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Abundance, species richness and diversity of forest bird assemblages – The relative importance of habitat structures and landscape context

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ABSTRACT

The variability in the amount and configuration of broad habitat types in the landscape, together with their structural complexity, influence observed biodiversity patterns. When considering structurally similar sites of the same habitat type, the variability in the abundance, species richness or diversity of organisms may be explained by the landscape context. To assess the numerical response of species to the landscape context, in terms of amount and configuration of forest environments, we investigated the bird assemblages of similarly structured forest habitats in an extensively managed forest region, encompassing different landscape contexts. We considered the numerical response of bird assemblages, in terms of abundance, species richness and diversity, and relative abundance of specific guilds, to the landscape context. We considered the forest cover at different spatial scales as a measure of habitat amount, while we quantified aspects of habitat configuration using various landscape metrics, and measured local forest structures. We found significant responses in multiple forest bird species to three important indices of forest structures: mean diameter of living trees, mean diameter of dead trees and volume of lying deadwood. Within similarly structured forest plots, bird assemblages showed responses linked with the landscape context, while plots with different habitat structure showed similar responses to the landscape context. In particular, there was a clear positive response of birds to the amount of broadleaf and mixed forest cover in the landscape. In addition, the distance between forest patches negatively affected species richness and diversity. Within landscapes, the increase of broadleaf in the existing forest area could boost abundance and diversity, decrease isolation levels for species dependent on broadleaves and enhance structural connectivity, generally favouring the majority of the species. Our findings suggest that the simple provision of habitat structures cannot represent a viable solution for biodiversity conservation and that the use of structural indicators of biodiversity like deadwood and age of canopy trees for assessing conservation value of forest needs to be integrated with landscape-scale indices. Our analysis clearly shows that the amount of habitat available in the surrounding landscape is linked with positive biodiversity responses. As human activities can alter both the provision of important habitat structures in stands across the landscape, as well as their overall landscape context, an integrated multi-scale biodiversity management is highly advisable.

1. Introduction

Species occurrences and abundances drive the assortment of biological communities, through local habitat structures, which make a site more or less suitable for species, and by the landscape context, which makes areas where habitat types occur more or less accessible to species (Lawton, 1999). The placement, diversity and size of habitat patches in landscapes, then, are generally recognised as major drivers of biodiversity (Tscharntke et al., 2012). In human-dominated landscapes, the amount of suitable habitat types has been altered across spatial scales. Local habitat structure has been often simplified by anthropogenic processes, such as management for timber production. In European forests, this process has been extensively described (Van Der Plas et al., 2016): it often begins with the loss of ecologically valuable structures

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that provide key resources to species (e.g. Kuuluvainen, 2002, 2009; Wesolowski, 2005). Older forests are generally characterized by higher structural complexity (Storch et al., 2018) and support many specialist species (e.g. Spies et al. 2006). Similarly, unmanaged or protected forests are often characterized by old-growth attributes, including structures that need time to develop (Hedwall and Mikusiński, 2015; Paillet et al., 2015; Uotila et al., 2002). Hence, forest management that emphasizes timber production, by depleting such structures, can become one of the main drivers of the abundance and diversity of forest organisms (Balestrieri et al., 2015; Fedrowitz et al., 2014; Villard and Foppen, 2018).

The influence of the landscape context on species has been described using birds as the most data-abundant taxon in many regions of the world (Bregman et al., 2014; Gaston et al., 2003; Jetz et al., 2007). A large body of research showed, indeed, that variation in bird numbers is often associated with variation in biodiversity of other taxa, with examples including urban biodiversity (Sattler et al., 2014), agricultural areas (Eglington et al., 2012), and mountain ranges (Valerio et al., 2016) and, consequently, birds have been used as broader environmental indicators (e.g. Gregory and Strien, 2010). In forest landscapes, large variation in forest birds' responses to different levels of intensity of forest management has been observed (Gregory et al., 2007; Paillet et al., 2010; Schulze et al., 2019). The current forest landscapes of Europe, in addition to inherent variation related to site conditions, have been affected by human activities mainly linked to silviculture, creating a complex mosaic of forest patches of different sizes, successional stages, tree species composition and vertical complexity (Bengtsson et al., 2000). In this context, forest cover and fragmentation result in large differences in environmental conditions available to forest birds across landscapes (Tellería et al., 2003). Moreover, the situation is dynamic due to the ongoing interplay between land-use change and climate change (Barbet-Massin et al., 2012; Lemoine et al., 2007).

The abundance of species at a local scale in forests is largely dependent on the local forest structures (Balestrieri et al., 2015; Czeszczewik et al., 2015; Díaz et al., 2005). However, the surrounding landscape may influence the local abundance of the species, due to e.g. spill-over of individuals from neighbouring patches (Tscharntke et al., 2012). The patchiness of a specific habitat type in the landscape influences the distribution of a given species (Basile et al., 2016; Hofmeister et al., 2017), and eventually, the species diversity of a given site (Koivula et al., 2018; Roth, 1976). The landscape context can also influence the relative abundance of specialist and generalist species, altering species composition (Uezu and Metzger, 2011). The amount of habitat in the landscape may affect species composition, as species have different habitat requirements, especially in relation to habitat area (e.g. Devictor et al. 2008). Assuming that higher abundances occur in optimal habitats, depending on the life histories of individual species and their ability to colonize and persist in a given area, similar landscapes could host similar assemblages. A reduced habitat area means also an increase in edge-area ratio with potentially negative consequences – generally referred to as 'edge effects' - for habitat specialist bird populations (Andrén and Angelstam, 1988; Donovan et al., 1997). In contrast, in forested areas, open habitat, edge and early-successional species might take advantage of altered habitats, depending on their traits (Borchtchevski et al., 2003; Żmihorski et al., 2019). Henceforth, the variability in the responses to environmental conditions makes forest bird assemblages a good case to study how anthropogenic landscapes drive species abundance, richness and diversity, i.e. the numerical response to habitat structure.

In this study, we investigated the relative influence of forest structures and landscape context, in terms of amount and configuration of forest environments, in shaping the numerical response of bird assemblages, considered as a proxy for biodiversity. Considering the potential influence of the landscape context on the responses of species to forest structures, we aim at comparing the bird assemblages of similarly structured forest habitats from an extensively managed forest region, encompassing different landscape contexts. To this regard, we formulate three hypotheses regarding the numerical response of birds to forest structure in managed forest landscapes:

1. The variability in species abundances from structurally similar forests depends on the landscape context.
2. Species richness and diversity of forest birds in structurally different forests can be similar due to similar landscape context, e.g. similar forest area in the landscape.
3. Species with similar habitat requirements are found in similar landscape contexts.

By investigating these three hypotheses, in addition to scrutinizing ecological theories, we also aim at providing evidence-based advices for landscape and habitat management for bird conservation in the context of multiple-use forestry, placing the emphasis on both single species at local scale and the entire bird assemblage at landscape scale.

2. Methods

2.1. Study area

The study was carried out in the forest landscape of the Black Forest (Fig. 1), southwest Germany, in 126 one-hectare plots (Latitude: 47.6°-48.3° N, Longitude: 7.7°-8.6° E; WGS 84). Plots were delineated within the ConFoBi research program (confobi.uni-freiburg.de) according to a set of conditions aimed at reducing the confounding factors not related with the forest environment (study area and plot selection are described in details in Storch et al. 2020), following a stratified-random selection along two environmental gradients, representing the local habitat structure (number of standing dead trees per plot) and the landscape context (forest cover in the 25 km^2 surrounding the plot), respectively. The plots were located in state owned forest at elevations between 443 and 1334 m above sea level. Plots were at least 1 km apart and were comprised of temperate mixed mountain forest, dominated by Norway spruce (*Picea abies*, 42.8%), European beech (*Fagus sylvatica*, 15.3%) and silver fir (*Abies alba*, 18.5%). All plots were located in mature stands managed with single tree selection under close-to-nature forest management leading to continuous cover forest (Bauhus et al., 2013; Gustafsson et al., 2020). Due to the forest management history of the study area, conifer and mixed forests occur throughout the entire elevation range.

2.1.1. Forest variables

We described the habitat structure of each 1-ha plot, with environmental variables representing forest structures, topography and productivity (Storch et al., 2020). We collected tree species identity and diameter at breast height (DBH) of all living trees and snags (with DBH > 7 cm), while lying deadwood volume data was collected using the line intersect method (Van Wagner, 1982). Altitude, slope, aspect and terrain ruggedness index (TRI) were derived from a digital terrain model with spatial resolution of 0.5 m (State Office for Geoinformation and Land Development Baden-Württemberg, Germany). The ruggedness index represented the overall ruggedness of the canopy layer and was computed using the surface model and processed using GDALDEM 2015. The normalized difference vegetation index (NDVI), which is a proxy for net primary productivity (Rafique et al., 2016; Wang et al., 2005), was computed from a satellite image retrieved from Sentinel 2A on 23 August 2016. Vegetation cover, including the herb and shrub layer, was measured on eight 25 m^2 subplots, systematically placed in every plot. In addition, data on tree-related microhabitats (TreMs) were collected based on a detailed typology proposed by Larrieu et al. (2018). TreMs are usually grouped into seven forms, including cavities, tree injuries and exposed wood, crown deadwood, excrescences, fruiting bodies of saproxylic fungi and slime molds, epiphytic, epixylic and parasitic structures, and fresh exudates such as sap run and heavy resinosis

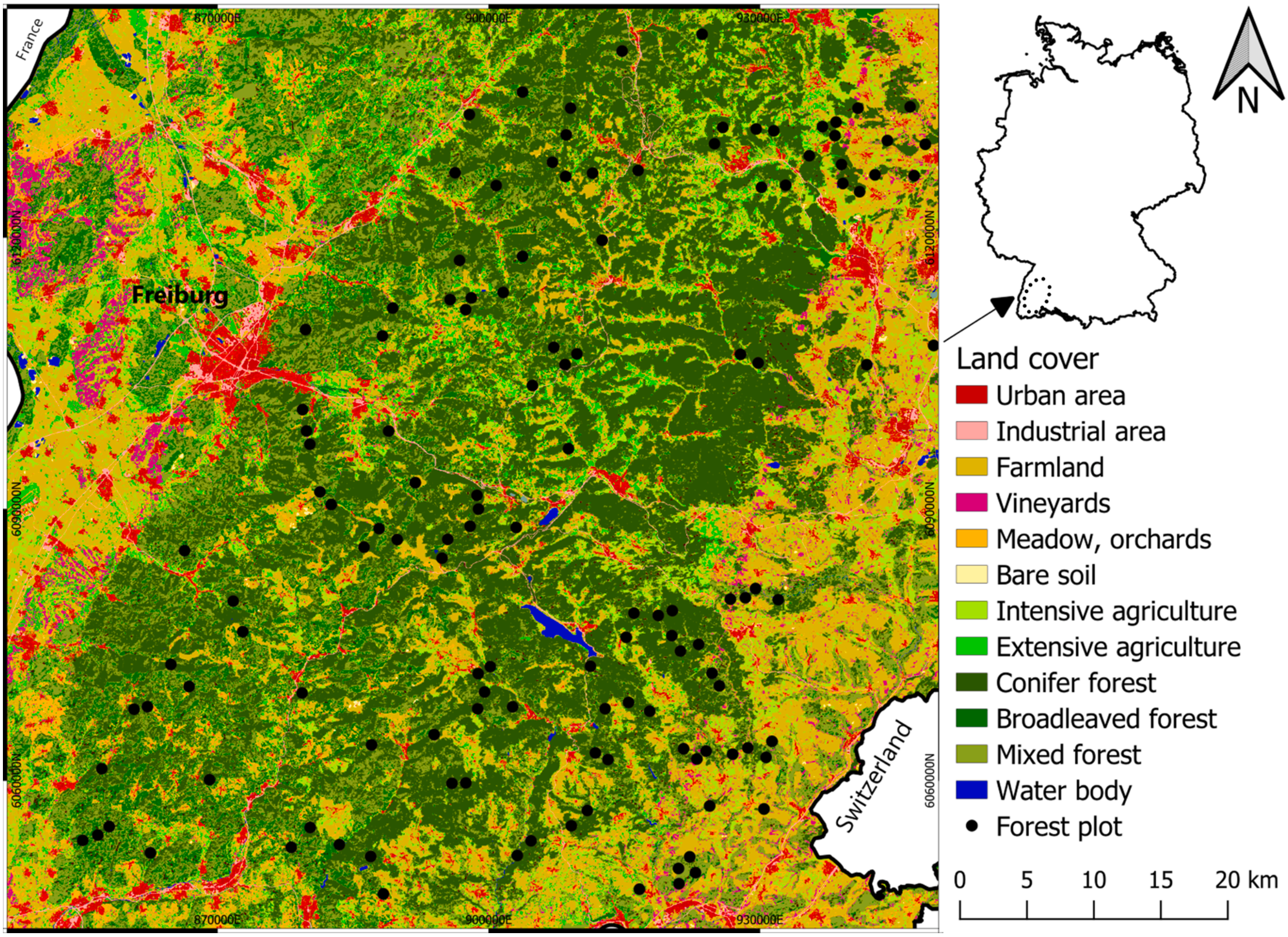

Fig. 1. Study area of the southern Black Forest, Germany, with main land cover classes and sampled 1-ha forest plots (black dots). Source: Geobasdata ©, www.lgl-bw.de, ref no: 2851.9–1/19.

(Asbeck et al., 2021). These microhabitats represent important structures for various forest organisms (Basile et al., 2020a; Paillet et al., 2018) and their abundance and richness was retrieved from previous research in the same area (Asbeck et al., 2019).

2.1.2. *Landscape variables*

To characterize the landscape context, we relied on a set of variables describing both the amount of forest habitat types and its configuration in the landscape surrounding each plot (Storch et al., 2020). The landscape-scale predictors spanned over multiple spatial scales. Forest cover was derived from the land cover map provided by the State Office for Geoinformation and Land Development Baden-Württemberg, Germany (Geobasdata ©, www.lgl-bw.de, ref no: 2851.9–1/19). Forest cover was assessed around each plot in circular buffer at five spatial scales: 5, 10, 15, 20 and 25 km^2, separately for broadleaf, mixed, conifer and total forest (including all forest types). Understanding the effects of the landscape context on biotic communities often requires adequate scaling (Thogmartin and Knutson, 2007; Wu, 2004). The multiple spatial scales in our study were chosen in order to approximate the portion of landscape where the community and meta-population processes linked to the given plot, such as spill-over or dispersal, potentially occur for forest bird species with different spatial requirements. A similar approach was used in other studies linking the landscape context with the abundance and diversity of forest birds (e.g. Mitchell et al. 2001, Morelli et al. 2013, Chiatante et al. 2019).

Landscape configuration was assessed using landscape metrics, computed with the software FRAGSTATS (McGarigal et al., 2012). By employing a square moving window and an edge depth of 100 m (Storch et al., 2005), the metrics were computed from the above-mentioned land cover map and considered only forests for the computation. We considered nine metrics in our study, selected because either evidence or experts suggest they have an effect on the numerical response of birds (Schindler et al., 2013). Also here, following the notion on the importance of appropriate scaling, the landscape metrics were computed at different spatial scales, based on empirical evidence (Schindler et al., 2013) or expert opinions and ranged from 10 ha (edge density) to 100 ha (contiguity area, core area, splitting index). The summary statistics of all environmental predictors describing the habitat structure and landscape context of each forest plot are included in supplementary material 1, table S1.

2.2. *Bird sampling protocol*

Birds were sampled by employing standardized point counts carried out from the center of each plot. Point counts were repeated up to three times/year during the period March-June 2017 and 2018, starting half an hour after sunrise with the latest ending at 12:00 CET (Balestrieri et al., 2017). Detected species were divided into those within and outside of the 50 m radius. To improve detectability and accuracy of data collection, a single count lasted 20 min, during which every bird heard or seen was recorded in both distance bands. Species were grouped, according to their habitat requirements, into common feeding and nesting guilds (Verner, 1984). We considered the nesting and feeding requirements to divide species into canopy, cavity, ground and shrub nesters, and aerial, canopy, ground and trunk feeders (table S2).

2.3. *Important forest structures*

To compare bird assemblages from similar forests in different landscape contexts, we assumed an assemblage-centred perspective to identify forest structures important for the entire assemblage. Forest birds have different requirements in terms of preferred habitat structures, and it is often challenging to synthesise which ones, if any, benefit the entire assemblage. Indeed, we aimed at finding those variables most important and most universal for forest species. We used hierarchical multi-species abundance models to identify important forest variables, based on the aggregate response of single species to selected predictors (Kéry and Royle, 2016; Yamaura et al., 2012). Developed from N-mixture models (Royle, 2004), such models estimate the abundance of species within an animal assemblage or community as a function of environmental predictors, taking into account the detectability error by employing repeated count data. To ensure reliable estimates, we included in the models only individuals recorded within the 50 m radius of sampling, excluding the species that occurred in < 10 plots and the species that are not suitable for robust detection through the count method employed (e.g. owls, birds of prey, crows, swallows). The model considered three main hierarchically organized processes; the single species abundance processes, dependent on the assemblage process and function of environmental predictors; and the detectability process, which assumes the observation dependent on the abundance process.

1. Assemblage process: $w_k \sim Bernoulli(\Omega)$
2. Single species abundance: $N_{ik}|w_k \sim Poisson(w_k\ \lambda_k)$
3. Detection process: $y_{ijk}|N_{ik} \sim Binomial(N_{ik}, p_{ijk})$

The assemblage process, i.e. if the species k belongs or not to the assemblage w, was modelled as a Bernoulli process. The latent abundance N of species k at plot i was modelled as a Poisson distribution, using the log link. The repeated counts y of species k at plot i during replicate j were used to model the detection process, as binomial distribution, using logit link. Species heterogeneity was included by modelling both abundance and detectability as a function of predictors. The environmental predictors encompassed by the species abundance model included the forest variables and were first checked with variance inflation analysis, to exclude those that could inflate variance, using as threshold the variance inflation factor ≤ 3 (James et al., 2014). The date and the time of the survey, instead, were used for modelling the detectability over time (both seasonal and daily, respectively). All the predictors were scaled prior to analysis. The full model was run by applying Bayesian inference. We used uninformative priors and ran three Markov chain Monte Carlo simulations of 250 000 iterations, discarding the first 100 000 and thinning by 100. We considered that chains reached convergence when the Gelman-Rubin statistic (r-hat) was ≤ 1.1 for all parameters (Gelman and Hill, 2007). A model selection procedure was then applied to select the best model, with the aim of retaining only those variables on which posterior estimates converged. First, we excluded from the model all community predictors that were not converging (r-hat > 1.1). Then we excluded the species whose estimates were not converging. We then considered the aggregate responses of species to forest variables to be significantly different from 0 when 90% of their posterior distribution did not overlap 0 ($f \geq 0.9$). The final model included only forest variables with a credible estimated effect on the entire assemblage. All the analyses were conducted in R environment. The community model was built with the package 'jagsUI' (Kellner, 2018).

2.4. *Landscape analysis*

In order to assess the effect of landscape context on the numerical response of forest birds to forest structures, we grouped together structurally similar plots, according to the forest variables identified by the multi-species abundance model. Given the number of plots, we aimed at identifying only two groups of plots and maximize the sample size of each group. We identified groups using K-Means clustering, which aims at grouping plots minimizing the sum of squares from the forest variables of the plots to the assigned group centers (Hartigan and Wong, 1979). We obtained two groups of forest plots characterized by high (HAB+) and low (HAB-) values of forest variables, representing plots rich and poor in forest structures important for the bird assemblage. To assess whether the numerical response of birds was influenced by the landscape context in these two groups of structurally similar plots, we employed a partial least square (PLS) regression (Wold et al., 2001). This technique groups variables into principal components, so that the covariance between components of two datasets is maximized (Carrascal et al., 2009). The contribution of each variable to the components is assessed via the respective loadings. The response variable can be single (e.g. species richness) or multiple (e.g. multi-species abundances), in which case, the species matrix is deflated according to the information from the local regression on the explanatory variables (Rohart et al., 2017). In addition, the variance in the response variables explained by each of the component can give a measure of the actual contribution of the components. PLS can handle noisy and correlated data, and model single or multiple response variables (Rohart et al., 2017). This technique has been useful in ornithological studies, when the aim was to disentangle the effects of different groups of variables on multiple species (Innangi et al., 2019). In our case, we included landscape metrics and forest cover variables in the predictor matrix to build the environmental components describing the multivariate landscape space. We selected landscape variables important for the bird assemblage according to their the Variable Importance for Projection (VIP ≥ 1) (Akarachantachote et al., 2014; Chong and Jun 2005). Then, we assessed the loadings of each landscape variable to understand its contribution to the components, and plotted the variability of the numerical response in the multivariate landscape space, according to the identified plot groups. Bird abundance was analyzed using two-block PLS regression, which allowed to analyze responses matrices and provides correlation values between single species and landscape variables. The analyses were performed using the R package 'mixOmics' (Rohart et al., 2017).

2.5. *Numerical response of birds*

The numerical response of birds to forest structures in different landscape contexts was modelled with the PLS regressions using abundance, species richness and Shannon diversity as response variables. Since this analysis targeted the entire assemblage at landscape scale, it included all the species for which at least 2 records were found and included all the individuals recorded within and beyond 50 m. However, species for which the sampling methods were not suitable (e.g. owls) were excluded from the analysis. The maximum count of individuals of each species at each plot was used as proxy for abundance. Species richness consisted of the simple species sums, whereas species diversity (i.e. Shannon diversity) was computed as asymptotic estimator based on single species abundances (Chao et al., 2014). This class of estimators uses sample-size-based rarefaction and extrapolation for calculating species richness (Colwell et al., 2012), and extends it to Shannon diversity by employing Hill numbers which differently weigh rare species. Analysis were conducted with the R package 'iNEXT' (Hsieh et al., 2016).

We considered that structurally similar plots with different fitted abundances would not overlap in the multivariate landscape space built with the PLS axis, in accordance with our first hypothesis. We also considered that an overlap in the multivariate space between structurally different plots with similar fitted abundances suggests that additional factors influence the numerical response of birds to forest structures. To examine our second hypothesis, we considered that structurally different plots would have similar species richness and diversity according to the forest cover in the landscape. We assessed also whether structurally different plots with similar species richness and diversity overlap in the multivariate landscape space, signalling a weak predictive ability of the landscape context to represent variability in the response of bird species to forest structures. Finally, we examined the fitted values of the PLS regression on bird abundance to identify plots with similar predicted abundances of each guild. We considered that plots with high fitted abundance (≥90th quantile) of a specific guild indicate optimal habitats and would occur in a clustered pattern in the multivariate landscape space.

3. Results

3.1. Important forest structures

The final multi-species abundance model encompassed 16 bird species. Three forest variables were retained in the final model, with ≥ 90% of the posterior distribution of the estimates not overlapping 0: mean DBH of living trees (95% interval of the mean effect: 0.01 – 0.28, $f = 1$), mean DBH of the dead trees (95% interval of the mean effect: 0.002 – 0.21, $f = 1$) and volume of the lying deadwood (95% interval of the mean effect: 0.001 – 0.09, $f = 1$). However, the magnitude and significance of effects differed among species (Fig. 2; see also supplementary material 2 figure S1). For instance, while uncertainty around the effect of mean DBH of living trees for black woodpecker (*Dryocopus martius*) was large (95% interval of the mean effect: −0.88 – 0.41, $f = 0.62$; Table 1), the same effect was reliably estimated for the Eurasian treecreeper (*Certhia familiaris*) (95% interval of the mean effect: −0.04 – 0.92, $f = 0.97$; Table 1).

The K-Means clustering identified two forest plot groups, including 104 and 22 plots, each characterized by low (HAB-) and high (HAB+) values of the three important forest variables previously identified.

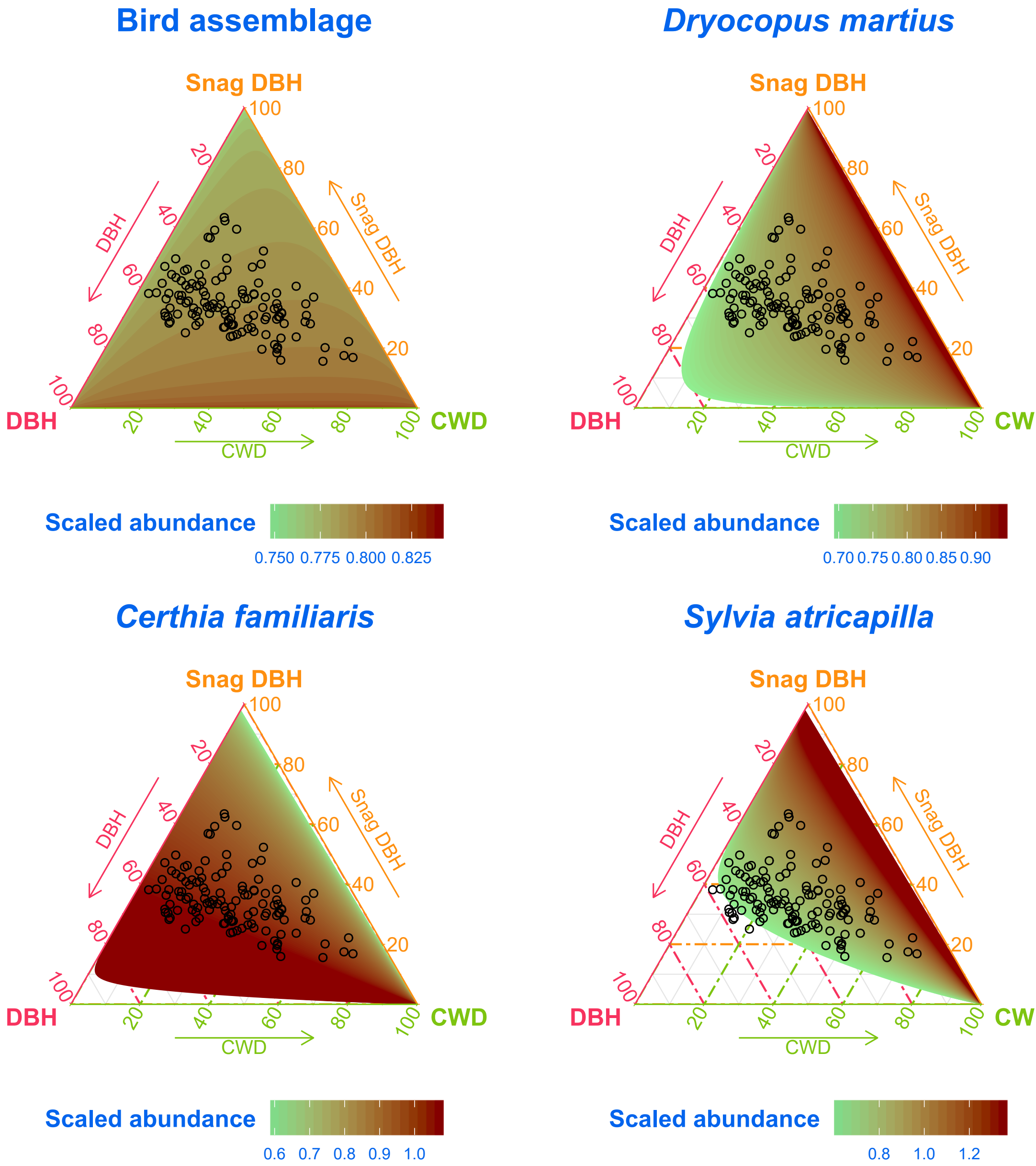

Fig. 2. Relationship between bird assemblage and selected species (top-right black woodpecker, bottom-right Eurasian blackcap, bottom-left Eurasian treecreeper) and the three important forest structures identified in the study. DBH = mean diameter at breast height; CWD = coarse woody debris (lying deadwood volume). The abundance is scaled to make the responses of different species comparable. Green-to-red areas indicate low-to-high abundances. Circles show the position of the study plots compared to the scaled predictors. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
Effect estimates of the three important forest structures identified by the bird abundance model. Bold indicates effects which posterior estimates have the same sign in >90% of the posterior distribution, $f \geq 0.9$. DBH = diameter at breast height.

Response		DBH of living trees		DBH of snags		Lying deadwood volume	
		Mean	SD	Mean	SD	Mean	SD
Bird assemblage		**0.104**	**0.316**	**0.066**	**0.288**	**0.032**	**0.089**
Scientific name	Common name						
Aegithalos caudatus	Long-tailed tit	−0.245	0.351	0.011	0.252	0.016	0.095
Certhia familiaris	Eurasian treecreeper	**0.414**	**0.239**	−0.027	0.177	−0.009	0.075
Columba palumbus	Woodpigeon	0.065	0.220	**−0.294**	**0.221**	0.008	0.078
Dendrocopos major	Great spotted woodpecker	0.072	0.219	0.223	0.196	−0.052	0.097
Dryocopus martius	Black woodpecker	−0.134	0.327	−0.008	0.261	0.041	0.093
Fringilla coelebs	Chaffinch	**0.396**	**0.173**	**−0.199**	**0.144**	−0.001	0.057
Garrulus glandarius	Eurasian jay	−0.093	0.246	0.163	0.195	0.059	0.076
Parus major	Great tit	−0.031	0.221	−0.078	0.183	0.026	0.072
Periparus ater	Coal tit	0.177	0.165	−0.031	0.139	0.018	0.058
Regulus ignicapilla	Firecrest	**0.273**	**0.217**	−0.048	0.182	−0.029	0.082
Sitta europaea	Nuthatch	0.057	0.227	−0.106	0.193	0.086	0.083
Sylvia atricapilla	Eurasian blackcap	−0.189	0.221	**0.362**	**0.176**	**0.096**	**0.073**
Troglodytes troglodytes	Eurasian wren	**0.319**	**0.244**	−0.216	0.197	**0.110**	**0.084**
Turdus merula	Eurasian blackbird	−0.001	0.196	**0.284**	**0.167**	0.010	0.067
Turdus philomelos	Song thrush	−0.049	0.222	0.205	0.184	−0.013	0.080
Turdus viscivorus	Mistle thrush	−0.011	0.257	−0.053	0.220	−0.045	0.103

3.2. Landscape effect on abundance

The final dataset for the landscape-level analysis of bird abundance included 42 species (table S2). The two-blocks PLS regression considered the matrices of bird counts and landscape variables as blocks, and reduced them to two components each. The final model included all conifer forest cover variables and mixed forest cover variables (except fcm_20 and fcm_25, see table S4), whereas landscape metrics scored a VIP < 1 and were excluded. The cumulative explained variance in the predictor components was 0.96. On the other side, the explained variance of the response/bird components was 0.14, indicating that the variability in bird abundances was difficult to reduce. The first predictor component was mainly built with the negative loadings of conifer forest cover across spatial scales and positive loadings of mixed forest cover (table S4). The second component was characterised by negative loadings of conifer forest and mixed forest cover (table S4). The variability in abundance of the bird assemblage between HAB+ and HAB- plots was similar across the multivariate landscape space (Fig. 3). However, the variability in abundances within HAB- and HAB+ plots only partly overlapped, indicating that higher abundances of birds are found when the landscape context favours mixed forest cover (Fig. 3). The correlation between individual species and landscape variables showed a clear distinction between species that are positively correlated with mixed forest cover and species positively correlated with conifer forest cover, and species that can have mixed responses to different types of forest cover (figure S2). None of the species was strongly correlated with conifer forest cover. Canopy nesters and feeders were the most abundant guilds across plots. They occurred at higher abundances in landscapes

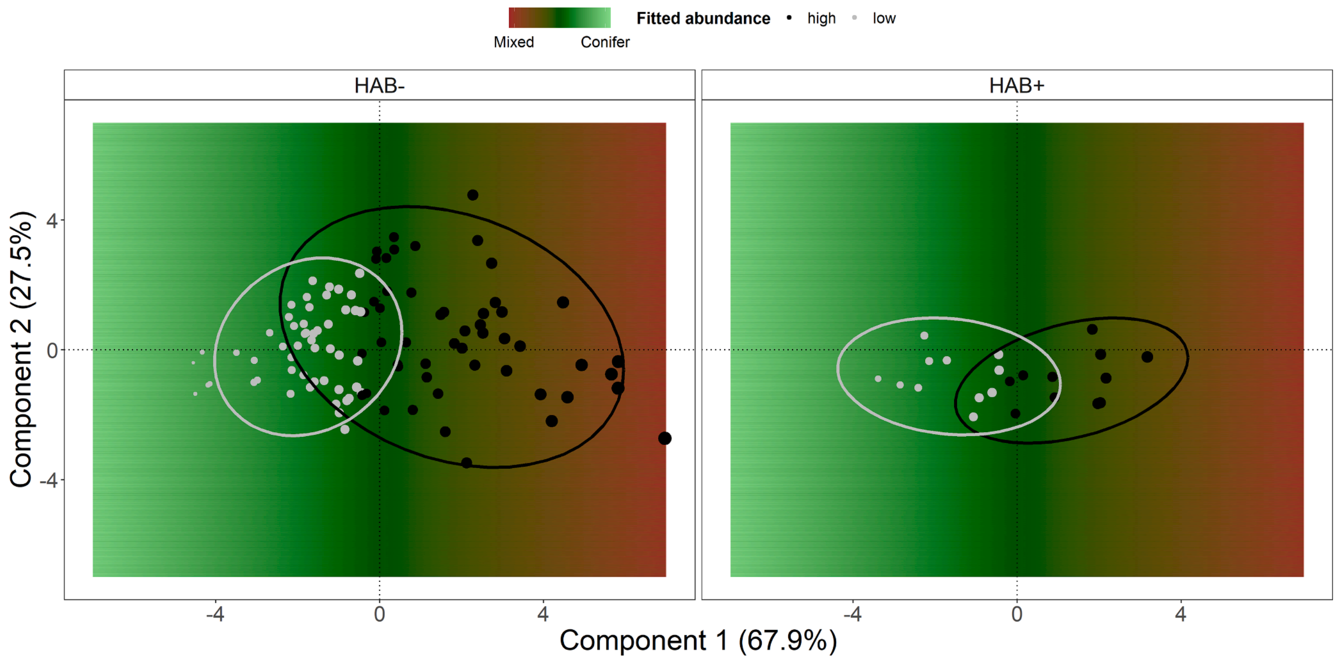

Fig. 3. Results of the two-block partial least square regression of the abundance of birds on landscape variables, for plots with low (HAB-) and high (HAB+) values of the important forest structures identified in the study. Circles show the position of each study plot in the multivariate landscape space and their size indicate plots with abundances greater (black) or smaller (grey) than the median fitted value. 95% ellipses group plots with high and low abundances. Red-to-green gradient shows the mixture of mixed and conifer forest cover in the multivariate landscape space. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

with higher mixed forest cover. Similar patterns were found for cavity and shrub nesters, ground feeders and trunk feeders. Contrastingly, ground nesters were more abundant when conifer forest cover prevailed in the landscape context (Fig. 4).

3.3. Landscape effects on species richness and diversity

Species richness and diversity values for each plot were returned with an average sample coverage of 0.67 (range = 0.38 – 0.9). For many plots, the accumulation rate of new species was slow, indicating a scarce turnover of species across samples (figure S3). The PLS for species richness included forest cover variables (total, conifer and broadleaf forest cover, see table S4) and one landscape metric, Euclidean nearest neighbor distance between patches. The landscape components could explain 80.4 % of the observed variance. The first landscape component was mostly determined by the negative loadings of conifer forest cover (table S4). The second component was characterized by the negative loading of Euclidean nearest neighbor distance, as well as the positive loading of broadleaf forest cover (table S4). Species richness in HAB+ and HAB- plots overlapped in the multivariate landscape space, indicating that similar species richness can be found despite the forest structure (Fig. 5). As for abundance, broadleaf forest cover favored species richness, while conifer forest cover constrained it to lower values (Fig. 5).

As for species richness, the PLS regression of species diversity included forest cover variables and Euclidean nearest neighbor distance as landscape metric (table S4). The multivariate landscape space accounted by the two components could explain 71.5 % of the observed variability. The first component was characterized by the negative loading of conifer forest cover across spatial scales (table S4). The second component, instead, was mainly characterized by the positive loading of broadleaf forest cover and the negative loading of Euclidean nearest neighbor distance (table S4). Different species diversity values were found in similarly structured plots across the landscape, but overall indicating an increase with broadleaf forest cover (Fig. 6), similarly to species richness.

4. Discussion

The main forest structures influencing the local abundance of forest birds were the sizes (DBH) of living and dead trees and the amount of lying deadwood. We used those structures to divide forest plots in high and low habitat quality, and looked at how the bird assemblages at each level of habitat quality expressed abundance, richness and diversity in different landscape contexts. We found that the numerical responses (abundance, richness and diversity) of the bird assemblages to forest structures were mainly dependent on the share of broadleaf forest in the surrounding landscape. In both high and low habitat quality plots, the bird assemblage occurred at higher abundance, richness and diversity when the landscape supported broadleaf or mixed forest cover. However, some guilds like ground nesters occurred at higher abundances in landscapes with higher conifer forest cover. Hence, local abundances were influenced by the amount and type of forest cover in the landscape, notwithstanding the local habitat quality. Species richness and diversity also depended mainly on the amount and type of forest in the landscape, although forest configuration had a smaller but significant effect.

4.1. Importance of the landscape context

The current debate on the moderation of biodiversity patterns in the landscape revolves mostly around the importance of habitat amount and habitat configuration (e.g. Fahrig, 2013; Fahrig, 2017; Hanski, 2015). For forest birds, the evidence for threshold-like responses to the amount of habitat in the landscape suggests it is the main determinant of their diversity patterns (Becker et al., 2011; Betts et al., 2007; De Camargo et al., 2018; Radford et al., 2005). The amount of habitat becomes particularly important when the habitat patches are surrounded by a matrix mainly composed of unsuitable habitat types (Shoffner et al., 2018). Theoretical frameworks suggest that, for a given species, habitat configuration may be more important at intermediate amounts of habitat in the landscape (Villard and Metzger, 2014). Evidence for the importance of habitat configuration exists for grassland bird species (Herse et al., 2018), and for bird assemblages encompassing heterogeneous landscapes (Halstead et al., 2019).

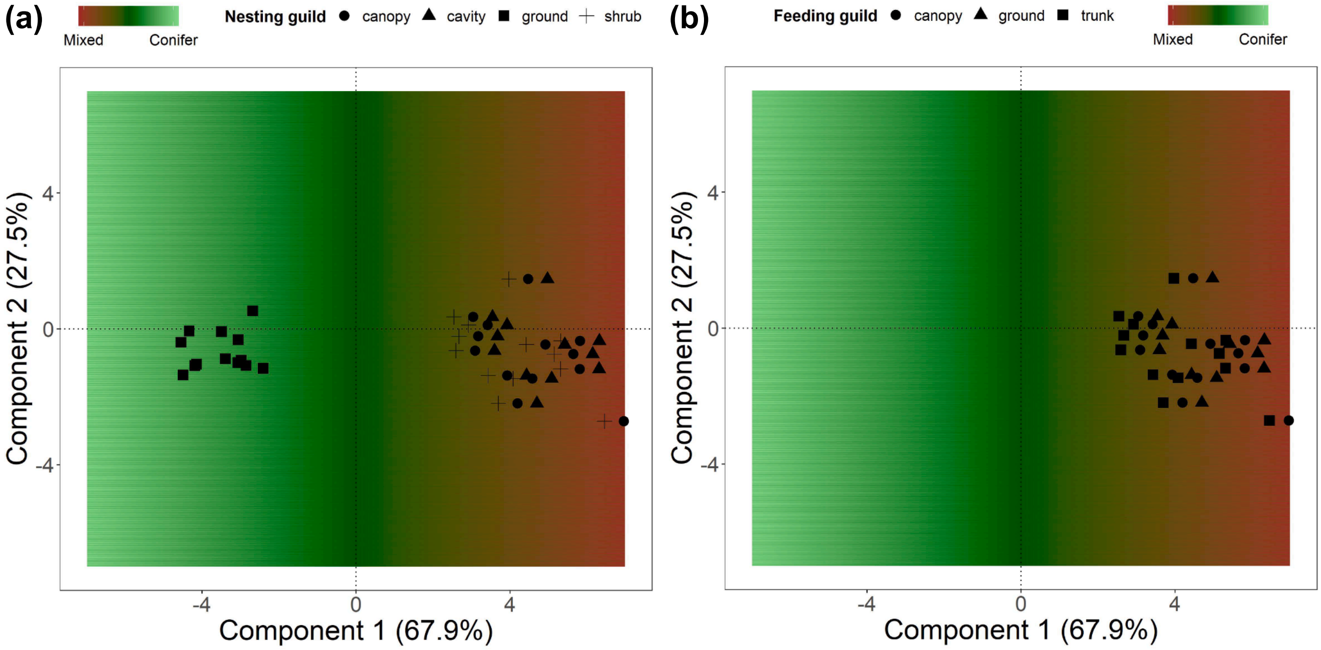

Fig. 4. Results of the two-block partial least square regression of the abundance of birds on landscape variables, for nesting and feeding guilds. Symbols show only optimal plots (plots with abundance ≥ 90th quantile) for the guilds, according to the legend. Triangles and squares are displayed with an offset 0.5 and −0.5 on the x-axis, for better representation.

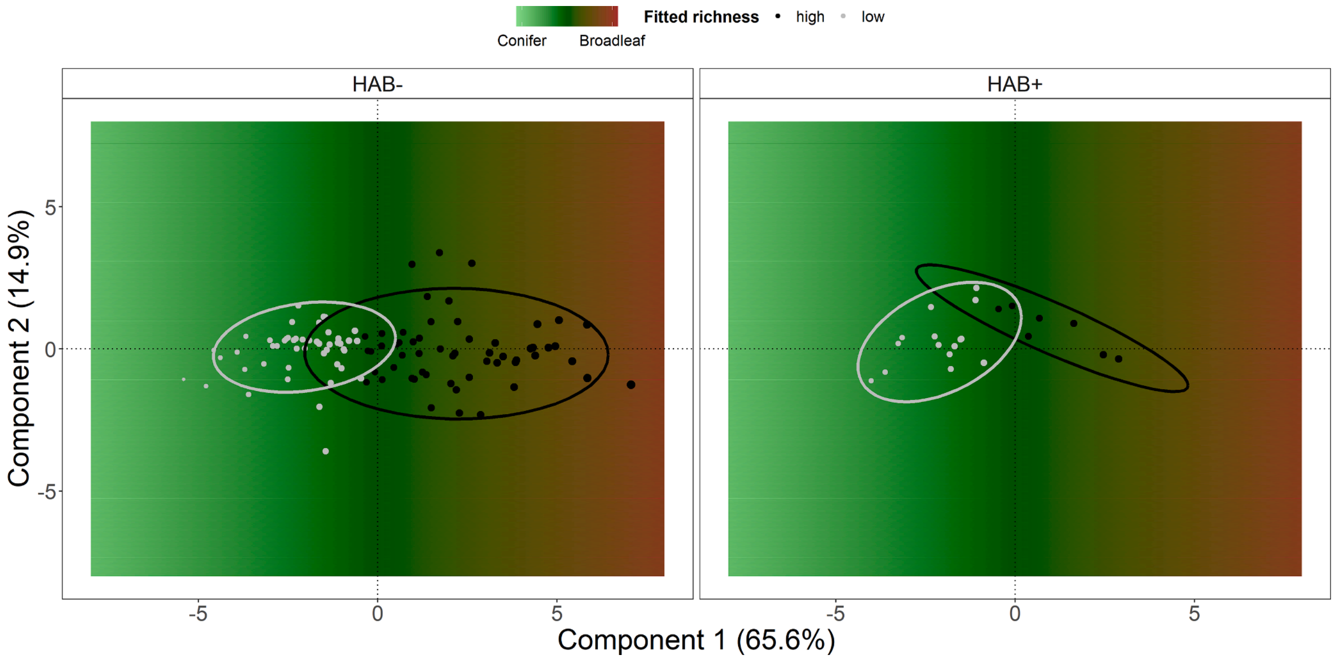

Fig. 5. Results of the partial least square regression of bird species richness on landscape variables, for plots with low (HAB-) and high (HAB+) values of the important forest structures identified in the study. Circles show the position of each study plot in the multivariate landscape space and their size indicate plots with richness greater (high) or smaller (low) than the median fitted value. 95% ellipses group plots with high (solid) and low (dashed) richness. Red-to-green gradient shows the mixture of broadleaf and conifer forest cover in the multivariate landscape space. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

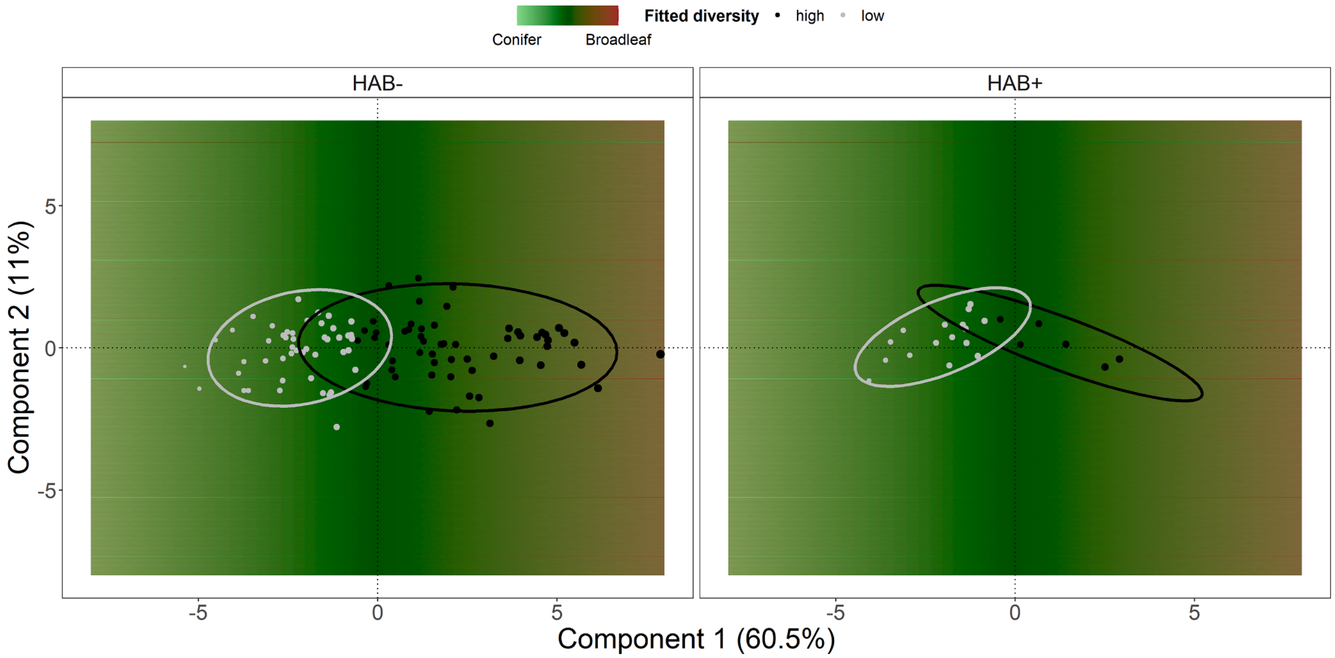

Fig. 6. Results of the partial least square regression of bird species diversity on landscape variables, for plots with low (HAB-) and high (HAB+) values of the important forest structures identified in the study. Circles show the position of each study plot in the multivariate landscape space and their size indicate plots with diversity greater (high) or smaller (low) than the median fitted value. 95% ellipses group plots with high (solid) and low (dashed) diversity. Red-to-green gradient shows the mixture of broadleaf and conifer forest cover in the multivariate landscape space. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

In our study, the amount of habitat described by forest cover was the main driver of the numerical responses of birds, whereas configuration played a minor role. Our findings may be influenced by the high number of species included, given our goal of targeting the entire bird assemblage. Our results showed a major role of broadleaf forest cover in influencing bird abundance, particularly of canopy and cavity nesting species, potentially buffering negative effects of insufficient local habitat structures. Only few of the species included in our analysis, mostly canopy feeders such as bullfinch (*Pyrrhula pyrrhula*), goldcrest (*Regulus regulus*) or crested tit (*Lophophanes cristatus*) showed positive correlations to conifer forest cover. Indeed, except for some conifer specialists, the importance of broadleaf forest in a landscape for the entire species assemblage can be linked to the availability of food (Vélová et al., 2021). This issue has a great importance for biodiversity conservation in anthropogenic landscapes: simple provisioning of habitat structures for species assemblages, such as deadwood or habitat trees (Bütler et al., 2013; Mölder et al., 2020), at the local scale may not match preferred landscape composition of forest birds (e.g. Holzkämper et al. 2006). In this respect, even if use of forest structural indicators of biodiversity like deadwood and age of canopy trees for assessing conservation value of forest may work well for some groups of organisms (Gao et al., 2015), our results indicate that landscape-scale indices are necessary to assess conservation value of forest stands for birds.

Considering that the composition of the studied bird assemblages was similar across plots (canopy nesters and feeders were always the dominant guilds), the differences in the landscape context determined the relative abundances of each guild. Similar results concerning different functional groups of birds in interior temperate forests in north-eastern USA showed that the landscape context influenced groups differently (Klingbeil and Willig, 2016). For example, functional diversity of resident birds was correlated with landscape diversity (Klingbeil and Willig, 2016). Moreover, Katayama et al. (2014) reported that for wide-ranging species of birds the species richness was highest in heterogeneous landscapes while the pattern was opposite for locally distributed species. However, there could be regional variability in responses to landscape characteristics associated with broad-scale environmental gradients. In Japan, for instance, cooler highly forested and homogeneous landscapes supported bird communities dominated by insectivorous forest specialists with narrow habitat breadths while warmer regions comprised communities dominated by generalists with wider habitat breadths, even in contiguous, highly forested landscapes (Spake et al., 2020).

Furthermore, the habitat of a species, especially in the case of birds, can enclose different types of vegetation associations (Hall et al., 1997). Like other studies, we adopted a very broad definition of habitat type, which equals the coarse vegetation type, i.e. forest. Contrary to both our expectations and several earlier findings (e.g. Mortelliti et al. 2010, Torrenta and Villard 2017), we found negative correlations between total forest cover and species richness and diversity, although we found positive effects specifically for broadleaf forest cover. Conifer stands dominate in our study system, while broadleaf and mixed forests are often found at the edge of conifer patches, where they increase landscape heterogeneity, resulting in higher species richness. Such results are actually expected when considering the entire bird assemblage and not just forest birds (Kmecl and Denac, 2018), as for our case. Similar results were earlier reported from Scandinavia (Berg, 1997; Enoksson et al., 1995), Japan (Yamaura et al., 2009), and the Czech Republic (Vélová et al., 2021).

4.2. *The role of landscape configuration*

In the case of less mobile animals, such as forest-dwelling non-volant small mammals, patch isolation has been found to have a weak but significant effect on species richness (Vieira et al., 2018). Their mobility makes it easier for birds to access distant patches and the distribution of individuals is controlled not only by habitat amount but also by the permeability of the matrix (Åberg et al., 1995; Geoffroy et al., 2019), which is a function of its configuration. Nevertheless, we found a negative response of species richness and diversity to the distance to the surrounding forest patches, though in our forest landscape even the most isolated plots are not far (as compared with the birds' mobility) from the nearest neighbouring forest patch, potentially suggesting that the matrix is not fully permeable (Salgueiro et al., 2021). The decrease of species richness and diversity with more distant forest patches may be a consequence of decreased spill-over among forest patches, mediated by distance, or of the landscape composition, due to a different mixture of forest and non-forest patches (Endenburg et al., 2019). Considering that we carried out our study in an extensively-managed forest landscape and that we did not restrict the species inventory to forest species only, we highlight that our results may also reflect the degree of permeability of the landscape.

The composition of biological assemblages is known to differ between production forests and unmanaged forests, as well as between different management types (Balestrieri et al., 2015; Fischer and Lindenmayer, 2002; Paillet et al., 2010; Weibull and Östman, 2003). The species composition can vary independently of species richness or diversity, meaning that in homogeneous forest landscapes, high local diversity can be associated with low turnover of species among sites (Schall et al., 2018). In heterogeneous landscapes, the spatial distribution of habitat types can determine higher species turnover and a larger regional pool of species, even though average diversity at sites can be low (Heikkinen et al., 2004; Schall et al., 2018; Söderström et al., 2001). Our results indicate homogeneous species assortment among plots, as expected for production forests (Freemark and Kirk, 2001). This homogeneity is usually driven by the most abundant guilds, in the case our study, the canopy nesters and feeders.

4.3. *Conservation implications*

Understanding the species-specific responses to habitat structure at local and landscape scales is the first step towards conservation-oriented forest management (Edman et al., 2011; Lichstein et al., 2002; Sanderson et al., 2002). The conservation of forest structures after logging operations (i.e. retention) has been proposed by multiple authors as an effective tool for preserving different species (Basile et al., 2017; Bütler et al., 2004; Lindenmayer et al., 1997). Consequently, many structural indicators have been proposed as a way to assess conservation value of forests and to monitor impact of forest management on biodiversity (Gao et al., 2015; Smith et al., 2008; Timonen et al., 2010).

Forest structures such as large living and dead trees, or lying deadwood, are fundamental in the supply of food resources and shelter to many species but their occurrence in forests is heavily conditioned by forestry. In our study system, these forest structures are important predictors of the abundance of the entire bird assemblage, but the homogeneous landscape context influence species assortment, so that similar assemblages are found across the landscape. Indeed, these structures may play a fundamental role for preserving the populations of forest specialist birds, such as many woodpecker species (Mikusiński et al., 2018b). Large trees lack from many forests, due to a combination of intensive timber production, altered disturbance regimes and climate change (Bennett et al., 2015; Lindenmayer and Laurance, 2017). In addition, the pulses of snags and lying deadwood in the landscapes linked to abiotic (e.g. wildfires or windthrows) and biotic disturbances (e.g. tree mortality due to bark beetle), are counteracted by salvage logging that, strikingly, is still applied also in protected areas (Mikusiński et al., 2018a; Müller et al., 2019). From a management perspective, this translates into the retention of large living trees above a certain diameter thresholds, suggested by different authors based on the conservation target (e.g. Gutzat and Dormann 2018, Basile et al., 2020b), and the retention of as many snags and logs as possible.

An increase in tree species mixture, favouring broadleaved trees in landscapes where such trees are scarce due to silviculture, coupled with extensive retention of snags and deadwood and trees with high ecological value (Basile et al., 2020a; Puverel et al., 2019), would benefit cavity excavators such as woodpeckers, and the potential benefit will extend to forest birds and the entire cavity-dependent community. The broadleaved trees, in contrast to coniferous species, are more likely to develop decay-formed cavities that provide safer nesting places than woodpecker-made cavities (Wesołowski and Martin, 2018). Increasing tree species mixtures, then, may positively feedback on resource provision, which is probably more important for keystone species, such as the black woodpecker (Brambilla et al., 2013; Hondong, 2016).

Moreover, such a measure has general positive impacts on biodiversity and the provision of ecosystem services (Gamfeldt et al., 2013). Current retention practices are often well below the habitat requirement of bird species (Basile et al., 2019), making even more important the adoption of a landscape perspective to implement conservation-oriented practices in managed forest landscapes. Our study confirms a need for integrated multi-scale biodiversity management that is based on simultaneous assessment of biodiversity at the stand and landscape scales. This requires further development of relevant sets of biodiversity indicators that encompass both the local and landscape requirements of different groups of organisms in a given region, as well as their interactions.

CRediT authorship contribution statement

MB conceptualized the research questions; IS conceptualized the overarching study design and secured the funding; MB and GM collected the data; MB cured the data, did the analysis, and prepared a first draft of the manuscript; GM and IS critically contributed to the writing. The authors read and approved the final manuscript.

Declaration of Competing Interest

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2021.108402.

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