *Tetrao urogallus cantabricus* revealed through stable isotopes analysis. J Ornithol 153 : 555-562.

Blondel J, Ferry C, Frochot B (1970) La méthode des indices ponctuels (I.P.A.) ou des relevés d'avifaune par « station d'écoute ». Alauda 38: 55-71.

Bowles IA, Rice RE, Mittermeier RA, da Fonseca GAB (1998) Logging and Tropical Forest Conservation. Science 280: 1899-1900.

Brawn JD, Robinson SK, Thompson FR (2001) The role of disturbance in the ecology and conservation of birds. Ann Rev Ecol Sys 32: 251-276.

Bull EL, Jackson JE (1995) Pileated Woodpecker (*Dryocopus pileatus*). In: Poole A, Gill F (eds) The Birds of North America. The Academy of Natural Sciences, nº 148, The American Ornithologists' Union, Washington, D.C.

Bütler R, Angelstam P, Ekelund P, Schlaepfer R (2004) Dead wood threshold values for the three-toed woodpecker presence in boreal and sub-Alpine forest. Biol Conserv 119: 305-318.

Camprodon J, Salvanya J, Soler-Zurita J (2008) The abundance and suitability of tree cavities and their impact on hole-nesting bird populations in beech forests of NE Iberian Peninsula. Acta Ornithologica 43: 17-31.

Caprio E, Ellena I, Rolando A (2008) Assessing habitat/landscape predictors of bird diversity in managed deciduous forests: a seasonal and guild-based approach. Biodivers Conserv 18: 1287-1303.

Caro TM, O'Doherti G (1999) On the use of surrogate species in conservation biology. Cons Biol 13: 805-814.

Caro T (2010) Conservation by Proxy: Indicator, Umbrella, Keystone, Flagship, and Other Surrogate Species. Island Press, Washington.

Carrascal LM, Cayuela L, Palomino D, Seoane J (2012) What species-specific traits make a bird a better surrogate of native species richness? A test with insular avifauna. Biol Conserv 152: 204-211.

Carignan V, Villard MA (2002) Selecting indicator species to monitor ecological integrity: a review. Environ Monit Assess 78: 45–61.

Castaño-Santamaría J, Crecente-Campo F, Fernández-Martínez JL, Barrio-Anta M, Obeso JR (2013) Tree height prediction approaches for uneven-aged beech forests in northwestern Spain. For Ecol Manage 307: 63-73.

Castedo-Dorado F, Creciente-Campo F, Álvarez-Álvarez P, Barrio-Anta M (2009) Development of a stand density management diagram for radiata pine stands including assessment of stand stability. Forestry 82: 1-16.

Dhôte J (2005) Implication of forest diversity in resistance to strong winds. In: Scherer-Lorenzen M, Körner C (eds) Forest Diversity and Function: Temperate and Boreal Systems. Springer-Verlag, Berlin. pp. 291-307.

Drever MC, Aitken K, Norris AR, Martin K (2008) Woodpeckers as reliable indicators of bird richness, forest health and harvest. Biol Conserv 141: 624 –634.

Drever MC, Marin K (2010) Response of woodpeckers to changes in forest health and harvest: Implications for conservation of avian biodiversity. For Ecol Manage 259: 958–966.

Fan ZF, Shifley SR, Spetich MA, Thompson FR, Larsen DR (2003) Distribution of cavity trees in midwestern old-growth and second- growth forests. Can J For Res 33: 1481-1494.

Farris KL, Huss MJ, Zack S (2004) The role of foraging woodpeckers in the decomposition of ponderosa pine snags. Condor 106: 50–59.

Gadow KV, Zhang CY, Wehenkel C, Pommerening A, Corral-Rivas J, Korol M, Myklush S, Hui GY, Kiviste A, Zhao XH (2011) Forest Structure and Diversity. In: Pukkala T, Gadow KV (eds) Continuous Cover Forestry. Springer-Verlag, Berlin, pp. 29-83.

García D, Quevedo M, Obeso J, Abajo A (2005) Fragmentation patterns and protection of montane forest in the Cantabrian range (NW Spain). For Ecol Manage 208: 29-43.

Genovart M, Tavecchia G, Enseñat JJ, Laiolo P (2013) Holding up a mirror to the society: Children recognize exotic species much more than local ones. Biol Conserv 159: 484-489.

Hagan JM, McKinley PS, Meehan AL, Grove SL (1997) Diversity and abundance of landbirds in a northeastern industrial forest. J Wildl Manage 61: 718-735.

Jactel H, Brockerhoff EG, Duelli P (2005) A test of the biodiversity-stability theory: meta-analysis of tree species diversity effects on insect pest infestations, and re-examination of responsible factors. In: Scherer-Lorenzen M, Körner C (eds)

Forest Diversity and Function: Temperate and Boreal Systems. Springer-Verlag, Berlin, pp. 235–262.

Järvinen O, Lokki J (1978) Indices of community structure in bird censuses based on single visit: effects of variation in species efficiency. Ornis Scand 9: 87–93.

Johnsson K, Nilsson SG, Tjernberg M (1993) Characteristics and utilization of old black woodpecker *Dryocopus martius* holes by hole-nesting species. Ibis 135: 410–416.

Kohyama T (1993) Size-structured tree populations in gap-dynamic forest--the forest architecture hypothesis for the stable coexistence of species. J Ecol 81: 131-143.

Laiolo P (2002) Effects of habitat structure, floral composition and diversity on a forest bird community in north-western Italy. Folia Zool 51: 121–128.

Laiolo P (2004) Diversity and structure of the bird community overwintering in the Himalayan subalpine zone: is conservation compatible with tourism? Biol Conserv 115: 251-262.

Laiolo P, Caprio E, Rolando A (2004) Can forest management have season-dependent effects on bird diversity? Biodivers Conserv 13: 1925-1941.

Laiolo P, Rolando A (2005) Forest bird diversity and skislopes: a case of negative edge effect. Anim Conserv 7: 9-16.

Laiolo P, Bañuelos MJ, Blanco-Fontao B, García M, Gutiérrez G (2011) Mechanisms Underlying the Bioindicator Notion: Spatial Association between Individual Sexual Performance and Community Diversity. PLoS ONE 6: e22724.

Landres PB, Verner J, Thomas W (1988) Ecological use of vertebrate indicator species: a critique. Conserv Biol 2: 316-328.

Laurance WF, Nascimento HEM, Laurance SG, Andrade A, Ribeiro JELS (2006) Rapid decay of tree-community composition in Amazonian forest fragments. Proc Natl Acad Sci USA 103: 19010–19014.

Lawton JH, Bignell DE, Bolton B, Bloemers GF, Eggleton P, Hammond PM, Hodda M, Holt RD, Larsen TB, Mawdsley NA, Stork NE, Srivastava DS, Watt AD (1998) Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forest. Nature 391: 72-76.

Levey DJ (1988) Tropical Wet Forest Treefall Gaps and Distributions of Understory Birds and Plants. Ecology 69: 1076-1089.

Martin K, Eadie JM (1999) Nest webs: a community-wide approach to the management and conservation of cavity-nesting forest birds. For Ecol Manage 115: 243-257.

Martin K, Aitken KEH, Wiebe KL (2004) Nest sites and nest webs for cavity-nesting communities in interior british Columbia, Canada: nest characteristics and niche partitioning. The Condor 106: 5–19.

Martínez AM (1993) Contribución al conocimiento de la eco-etología del urogallo cantábrico. PhD Thesis, León University. 398 p.

Mikusiński G, Gromadzki M, Chylarecki P (2001) Woodpeckers as Indicators of Forest Bird Diversity. Conserv Biol 15: 208–217.

Mols CMM, Visser ME (2002) Great tits can reduce caterpillar damage in apple orchards. J Appl Ecol 39: 888–899.

Moning C, Muller J (2008) Environmental key factors and their thresholds for the avifauna of temperate montane forests. For Ecol Manage 256: 1198-1208.

Motz K, Sterba H, Pommerening A (2010) Sampling measures of tree diversity. For Ecol Manage 260: 1985-1996.

Nair KSS (2007) Tropical forest insect pests: ecology, impact and management. Cambridge University Press, Cambridge.

Newton I (1994) The role of nest sites in limiting the numbers of hole-nesting birds—a review. Biol Conserv 70: 265–276.

Noss RF (1999) Assessing and monitoring forest biodiversity: a suggested framework and indicators. For Ecol Manage 115: 135–146.

Obeso JR, Fernández-Calvo IC (2002) Fruit removal, pyrene dispersal, post-dispersal predation and seedling establishment of a bird-dispersed tree. Plant Ecol 16: 223-233.

Obeso JR, Bañuelos MJ (2003) El urogallo (*Tetrao urogallus cantabricus*) en la Cordillera Cantábrica. Parques Nacionales, Ministerio de Medio Ambiente, Madrid.

Oxbrough A, French V, Irwin S, Kelly TC, Smiddy P, O'Halloran J (2012) Can mixed species stands enhance arthropod diversity in plantation forests? For Ecol Manage 270: 11-18.

Pakkala T, Pellikka JT, Lindén H (2003) Capercaillie *Tetrao urogallus* – a good candidate for an umbrella species in taiga forests. Wildl Biol 9: 309–316.

Pautasso M, Holdenrieder O, Stenlid J (2005) Susceptibility to fungal pathogens of forests differing in tree diversity. In: Scherer-Lorenzen M, Körner C (eds) Forest Diversity and Function: Temperate and Boreal Systems. Springer-Verlag, Berlin, pp. 263–289.

Pearson LD (1995) Selecting indicator taxa for the quantitative assessment of biodiversity. In: JL Harper, DL Hawksworth (eds.). Biodiversity-Measurement and estimation. Chapman and Hall, London, pp. 75-80.

Petty SJ, Avery MI (1990) Forest Bird Communities. Occasional Papers 26. Forestry Commission, Edinburgh.

Pommerening A (2002) Approaches to quantifying forest structures. Forestry 75 (3): 305-324.

Pommerening A, Stoyan D (2006) Edge-correction needs in estimating indices of spatial forest structure. Can J For Res 36: 1723-1739.

Pretzsch H (2009) Forest dynamics, growth and yield. Springer-verlag Berlin-Heidelberg. Milton-Keynes.

Quevedo M, Bañuelos MJ, Obeso JR (2006a). The decline of cantabrian capercaillie: How much does habitat configuration matter? Biol Conserv 127: 190-200.

Quevedo M, Bañuelos MJ, Sáez O, Obeso JR (2006b) Habitat selection by cantabrian capercaillie Tetrao urogallus cantabricus at the edge of the species distribution. Wildl Biol 12: 269-278.

Ranius T, Fahrig L (2006) Targets for maintenance of dead wood for biodiversity conservation based on extinction thresholds. Scand J For Res 21: 201-208.

Remm J, Lohmus A (2011) Tree cavities in forests – The broad distribution pattern of a keystone structure for biodiversity. For Ecol Manage 262: 579-585.

Robles H, Ciudad C, Vera R, Olea PP, Purroy FJ, Matthysen E (2007) Sylvopastoral management and conservation of the middle spotted woodpecker at the South western edge of its distribution range. For Ecol Manage 242: 343-352.

Rolstad J, Rolstad E, Stokke PK (1995) Feeding habitat and nest-site selection of breeding Great Spotted Woodpeckers *Dendrocopos major*. Ornis Fenn 72: 62-71.

Sabo SR, Holmes RT (1983) Foraging niches and the structure of forest bird communities in contrasting montane habitats. Condor 85: 121-138.

Sánchez S, Cuervo JJ, Moreno E (2007) Suitable cavities as a scarce resource for both cavity and non-cavity nesting birds in managed temperate forests. A case study in the Iberian Peninsula. Ardeola 54: 261-274.

Sekercioglu CH (2006) Increasing awareness of avian ecological function. Trends Ecol Evol 21: 464–471.

Shiu H, Lee P (2003) Assessing avian point-count duration and sample size using species accumulation functions. Zool Stud 42: 357-367.

Schröter D, Cramer W, Leemans R, Prentice I C, Araújo, MB, Arnell NW,   Bondeau A, Bugmann H, Carter TR, Gracia CA, de la Vega-Leinert AC, Erhard M, Ewert F, Glendining M, House JI, Kankaanpää S, Klein RJT, Lavorel S, Lindner M, Metzger MJ, Meyer J, Mitchell TD, Reginster I, Rounsevell M, Sabaté S, Sitch S, Smith B, Smith J, Smith P, Sykes MT, Thonicke K, Thuiller W, Tuck G, Zaehle S, Zierl B (2005) Ecosystem service supply and vulnerability to global change in Europe. Science 310: 1333-1337.

Sonerud GA (1985) Nest hole shift in Tengmalm's owl *Aegolius funereus* as defence against nest predation involving long-term memory in the predator. J Anim Ecol 54: 179-192.

Storch I (1995) Annual home ranges and spacing patterns of capercaillie in central Europe. J Wildl Manage 59: 392-400.

Suter W, Graf RF, Hess R (2002) Capercaillie (*Tetrao urogallus*) and avian biodiversity: testing the umbrella-species concept. Conserv Biol 16: 778–788.

Swenson JE, Angelstam P (1993) Habitat separation by sympatric forest grouse in Fennoscandia in relation to boreal forest succession. Can J Zool 71: 1303-1310.

Thomas JW, Anderson RG, Maser C, Bull EL (1979) Snags. In Thomas JW (ed) Wildlife habitats in managed forests: the Blue Mountains of Oregon and Washington. Agriculture Handbook No 553. Portland, OR; US Department of Agriculture, pp. 60–77.

Tremblay JA, Bélanger L, Desponts M, Brunet G (2007) La restauration passive des sapinières mixtes de seconde venue: une alternative pour la conservation des sapinières mixtes anciennes. Can J For Res 37: 825-839.

Tyrrell LE, Crow TR (1994) Dynamics of dead wood in old-growth hemlock hardwood forests of northern Wisconsin and northern Michigan. Can J For Res 24: 1672-1683.

Van Bael SA, Brawn JD, Robinson SK (2003) Birds defend trees from herbivores in a Neotropical forest canopy. Proc Natl Acad Sci 100: 8304–8307.

Veríssimo D, Fraser I, Groombridge J, Bristol R, MacMillan DC (2009) Birds as tourism flagship species: a case study of tropical Islands. Anim Conserv 12: 549-558.

Virkkala R, Rajasärkka A, Väisänen RA, Vickholm M, Virolainen E (1994) Conservation value of nature reserves: Do hole-nestingbirds prefer protected forests in southern Finland? Ann Zool Fenn 31: 173-186.

Vitousek PM (1984) Litterfall, Nutrient Cycling, and Nutrient Limitation in Tropical Forests. Ecology 65: 285–298.

Waring RH, Schlesinger WH (1985) Forest ecosystems. Concepts and management. Academic Press, Orlando.

Welsh HH (1990) Relictual amphibians and old-growth forests. Conserv Biol 4: 309-319.

Wirth C (2005) Fire regime and tree diversity in boreal forests: implications for the carbon cycle. In: Scherer-Lorenzen M, Körner C (eds) Forest Diversity and Function: Temperate and Boreal Systems. Springer-Verlag, Berlin, pp. 309-344.

Tables

Table 1. List of the bird indicators considered in this study, the species comprising them and their relevance in forest conservation and ecology.

Indicators	Species	Significance
Cavity nesting birds	*Sitta europea* *Certhia barchydactyla* *Certhia familiaris* *Cyanistes caeruleus* *Parus major* *Poecile palustris* *Lophophanes cristatus* *Periparus ater*	Resource-limited species (Noss, 1999) Diversity indicator (Laiolo, 2002; Moning and Muller, 2008; Virkkala et al., 1994)
Woodpeckers	*Dendrocopos major* *Picus viridis* *Dryocopus martius*	Keystone species providing holes for cavity nesting species (Drever et al., 2008, 2010; Jonsson, 1993; Mikusiński et al., 2001)
Capercaillie	*Tetrao urogallus*	Flagship species (Obeso and Bañuelos, 2003) Umbrella species (Laiolo et al., 2011; Pakkala et al., 2003; Suter et al., 2002)

Table 2. Results of generalized linear mixed models explaining variation in cavity nesting bird density, woodpecker occurrence and Capercaillie occurrence. The best models (i.e. those with the lowest AIC, Akaike Information Criterion) are shown. See Appendix 3 for the full list of models tested. D = Tree species diversity; S = Shrub species richness; D_v = Vertical species mingling; CV_{dbh} = Tree diameter variation; CV_h = Tree height variation, BA_d = Standing dead wood; R = Regularity.

	Model 1	AIC = 169	
	Predictors	Estimate	SE
	D	1.242	0.350
	D_v	2.550	0.926
	CV_{dbh}	1.517	0.487
Cavity nesting birds	CV_h	-1.766	0.447
	Model 2	AIC = 170.7	
	Predictors	Estimate	SE
	D	1.207	0.353
	D_v	2.497	0.926
	CV_{dbh}	1.506	0.487
	CV_h	-1.705	0.457
	R	0.102	0.172
	Model 1	AIC = 152.4	
	Predictors	Estimate	SE
	BA_d	1.003	0.544
	Model 2	AIC = 153.3	
	Predictors	Estimate	SE
Woodpeckers	BA_d	1.026	0.532
	R	0.959	0.91
	Model 3	AIC = 153.4	
	Predictors	Estimate	SE
	BA_d	1.113	0.561
	D_v	3.963	4.060
	Model 4	AIC = 153.9	
	Predictors	Estimate	SE
	CV_h	-2.367	1.876
Capercaillie	Model 1	AIC = 48.02	
	Predictors	Estimate	SE

S	0.530	0.240
Elevation	0.013	0.004
Model 2	**AIC = 49.46**	
Predictors	**Estimate**	**SE**
S	0.535	0.251
D_v	-6.905	9.467

Table 3. Summary of forest structural and spatial variables affecting each indicator. + positive association; - negative association; D = Tree species diversity; S = Shrub species richness; D_v = Vertical species mingling; CV_{dbh} = Tree diameter variation; CV_h = Tree height variation, BA_d = Standing dead wood.

Cavity nesting birds		Woodpeckers		Capercaillie	
D	(+)	BA_d	(+)	Elevation	(+)
D_v	(+)			S	(+)
CV_{dbh}	(+)				
CV_h	(-)				

Figure captions

Figure 1. Cavity nesting birds were more abundant in plots with high vertical species mingling (a), woodpeckers were more common in plots with large amounts of standing dead trees (b), and Capercaillie preferred plots with a complex shrub layer (c). Mean values and standard errors are shown for woodpeckers and Capercaillie data.

Figures

Figure 1

(a)

Density of cavity nesting birds

Vertical species mingling

(b)

Standing dead trees (m^2 ha^{-1})

Plots without Woodpeckers   Plots with Woodpeckers

(c)

Shrub species richness

Plots without Capercaillie   Plots with Capercaillie
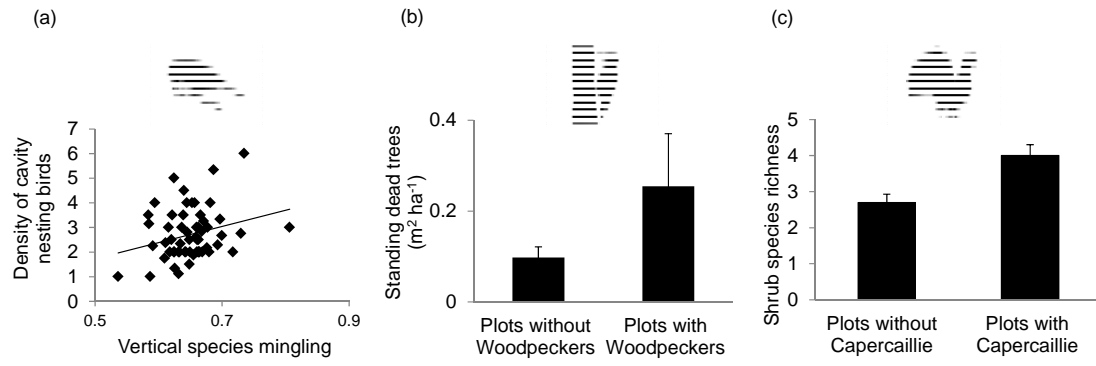
Appendices

Appendix 1. Distribution of beech forests in the Cantabrian Mountains in Asturias (green areas) and location of the bird study plots (red).
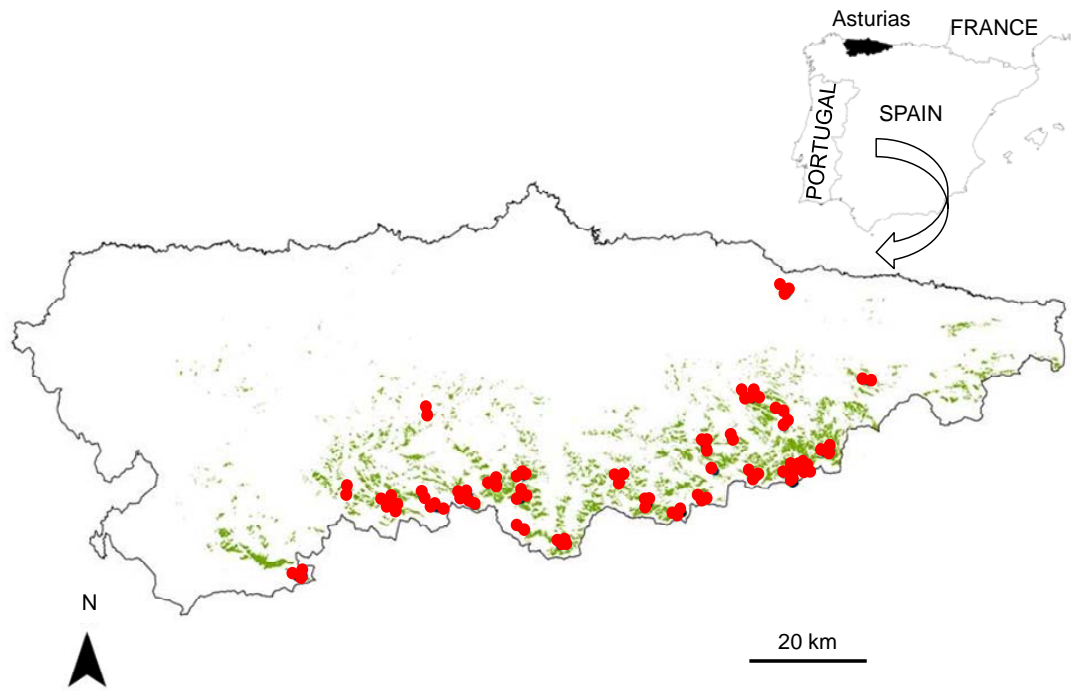
Appendix 2. List of the structural and spatial vegetation indexes used in this study, in keeping with Motz, Sterba and Pommerening (2010), Pretzsch (1996) (for D_v) and Weber (2000) (for D_{st}).

Index	Variable definition	
Aggregation index (R) *Regularity*		
$R = \dfrac{\bar{r}_{observed}}{E(r)}$	$\bar{r}_{observed}$	Arithmetic mean of distances between a reference tree in the woodlot and its four nearest neighbors.
	$E(r) = 0.5\sqrt{\dfrac{A}{N}}$	N: number of trees in the woodlot; A: woodlot area
Simpson vertical index (D_v) *Vertical species mingling*		
$D_v = 1 - \displaystyle\sum_{i=1}^{s}\sum_{j=1}^{z} p_{ij}^{\,2}$	p_{ij}	Relative frequency of species i in height stratum j referring to the overall stem number in the woodlot [three strata were considered: 0-50%, 50-80% and 80-100% canopy height (Pretzsch, 1996)]
Simpson stratified index (D_{st}) *Horizontal species mingling*		
	p_i	Relative frequency of stratum i referring to the overall stem number in the woodlot.
$D_{st} = 1 - \displaystyle\sum_{i=1}^{n}\left(\dfrac{h \cdot p_i}{n \cdot h_i}\right)^2$	$\left(\dfrac{h}{n \cdot h_i}\right)$	hi = height of tree i ; h = maximum height of the woodlot. A weighting factor was used to correct for differences between the intervals used.
Simpson species richness (D)		
$D = 1 - \displaystyle\sum_{i=1}^{s} p_i^{\,2}$	p_i	Relative frequency of species i in the forest referring to stem number in the woodlot.
Coefficient of variation of tree diameters at breast height (1.3 m above the ground); (V_{dbh})		

	SDD	Standard deviation of four tree diameters measured at breast height
$CV_{dbh} = \dfrac{SDD}{D_m}$		
	D_m	Mean diameters of 32-81 trees measured at breast height.

Coefficient of variation of tree height (CV$_h$)		
	SDH	Standard deviation of four tree heights.
$CV_h = \dfrac{SDH}{H_m}$		
	H_m	Mean height of 32-81 trees.

Standing dead wood (BA$_d$)		
$BA_d = \dfrac{\pi}{4}\sum_{i=1}^{n} d_i^{\,2}$	d_i	Diameter at breast height of standing dead tree *i*.

Cited References

Motz, K., Sterba, H. and Pommerening, A. 2010. Sampling measures of tree diversity. For Ecol Manage 260: 1985-1996.

Pretzsch, H. 1996. Strukturvielfalt als Ergebnis waldbaulichen Handelns. Allg. Forst. -u. J. –Ztg., 167: 213-221.

Weber, 2000. Geostatistiche Analyse der Structur von Waldbestonden am Beispiel augerwahlter Banwalder in Baden-Wurttemberg. Berichte Freiburger Forstliche Forschung Heft 20. FVA Baden-Wurttemberg. Freiburg.133

Appendix 3. List of the 20 models tested per indicator group and their AIC (Akaike Information Criterion) values. The best models (separated by less than 2 AIC points) are highlighted in bold. R = Regularity; D = Tree species diversity; S = Shrub species richness; D_v = Vertical species mingling; D_{st} = Horizontal species mingling; CV_{dbh} = Tree diameter variation; CV_h = Tree height variation, BA_d = Standing dead wood.

Cavity nesting birds	**AIC**
D + D_v + CV_h+ CV_{dbh}	**169**
R + D + D_v + CV_h+ CV_{dbh}	**170.7**
R + D + D_v + CV_h + CV_{dbh} + BA_d	172.4
R + D + D_v+ D_{st} + CV_h+ CV_{dbh}	172.6
R + D + D_v + CV_h+ CV_{dbh} + S+ BA_d	174
R + D+ D_v + D_{st} + CV_h+ CV_{dbh} + S + BA_d	176
CV_h	182.3
Elevation + Slope + Orientation	180.5
D_{st}	181.9
BA_d	184.7
R	186.7
D	187.6
D_v	187.8
S	189.5
CV_{dbh}	189.7
CV_h + Elevation + Longitude	232.5
CV_h + Elevation + Longitude + Latitude	232.4
CV_h + CV_{dbh} + Elevation + Longitude + Latitude	232.1
D_v + CV_{dbh} + CV_h + Elevation + Longitude + Latitude	231.7
D + D_v + CV_{dbh} + CV_h + Elevation + Longitude + Latitude	229.6
D + D_v + CV_{dbh} + CV_h + S + Elevation + Longitude + Latitude	229.5
D + D_v + D_{st} + CV_{dbh} + CV_h + S + Elevation + Longitude + Latitude	231.5
D + D_v + D_{st} + CV_{dbh} + CV_h + S + BA_d + Elevation + Longitude + Latitude	232.4
R + D + D_v + D_{st} + CV_{dbh} + CV_h + S + BA_d + Elevation + Longitude + Latitude	234.3
R + D + D_v + D_{st} + CV_{dbh} + CV_h + S + BA_d + Elevation + slope + Orientation + Longitude + Latitude	238.5
Elevation + Slope + Orientation + Longitude + Latitude	240.3
Longitude + Latitude	246.6

Woodpeckers	**AIC**
BA_d	**152.4**
R + BA_d	**153.3**
D_v+ BA_d	**153.4**
CV_h	**153.9**
R + CV_{dbh}+ BA_d	154.5
R	154.6
D_{st}	154.8
R + D_{st}+ CV_{dbh} + BA_d	156.1

$R + D + D_{st} + CV_{dbh} + BA_d$	157.2
D_v	155
CV_{dbh}	155.3
D	155.3
S	155.5
Longitude + Latitude	157.4
Elevation + Slope + Orientation	158.7
$R + D + D_{st} + CV_{dbh} + S + BA_d$	158.9
$R + D + D_{st} + CV_{dbh} + S + BA_d$	158.9
$R + D + D_v + D_{st} + CV_{dbh} + S + BA_d$	160.5
$R + D + D_{st} + CV_{dbh} + S + BA_d + Elevation$	160.8
$R + D + D_v + D_{st} + CV_h + CV_{dbh} + S + BA_d$	162.2
Elevation + Slope + Orientation + Longitude + Latitude	162.4
$R + D + D_v + D_{st} + CV_{dbh} + S + BA_d + Elevation$	162.5
$R + D + D_v + D_{st} + CV_{dbh} + S + BA_d + Elevation + Longitude$	164.5
$R + D + D_v + D_{st} + CV_{dbh} + S + BA_d + Elevation + Longitude + Latitude$	166.1
$R + D + D_v + D_{st} + CV_{dbh} + CV_h + S + BA_d + Elevation + Longitude + Latitude$	168
$R + D + D_v + D_{st} + CV_{dbh} + CV_h + S + BA_d + Elevation + Slope + Orientation + Longitude + Latitude$	171.9

Capercaillie	**AIC**
S + Elevation	**48**
D_v + S + Elevation	**49.4**
$D + D_v + Dst + S + Elevation$	**50.3**
$D_v + D_{st} + S + Elevation$	51.3
$D + D_v + D_{st} + S + BA_d + Elevation$	51.8
Elevation	52.1
$D + D_v + D_{st} + CV_h + S + BA_d + Elevation$	52.1
$D + D_v + D_{st} + CV_{dbh} + CV_h + S + BA_d + Elevation$	52.2
$R + D + D_v + D_{st} + CV_{dbh} + CV_h + S + BA_d + Elevation$	52.5
Elevation + Slope + Orientation	54.1
$R + D + D_v + D_{st} + CV_{dbh} + CV_h + S + BA_d + Elevation + Longitude$	54.9
$R + D + D_v + D_{st} + CV_{dbh} + CV_h + S + BA_d + Elevation + Longitude + Latitude$	56.3
$R + D + D_v + D_{st} + CV_{dbh} + CV_h + S + BA_d + Elevation + Longitude + Latitude + Slope + Orientation$	58.3
S	59.7
$R + D + D_v + D_{st} + CV_{dbh} + CV_h + S + BA_d$	59.7
D_v	60.4
D_{st}	60.9
CV_h	61.4
Longitude + Latitude	61.5
BA_d	62.2
CV_{dbh}	62.4
R	62.4
D	62.4

Appendix 4. Relationships between the diversity of cavity nesting birds and tree species diversity (D), tree height variation (CV_h) and tree diameter variation ($CV_{dbh)}$) in woodlots.