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Forest type consistently shapes bird communities across seasons: Insights from passive acoustic monitoring

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ABSTRACT

Forest management affects forest-dwelling taxa, such as birds, which play diverse roles in ecosystem functioning. While birds are frequently studied, surveys typically are conducted during the breeding season, overlooking non-breeding periods during which birds may have different resource requirements. Understanding year-round dynamics of habitat use is essential to inform management practices that support bird communities. We used passive acoustic monitoring to study bird assemblages across a gradient from deciduous broadleaved to coniferous forest stands around the city of Jena (Thuringia, Germany). We investigated how season, forest type, and environmental variables influence species taxonomic diversity, community composition, and functional diversity. Birds were monitored in 30-day periods during winter, spring, summer, and autumn 2024 using AudioMoth recorders and BirdNET for species identification. Species diversity varied significantly by season, peaking in spring and summer and declining in autumn and winter; forest type had no effect. Community composition was primarily driven by season, but within seasons, birds clustered by forest type. Season influenced functional dispersion and dissimilarity, but not evenness; forest type influenced only functional dispersion. Overall, seasonality, especially migration dynamics, most strongly impacts bird diversity. Within seasons, forest type structures community composition but does not affect taxonomic or functional diversity. Persistent functional diversity despite taxonomic shifts suggests functional redundancy, indicating resilience to habitat change. Coniferous stands emerged as harbouring distinct, but equally diverse bird species compared to deciduous stands. Forest managers should prioritise a mix of forest types to sustain rich bird communities and ensure long-term ecosystem functionality.

1. Introduction

Temperate forests in Central Europe cover a significant portion of the landscape, with Germany having 32 % of its area forested (BMEL, 2024). These forests provide essential habitats for a wide variety of species and play a crucial ecological role (Brocknerhoff et al., 2017). However, most forests are intensively managed, which profoundly alters their structure and the patterns of natural disturbances and regeneration. This influences both the abiotic and the biotic environments (Chaudhary et al.,

2016). Moreover, climate change is further modifying forest conditions (Seidl et al., 2017). Together, this can cause biodiversity decline and the loss of ecosystem functions (Mori et al., 2017). Accordingly, these challenges require sustainable forest management that balances timber production with biodiversity preservation (Castaño-Villa et al., 2019; Mori et al., 2017; Penone et al., 2019).

Birds represent a key group of forest-dwelling organisms and are widely used as indicators of biodiversity due to their sensitivity to environmental change, their trophic position in food webs, their reliance

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on a broad range of habitat features, the numerous ecosystem functions they fulfil, and the relative ease with which they can be monitored (Gao et al., 2015; Lees et al., 2022; Sekercioglu, 2006; Zeller et al., 2023). In Europe, forest bird populations have been reported to decline significantly (Burns et al., 2021), although trends vary regionally, with Germany reporting stable forest bird populations (Kamp et al., 2021). This highlights the need for forest management strategies that account for avian habitat requirements (Burrascano et al., 2023; Schuldt et al., 2022). Forest bird occurrences are influenced by a wide range of abiotic factors, including temperature, precipitation, light, and the availability of microclimatic refuges, all of which are related to forest vertical structure, tree species composition, and canopy closure. Biotic conditions affect bird abundance and diversity, in addition to the factors mentioned above, by the availability of nesting sites (e.g., cavities, shrubs), or provisioning of food resources such as arthropods, seeds, and fruits (Gutzat and Dormann, 2018; Penone et al., 2019; Zeller et al., 2023; Zellweger et al., 2016).

To minimise sampling effort, most previous studies of bird diversity have focused solely on the breeding season. This is understandable, as breeding is a crucial stage in bird life cycles and also the period when birds are most conspicuous due to vocal activity, making them easier to survey (Gil and Llusia, 2020). However, focusing exclusively on the breeding season risks overlooking birds' resource requirements during other seasons, which may differ from those during the breeding season. For instance, Michielsen et al. (2024) found that bird communities in the Białowieża Forest were more abundant in coniferous stands in winter than in spring, but more abundant in deciduous forests in spring. This shift likely reflects the greater availability of foliage in winter in conifers, providing shelter and food (Zhao et al., 2024), whereas most bird species rely on insect prey during breeding, which may be higher in deciduous forests (Hinks et al., 2015; Pedley et al., 2014; Piel et al., 2021). Moreover, migratory species may use forests as stopover or wintering sites, further altering community composition. Gaining a comprehensive understanding of how forests can support diverse bird communities, therefore, requires extending research beyond the breeding period to encompass other critical phases of avian annual cycles (Alba et al., 2025; Barbe et al., 2018; Keller et al., 2009; Michielsen et al., 2024).

Biodiversity assessments of forest birds often focus only on taxonomic diversity, typically expressed as species richness or abundance. While this provides valuable information, it may be insufficient to capture the ecological complexity of bird communities. Community composition – that is, *which* species are present at which abundances – can provide additional insights into temporal species turnover, which may be masked when only taxonomic richness is considered (Sommer and Fichtner, 2023). At the same time, it is essential to assess functional diversity, which reflects the range of ecological strategies and adaptations in a community, such as foraging strategies, dietary niches, or nesting behaviours. This functional perspective is particularly relevant in managed forests, because it helps clarify whether species that perform similar ecological roles persist, and whether critical ecosystem functions – such as insect predation or seed dispersal – are maintained (Alba et al., 2025; Bae et al., 2018; Böhm et al., 2011).

Recent advances in bioacoustics have enabled the extended monitoring of vocalising species with minimal additional sampling effort through Passive Acoustic Monitoring (PAM) (Darras et al., 2025; Gibb et al., 2019; Ross et al., 2023). Unlike traditional monitoring methods, PAM involves deploying sound recorders at monitoring sites, with the resulting recordings subsequently analysed either manually or using automated species identification tools. This approach is increasingly adopted, as it allows simultaneous monitoring across multiple sites over extended periods (Sugai et al., 2019). PAM has been shown to yield results comparable to those from conventional point counts (Fairbairn et al., 2025) or even outperform observer-based methods (Darras et al., 2016). It has been demonstrated that PAM is well-suited to studying the phenology of forest birds during the breeding season (Singer et al.,

2025); however, PAM has rarely been used to study the phenology of acoustic bird communities across seasons. We use the term “acoustic community” as coined by Farina and James (2016) to account for the fact that we assess bird communities based on their acoustic expressions.

In this study, we investigated the seasonality of acoustic bird communities in Central European forest ecosystems using passive acoustic monitoring. We analysed the effects of season, forest structure, and microclimate on three features of acoustic bird assemblages: 1) species diversity, 2) community composition, and 3) functional diversity. We hypothesised that season has a significant effect on all three metrics due to bird migration patterns, whereas habitat parameters (forest structure, microclimate) have minor effects. However, apart from the main impact of season, we further hypothesised that forest structure, especially tree species, shows consistent effects on community composition across seasons.

2. Materials & methods

2.1. Study sites

The study took place at 20 forest sites around Jena, Thuringia, Germany. Located in the Saale valley, Jena (50° 92' N, 11° 58' E) experiences a continental climate with mean annual temperatures of 11.3 °C and mean annual precipitation of 583 mm (mean values for the period 2015–2024, Ernst-Abbe-Hochschule Jena, 2025). The study sites are located around Jena, in an area with comparably steep slopes arranged around four valleys with different aspects (see Fig. 1). The sites form part of a long-term forest condition survey (“Waldzustandserhebung”, project WZE@Jena), which enhances the resolution of the national monitoring program since 2023. The sites are largely characterised by shallow soils on calcareous ground. They are located in managed municipal forests, except for the northernmost site (site 544), which is in a total reserve where no management happened for at least 40 years.

Across the 20 sites, six forest types are represented (see Fig. 1 for site and type locations), including three European Union's Natura 2000 habitat types (“Lebensraumtypen”, LRT; Szymank et al., 2023) and three biotope types as classified by the federal state of Thuringia (“Biotoptypen”, BT; Thüringer Ministerium für Landwirtschaft, Naturschutz und Umwelt, 1999). Woodruff Beech forests (Habitat type, “Lebensraumtyp”, LRT 9130, Galio-odorati Fagetum; turquoise) are dominated by pure beech stands with high tree cover and a high proportion of deciduous trees (hereafter “deciduous” refers to deciduous broadleaved trees). These stands have minimal understory species richness and cover, with notably high tree height and microhabitat density. Similarly, Oak-Hornbeam forests (LRT 9170, Galio-Carpinetum; green), another EU Natura 2000 habitat type, have a high deciduous share and the highest microhabitat density, with pronounced vertical stratification and shrub cover ranging from 3 % to 86 %. Calcareous Beech forests (LRT 9150, Carici-Fagetum; orange) are also EU-recognised habitat types, typically found on slopes; they are the lightest, have moderate vertical cover across all layers, high microhabitat density, and slightly elevated crown defoliation. Among the three biotope types are Hardwood Beech forests (BT 7103–60x, Beech/deciduous mixed forest; pink), which are distinguished by above-average stand height and microhabitat density, a high proportion of deciduous species, and variable understory cover. Pine-mixed forests (BT 7203–20x, Mixed pine forest; yellow) display variable tree and understory cover but high herb species richness, high crown defoliation, and relatively few microhabitats per tree. Mixed deciduous-conifer forests (BT 7403–40x, Mixed deciduous-evergreen forest; blue) are dominated by conifers such as pine and spruce, with moderate tree and shrub richness and cover, variable herb layer cover, and moderate crown defoliation. Other than the three Natura 2000 habitat types, these three biotope types are more strongly influenced by forestry; this is evident in the admixture of non-native black pine (*Pinus nigra*) with Scots pine (*Pinus sylvestris*)

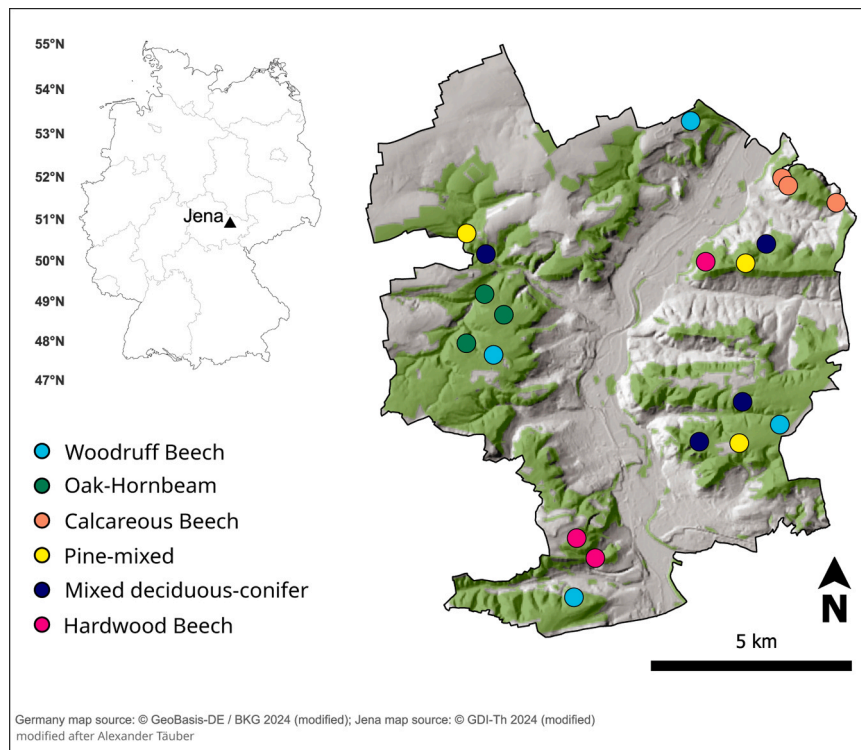


Fig. 1. The 20 study sites in Jena, Thuringia, Germany. The map extent shows the city boundaries, the hill shades represent elevation, and the green area shows forest cover. Coloured dots show the (randomly chosen) study site locations and their classification as forest types. The Germany map in the upper-left corner shows Jena's location in Germany.

stands and the isolated occurrence of spruce (*Picea abies*), which is not typical for the location. Please see the pictures Fig. A1 in the Appendix A for an impression of the six forest types.

2.2. Bird data

Bird occurrences were monitored around the year using passive acoustic monitoring with AudioMoths (version 1.2.0) (A. P. Hill et al., 2019). On each site, one AudioMoth was attached to a tree, either the tree in the centre of the plot or a nearby one, with the microphone directed towards the plot centre, at approximately 2 m above the ground, in a waterproof IPX7 case. We programmed them to record every 15 min for 25 s, starting at the full hour. While standards in recording regimes have yet to be developed, some comparable studies found advantages of recording smaller but more snippets as we did, as this can lead to a faster accumulation of species while saving battery and storage resources (Cook and Hartley, 2018; Metcalf et al., 2022). The devices recorded with a sample rate of 192 kHz and with the gain set to medium. They recorded for one continuous 30-day period per season: the winter period was January 1–30, the spring period was March 25–April 23 – a period covering the main activity periods of forest species (Singer et al., 2025) –, the summer period was July 1–30, and the autumn period was November 1–30, all in 2024. Due to SD card failures, one device did not record for the first nine days in winter, one did not record at all in spring, three did not record in summer, and three did not record in autumn.

We analysed the recordings with the artificial neural network BirdNET Analyzer version 2.4 (Kahl et al., 2021) using a minimum confidence value of 0.1, a sensitivity of 1, an overlap of 0, and a latitude and longitude of 50.92 and 11.58. BirdNET provides detections for 3-sec snippets with a confidence score between 0.1 and 1. We excluded all species associated with habitats other than forest, shrubland, human-modified, grassland, woodland, and rock, according to the AVONET eBird trait table (Tobias et al., 2022), and also additionally

excluded *Aix galericulata* and *Anser albifrons*, as these species require an aquatic habitat nearby, which is not present near any of our study sites. This was done to ensure that we excluded species unlikely to use our study sites as habitat, but that were instead detected flying over the sites.

We used the methodology described in Wood and Kahl (2024) to select a species-specific threshold above which we counted all detections to minimise the number of false detections included. To do that, ESF manually validated a sample of up to 45 detections per species, five per confidence “class” (i.e., confidence values of 0.1–0.2, 0.2–0.3, etc., up to 0.9–1), by listening to them. Confirming true detections and rejecting false ones, we then back-transformed the confidence scores to logit scores, fitted a logistic regression of the confidence score for each species, and extracted the confidence score at $p = 0.9$, where p is the probability that the predictions are correct. The resulting detections are thus true detections with a 90 % probability. We then manually reviewed detections of migrating birds in seasons when detections were unlikely, listened to those unlikely detections, and, if they were false, manually removed them. 78 species were detected by BirdNET and, during validation, confirmed to have at least one true positive detection. In 20 cases, the threshold was set so high that all detections were excluded (this happened for *Accipiter gentilis*, *Asio otus*, *Corvus monedula*, *Coturnix coturnix*, *Cuculus canorus*, *Curruca communis*, *Curruca curruca*, *Delichon urbichon*, *Emberiza citronella*, *Hippolais icterina*, *Lanius collurio*, *Merops apiaster*, *Milvus milvus*, *Motacilla alba*, *Oriolus oriolus*, *Phoenicurus ochruros*, *Poecile montanus*, *Streptopelia decaocto*, *Streptopelia turtur*, *Sylvia borin*; see Tab. A1 in the Appendix A). Our final detections table, which we used in the following analyses, thus included 58 species. We transformed the detections into “activity days” by counting the number of days per species and site (within each of the four seasons) on which the species was detected at least once. We then log-transformed the activity days. This was done to account for the large differences between vocally very active (and often detected) species and those that are quieter due to their specific behaviour. The table of all detections included in the analysis is in Appendix B.

We extracted data on eight traits relevant for resource requirements and habitat use from trait tables; diet (trophic niche) and habitat from AVONET (Tobias et al., 2022), and body mass, clutch size, broods per year, bill length, nest type, and migration status from Storchová and Horák (2018). We tested for correlation between the traits using Spearman's correlation for continuous traits, Cramér's V for categorical traits, and mixed correlation tests for combinations of both (method = auto). We removed bill length because of its strong correlation with body mass ($\rho = 0.73$, $p < 0.001$).

2.3. Environmental variables

Altitude, aspect, and inclination values of the sites were taken from Ixas (2023). One temperature logger (Hobo MX2301A) was attached to a tree in the centre of each site, approximately 1.5 m above ground, measuring air temperature every 20 min. In March 2024, a light logger (Hobo MX2202) was installed 15 cm above ground, located 2 m north of the plot centre. As the logger was installed after the winter measuring period in January 2024, we used light data from the same days in January 2025 instead. We acknowledge that this is not perfect; however, we consider it the best solution. From these, we calculated the mean values of air temperature and light.

On a 10×10 m plot near the central tree, vegetation surveys were conducted in spring and summer 2023. For the herb, shrub, and tree layer, species identity and cover estimates were noted. These were used to calculate the Shannon index of vegetation stratification, using the respective cover values for the three layers (MacArthur and MacArthur, 1961). We used mappings of all trees within a 15 m radius (707 m^2) around the central tree with the temperature logger to calculate the proportion of deciduous to coniferous trees. The diameter at breast height (DBH) was measured at 1.30 m above ground, including all trees with a DBH of at least 7 cm. We calculated the basal area ($\pi \times (\text{DBH}/2)^2$) for each tree and summed these values separately for deciduous and coniferous trees per site. The relative share of basal area of deciduous and coniferous trees was then quantified as the proportion of the total basal area of each of these two tree types to the site's overall basal area, hereafter referred to as "deciduous/coniferous BA share".

We used crown defoliation estimates from the forest condition survey conducted in summer 2024. This was done for four groups of (usually) six trees each, situated 25 m away in each cardinal direction from the plot's centre tree, following the standard protocol for forest condition surveys (Thüringer Ministerium für Infrastruktur und Landwirtschaft, 2024). We calculated the mean crown defoliation across all trees in each plot. On these same trees, the number of microhabitats (such as cavities, fractures, bark structures, deadwood, etc.; see Kraus et al., 2016) was gathered, which we transformed into the number of microhabitats per tree. Spearman correlation tests revealed high positive ($\rho > 0.7$) correlations between aspect and inclination and between microhabitats per tree and coniferous BA share, and high negative ($\rho < -0.7$) correlations between aspect and altitude, between coniferous BA share and microhabitats per tree, and between coniferous and deciduous BA share. We therefore removed inclination, altitude, microhabitats per tree, and coniferous BA share. The selection of environmental predictors included in the analyses was thus: aspect, mean crown defoliation, tree species richness, shrub species richness, herb species richness, tree cover, shrub cover, herb cover, Shannon index of vegetation stratification, deciduous BA share, mean temperature, and mean light. The table of predictor variables is in Appendix C.

2.4. Data analysis

We calculated and visualised species richness and the effective numbers of common and dominant species (Hill number orders $q = 0, 1, 2$) for the four seasons and the six forest types. Rather than using the nonlinear Shannon entropy and Simpson index directly, converting these indices into effective numbers of species makes diversity values

more intuitive and comparable across communities. The effective number of species is the number of equally abundant species that would yield the observed value of a given diversity index (Shannon or Simpson, in our case). This allows that one community can be meaningfully described as, for example, "three times as diverse" as another. In this framework, species richness corresponds to the so-called Hill number of order $q = 0$; the effective number of common species is the exponential of the Shannon entropy ($q = 1$); and the effective number of dominant species is the reciprocal of the Simpson index ($q = 2$). These three measures are members of the same family of diversity indices, differing only in the value of q , which controls the degree to which rare species are down-weighted when quantifying diversity. The concept of effective numbers of species dates back to MacArthur (1965), was formalised by Hill (1973), and was later revived and promoted by Jost (2006) as a preferred way to express diversity in ecology.

We tested for significant differences between groups using ANOVA and Tukey's HSD tests. As the sampling coverage was very high (between 89 % and 99 %, calculated per site and season using the iNEXT package; Hsieh et al., 2025), we used our observed values. To analyse relationships between environmental variables and species richness across seasons, we fitted linear models for each season using R's *lm* function. We included the deciduous BA share, tree cover, vegetation stratification, shrub cover, temperature, and light as predictors. We first fitted a full model with these predictors, then used the *dredge* function from the MuMIn package (Bartón, 2025) to identify the models that best explain the observed variation, based on AICc (Akaike's Information Criterion corrected for small sample sizes). When several best models ($\Delta \text{AICc} < 2$) were available, we averaged them using *model.avg*.

To analyse the community composition, we fitted a non-metric multidimensional scaling (NMDS) with *metaMDS* from the *vegan* package (Oksanen et al., 2025) on the matrix with the activity days using chord distance, as this distance metric also accounts for double zeros between two assemblages (i.e., species absent in two assemblages; "assemblage" hereafter referring to the bird community at a given site and season). We then plotted the NMDS and included significant predictors ($p < 0.05$) identified with *envfit*, both for all assemblages and separately per season. To assess variation in community composition among seasons and forest types, as well as the effect of deciduous BA share, we used permutational multivariate analysis of variance (PERMANOVA, functions *adonis2* and *pairwise.adonis2* from packages *vegan* and *pairwiseAdonis*; Martínez Arbizu, 2017). We also ran PERMANOVA analyses and pairwise Adonis tests for each season separately to evaluate the influence of forest type and deciduous BA share on within-season community variation. We then did an indicator species analysis, once per season and once per forest type, using the *multipatt* function from the *indicspecies* package (Cáceres and Legendre, 2009).

Based on the selected traits (habitat, diet, body mass, clutch size, broods per year, nest type, migration status), we calculated functional traits-based distances between all species pairs using Gower's distance as we had a mixture of continuous and categorical traits using the *funct.dist* function, which is, like all functions used for the calculation of functional diversity measures described hereafter, from the *mFD* package (Magneville et al., 2022). We then calculated the position of each species in a multidimensional functional space based on the *quality.fspaces* function using this species-traits distance matrix. This, along with the log-transformed assemblage-species matrix, was used to calculate functional alpha diversity indices (function *alpha.fd.multidim*). Due to high correlations among each other or with species richness, we subsequently included only functional dispersion (FD_{is}, the species activity-days-weighted deviation of trait values from the centre of the functional trait space) and functional evenness (FE_{ve}, how evenly species activity days are distributed across the functional trait space) (Moullot et al., 2013). We plotted boxplots for the four seasons and the six forest types, and tested for significant differences between groups using ANOVA and Tukey's HSD tests. To assess functional beta dissimilarity, we calculated a distance matrix for each pair of assemblages

using the Jaccard distance metric with the *beta.fd.multim* function, based on a presence-absence matrix of species per assemblage and the position of each species in the multidimensional functional space. For this Jaccard beta dissimilarity matrix, we fitted and plotted an NMDS using chord distances and identified significant predictors using *envfit* (vegan package), both for all assemblages and separately per season. We again used PERMANOVA and pairwise Adonis tests to assess significant differences in functional dissimilarity among assemblages for both seasons and forest types.

3. Results

In total, 11,080 activity days (AD) of 58 species were included in the analysis. Of these, 38 species were detected on 2105 AD in winter, 52 species on 5024 AD in spring, 48 species on 2673 AD in summer, and 33 species on 1278 AD in autumn. The species with the most AD were *Poecile palustris* (835 AD), *Regulus regulus* (778 AD), *Sitta europaea* (776 AD), *Cyanistes caeruleus* (759 AD), and *Erithacus rubecula* (762 AD). *Jynx torquilla* (2 AD) is highly threatened in Thuringia (Red List Status 2), and *Alauda arvensis* (11 AD), *Dendrocoptes medius* (45 AD), *Lullula arborea* (3 AD), and *Phoenicurus phoenicurus* (38 AD) are listed as near threatened. For a species list of detected and confirmed species, see [Tab. A1](#) in the appendix.

3.1. Species diversity across seasons

The comparison of species diversity between seasons showed significant differences in species richness (q_0) and in the effective number of common and dominant species (q_1 and q_2 ; [Fig. 2](#)).

Species richness was between 15 and 25 for most autumn and winter communities and between 20 and 35 for most spring and summer communities. The spring communities had significantly higher species richness than the summer communities, which in turn had significantly more species than the winter and autumn communities. The effective numbers of common and dominant species were lower, but the pattern is the same as for species richness. For q_1 and q_2 , the spring and summer communities showed significantly higher species diversity than the winter and autumn communities. Species accumulation curves are shown in [Fig. A2](#) in the appendix.

The species diversity exhibited slight differences among some forest types, but no significant effect was found ([Fig. 3](#)). Hardwood Beech forest sites showed a non-significant tendency towards higher species diversity.

Model selection outcomes differed among seasons (see [Tab. A4](#) in the

appendix for the full output). In winter and summer, the null model was best supported, indicating that habitat or microclimatic variables had no explanatory power. In spring, several predictors appeared in competing models, but their effects were weak and uncertain. In autumn, shrub cover consistently explained variation in species richness, with higher shrub cover associated with greater richness.

3.2. Community composition

Community compositions differed markedly between the four seasons ([Fig. 4](#)). Autumn and winter, as well as spring and summer, communities were similar to each other. As indicated in [Fig. 2](#), a gradient from low to high species richness from winter and autumn towards spring and summer is visible in the ordination, illustrated by the grey contour lines.

Within the seasonal communities, clusters of communities of different forest types became visible (see [Fig. A3](#) in the appendix, which shows connecting lines between the same sites across seasons). Woodruff Beech and Oak-Hornbeam communities occupied the lower region of the ordination, whereas mixed and pine forests were located towards the upper area. This gradient is reflected by the significant predictors: deciduous BA share, tree cover, and the Shannon index of layer stratification point downwards, while herb and shrub species richness point upwards towards the mixed and pine communities.

The PERMANOVA analysis revealed significant differences in community composition between seasons (Bray-Curtis, $F_{3,69} = 14.54$, $R^2 = 0.39$, $p < 0.001$; 9999 permutations). Multilevel pairwise comparisons using pairwise Adonis tests confirmed significant differences between all seasonal pairs ($p_{\text{adjusted}} = 0.006$; see [Tab. A5](#) in the appendix for full details). Additionally, the PERMANOVA indicated significant differences among forest types (Bray-Curtis, $F_{5,67} = 2.93$, $R^2 = 0.18$, $p < 0.001$; 9999 permutations). Pairwise Adonis tests revealed significant differences between Pine-mixed and Oak-Hornbeam, Pine-mixed and Woodruff Beech, Oak-Hornbeam and Mixed Deciduous-Conifer, and Mixed Deciduous-Conifer and Woodruff Beech forest types ($p_{\text{adjusted}} < 0.05$; see [Tab. A6](#) in the appendix for full outputs). Basal area share of deciduous trees explained 7.6 % of community variance (PERMANOVA, $p < 0.001$, see [Tab. A7](#) in the appendix). When looking at individual communities per season and significant environmental variables, the patterns differed from those for the community year-round ([Fig. 5](#)).

Within seasons, different factors played a role in shaping the communities than when looking at the dataset of the whole year. These factors varied by season, indicating that different environmental variables drive community structure at different times. The deciduous BA

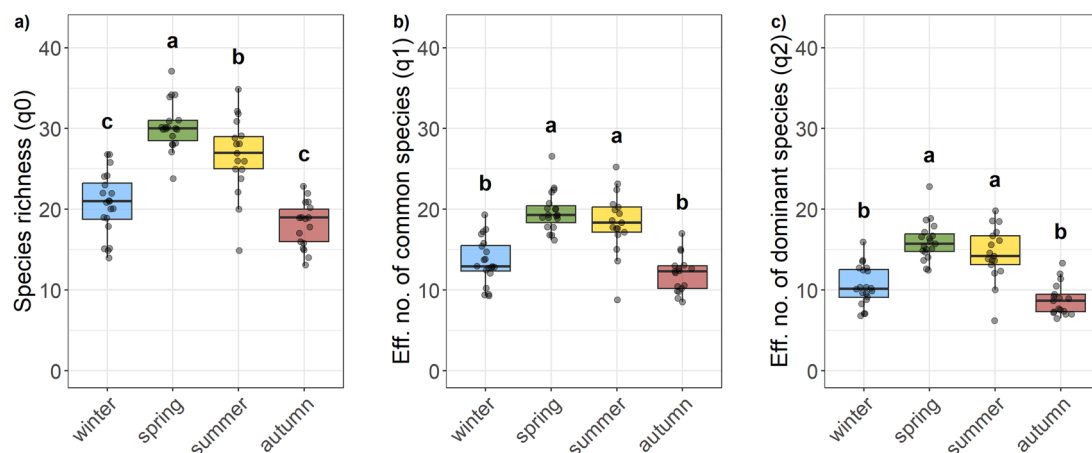


Fig. 2. Hill numbers of bird species diversity between seasons. (a) Species richness, (b) Effective number of common species, (c) Effective number of dominant species. The letters above the boxplots indicate significant differences between seasons. Boxplots display the median (black line), first and third quartiles (box hinges), and whiskers extending to 1.5 x the interquartile range. Group differences were assessed using ANOVA followed by Tukey post hoc comparisons (significance level 0.05). See [Tab. A2](#) in the appendix for the full output.

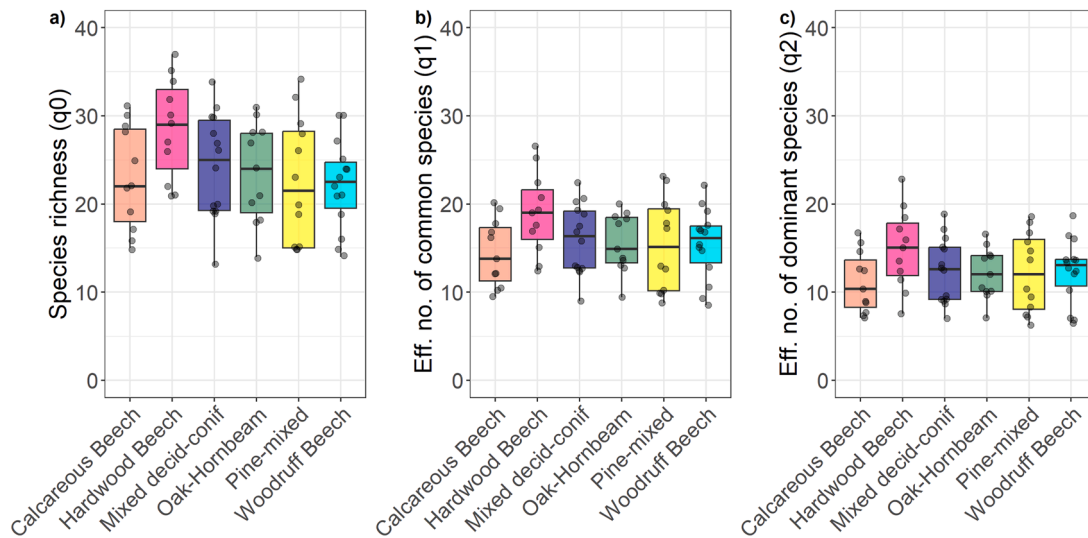


Fig. 3. Hill numbers of bird species diversity between forest types. (a) Species richness, (b) Effective number of common species, (c) Effective number of dominant species. Boxplots display the median (black line), first and third quartiles (box hinges), and whiskers extending to 1.5 x the interquartile range. Group differences were assessed using ANOVA ($p = 0.05$), but none of the differences among forest types were significant. See Tab. A3 in the appendix for full output.

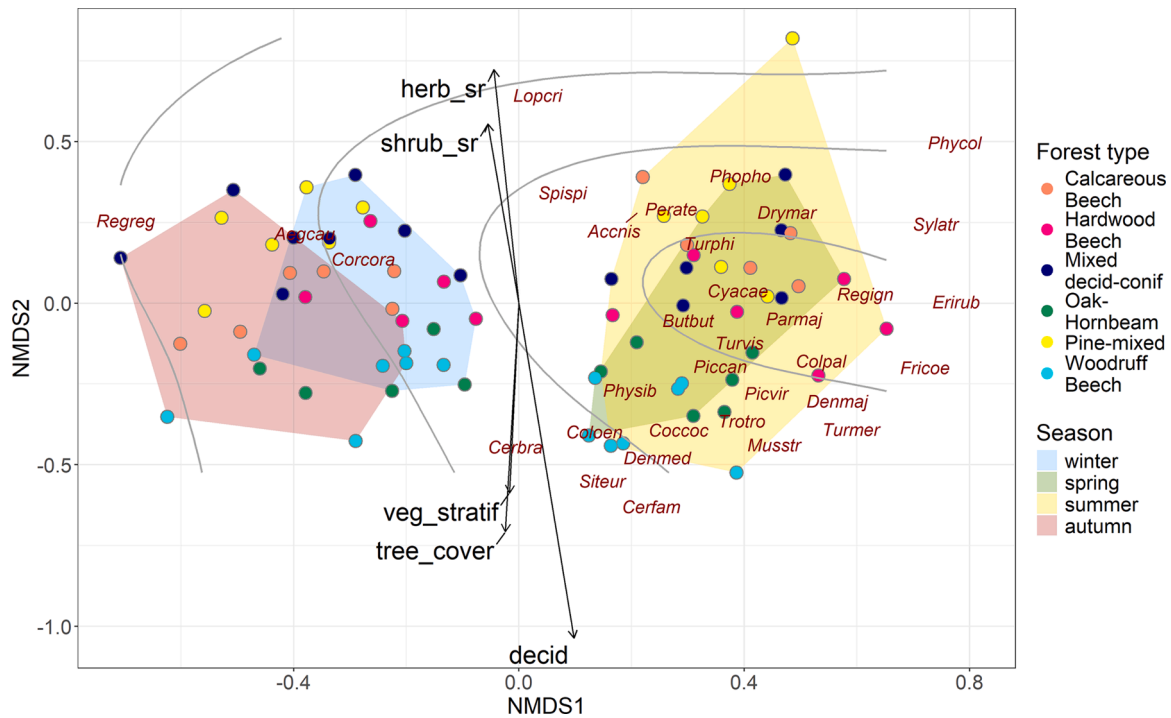


Fig. 4. Non-metric multidimensional scaling of bird communities based on chord distance in 3 dimensions, final stress = 0.15. Points represent the community of one site in one of the four seasons (meaning that each site is represented up to four times). Coloured convex hulls enclose communities of the four seasons. The grey contour lines illustrate species richness gradients, with innermost circles representing highest richness. Only significant predictors ($p < 0.05$) are shown; herb_sr: herb species richness, shrub_sr: shrub species richness; veg_stratif: Shannon index of vegetation stratification, tree_cover: tree cover; decid: basal area share of deciduous trees. Only significant species are shown; Accnis: *Accipiter nisus*; Aegcau: *Aegithalos caudatus*; Butbut: *Buteo buteo*; Cerbra: *Certhia brachydactyla*; Cerfam: *Certhia familiaris*; Coccoc: *Coccothraustes coccothraustes*; Colpal: *Columba palumbus*; Corcora: *Corvus corax*; Cyacae: *Cyanistes caeruleus*; Denmaj: *Dendrocopos major*; Denmed: *Dendrocoptes medius*; Drymar: *Dryocopus martius*; Erirub: *Erithacus rubecula*; Fricoe: *Fringilla coelebs*; Lopcri: *Lophophanes cristatus*; Musstr: *Muscicapa striata*; Parmaj: *Parus major*; Perate: *Periparus ater*; Phopho: *Phoenicurus phoenicurus*; Phycol: *Phylloscopus collybita*; Physib: *Phylloscopus sibilatrix*; Piccan: *Picus canus*; Regign: *Regulus ignicapilla*; Regreg: *Regulus regulus*; Siteur: *Sitta europaea*; Spispi: *Spinus spinus*; Sylatr: *Sylvia atricapilla*; Turmer: *Turdus merula*; Turphi: *Turdus philomelos*; Turvis: *Turdus viscivorus*. The same ordination, plotted with NMS1 vs. NMS3 and NMS2 vs. NMS3, can be found in the appendix (Fig. A4 and Fig. A5).

share was a significant predictor in winter, spring, and summer, while herb cover and/or herb species richness were significant in spring, summer, and autumn. Vegetation stratification seemed to drive the communities in winter and tree cover those in summer. The only significant effect of one of the microclimatic variables was observed in

spring with light. There was no apparent gradient of low to high species richness across seasons, which would be explained by the predictors. The PERMANOVA analysis by season revealed that forest type explained much of the community variance in all seasons except autumn where it was non-significant: 41 % in winter, 48 % in spring, 47 % in summer (all

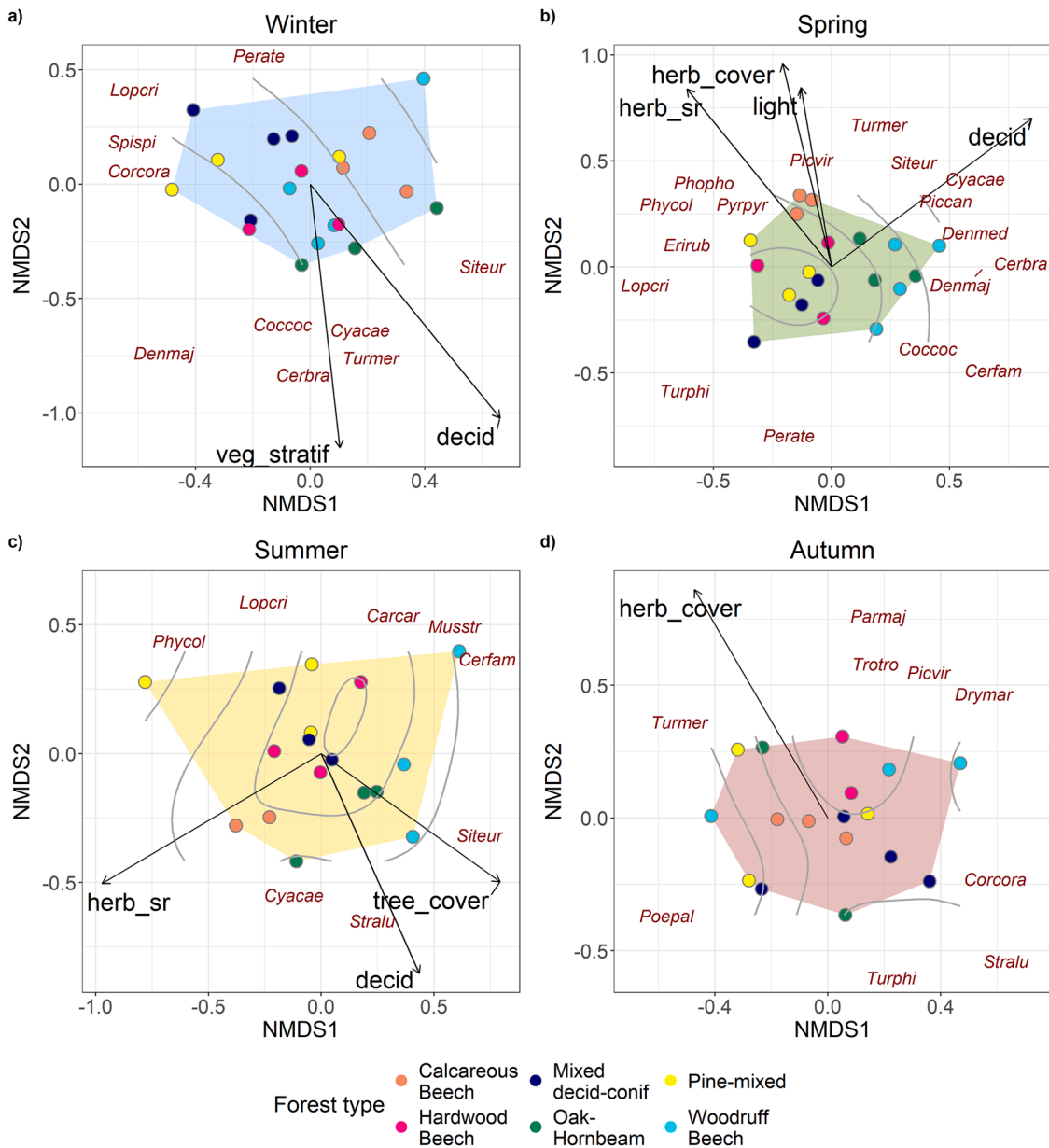


Fig. 5. Non-metric multidimensional scaling of bird communities for (a) winter (3 dimensions, final stress = 0.12), (b) spring (2 dimensions, final stress = 0.18), (c) summer (2 dimensions, final stress = 0.15), (d) autumn (2 dimensions, final stress = 0.18), all based on chord distance. The grey contour lines illustrate species richness gradients, with innermost circles representing highest richness. Only significant predictors ($p < 0.05$) are shown; veg_stratif: Shannon index of vegetation stratification, herb_cover: herb cover, herb_sr: herb species richness, light: light availability; decid: basal area share of deciduous trees. Only significant species are shown; Carcar: *Carduelis carduelis*; Cerbra: *Certhia brachydactyla*; Cerfam: *Certhia familiaris*; Coccoc: *Coccothraustes coccothraustes*; Corcora: *Corvus corax*; Cyacae: *Cyanistes caeruleus*; Denmaj: *Dendrocopos major*; Denmed: *Dendrocoptes medius*; Drymar: *Dryocopus martius*; Erirub: *Erithacus rubecula*; Loperri: *Lophophanes cristatus*; Musstr: *Muscicapa striata*; Parmaj: *Parus major*; Perate: *Periparus ater*; Phopho: *Phoenicurus phoenicurus*; Phycol: *Phylloscopus collybita*; Piccan: *Picus canus*; Picvir: *Picus viridis*; Poepal: *Poecile palustris*; Pyrpyr: *Pyrrhula pyrrhula*; Siteur: *Sitta europaea*; Spispi: *Spinus spinus*; Stralu: *Strix aluco*; Trotro: *Troglodytes troglodytes*; Turmer: *Turdus merula*; Turphi: *Turdus philomelos*; Turpil: *Turdus pilaris*. The winter ordination, plotted as NMDS1 vs. NMDS3 and NMDS2 vs. NMDS3, is shown in Fig. A6 in the appendix.

$p < 0.001$; see Tab. A8 in the appendix). Deciduous BA share explained 16 % in winter, 17 % in spring, 14 % in summer, and 14 % in autumn (all $p < 0.01$; see Tab. A9 in the appendix).

3.2.1. Indicator species analysis

The indicator species analysis identified several species characteristic of the different seasons. *Turdus pilaris* was the only species mainly found in winter (Table 1). In contrast, several species were typical for spring (*Picus canus*, *Turdus viscivorus*, *Chloris chloris*, *Lullula arborea*) and for summer (*Muscicapa striata*, *Phoenicurus phoenicurus*, *Accipiter nisus*, *Apus apus*, *Falco tinnunculus*). Multiple species were associated with two

or three consecutive seasons, notably *Parus major* for winter, spring, and summer, and *Troglodytes troglodytes* for spring, summer, and autumn. No typical species for autumn only was found (Table 1).

3.3. 3.3 Functional diversity

In functional dispersion (FD_{is}, the species activity-days-weighted deviation of trait values from the centre of the functional trait space), there were significant differences between the seasons, but not for functional evenness (FE_{ve}, how evenly species activity days are distributed across the functional trait space). FD_{is} was highest in

Table 1

Results of the indicator species analysis for the different seasons, both individually and in combinations.

Species	Square root of the indicator value	p-Value
Winter		
<i>Turdus pilaris</i>	0.59	< 0.001***
Spring		
<i>Picus canus</i>	0.84	< 0.001***
<i>Turdus viscivorus</i>	0.74	< 0.001***
<i>Chloris chloris</i>	0.41	< 0.05*
<i>Lullula arborea</i>	0.40	< 0.05*
Summer		
<i>Muscicapa striata</i>	0.80	< 0.001***
<i>Phoenicurus phoenicurus</i>	0.59	< 0.001***
<i>Accipiter nisus</i>	0.47	< 0.05*
<i>Apus apus</i>	0.42	< 0.05*
<i>Falco tinnunculus</i>	0.39	< 0.05*
Winter + Spring		
<i>Spinus spinus</i>	0.70	< 0.001***
Spring + Summer		
		< 0.001***
<i>Fringilla coelebs</i>	0.95	< 0.001***
<i>Erethacus rubecula</i>	0.94	< 0.001***
<i>Phylloscopus collybita</i>	0.93	< 0.001***
<i>Turdus merula</i>	0.89	< 0.001***
<i>Sylvia atricapilla</i>	0.85	< 0.001***
<i>Regulus ignicapilla</i>	0.83	< 0.001***
<i>Picus viridis</i>	0.77	< 0.001***
<i>Columba palumbus</i>	0.75	< 0.001***
<i>Turdus philomelos</i>	0.69	< 0.01**
<i>Dendrocoptes medius</i>	0.59	< 0.05*
<i>Phylloscopus sibilatrix</i>	0.44	< 0.05*
Winter + Spring + Summer		
<i>Parus major</i>	0.95	< 0.001***
<i>Periparus ater</i>	0.73	< 0.001***
Winter + Summer + Autumn		
<i>Aegithalos caudatus</i>	0.78	< 0.05*
Spring + Summer + Autumn		
<i>Troglodytes troglodytes</i>	0.82	< 0.001***

summer, followed by spring, and autumn and winter were on the lower end. This trend was the opposite for FEve, where values were lowest in spring and summer and highest in winter and autumn (Fig. 6). For full ANOVA and post hoc test outputs, see Tab. A10 in the appendix.

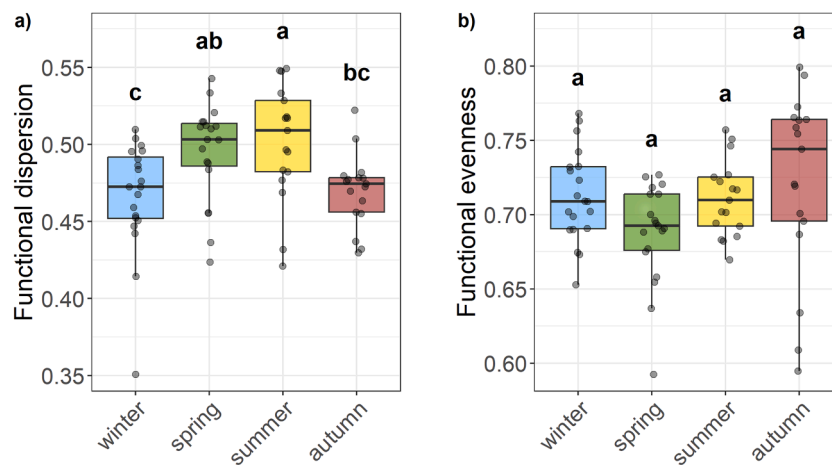


Fig. 6. Functional diversity of bird communities in different seasons, (a) Functional dispersion, (b) Functional evenness. Boxplots display the median (black line), first and third quartiles (box hinges), and whiskers extending to 1.5 x the interquartile range. Group differences were assessed using ANOVA followed by Tukey post hoc comparisons (significance level 0.05).

For FDis, significant differences between the forest types could be found, but not for FEve (Fig. 7). For full ANOVA and post hoc test outputs, see Tab. A11 in the appendix.

The bird communities, plotted according to functional dissimilarity, show partial differentiation by season, with some overlap, especially between spring communities and all other communities (Fig. 8). Forest types contribute to structuring functional assemblages to some extent, as evident from the point colours. When considering all seasons together, no environmental predictors were significant.

The PERMANOVA indicated significant differences in functional community composition among seasons (Bray–Curtis, $F_{3,69} = 10.62$, $R^2 = 0.32$, $p < 0.001$; 9999 permutations). Post hoc pairwise comparisons (using pairwise Adonis) revealed significant differences between winter and spring, winter and summer, spring and autumn, spring and winter, and summer and autumn (see Tab. A12 in the appendix for full output). In contrast, the PERMANOVA revealed no significant differences in functional community composition among forest types (Bray–Curtis, $F_5, 67 = 1.21$, $R^2 = 0.08$, $p = 0.20$; 9999 permutations; see Tab. A13 in the appendix for full output).

To investigate seasonal changes in environmental variables, we performed NMDS ordinations separately for each season. The only significant predictor for the spring communities was temperature. See Fig. A7 in the appendix for the ordination plots.

4. Discussion

Our study revealed that season is the main driver for species diversity, species composition, and functional diversity of bird assemblages in Central European forests. Winter and autumn assemblages differed significantly from spring and summer assemblages in both species diversity and composition. Functional diversity – as measured by functional dispersion and functional originality – was highest in spring and summer and lowest in autumn and winter, reflecting greater variation from central functional trait space and the presence of more species with rare or unique traits during warmer seasons. However, species composition was also consistently affected by the gradient from deciduous to coniferous forest types across seasons, revealing a strong effect of forest management on acoustic bird assemblages throughout the year.

4.1. Taxonomic diversity

We found significant differences in bird diversity across seasons, but not between forest types. Seasonal variation was primarily driven by migratory species that arrived in spring and remained through summer

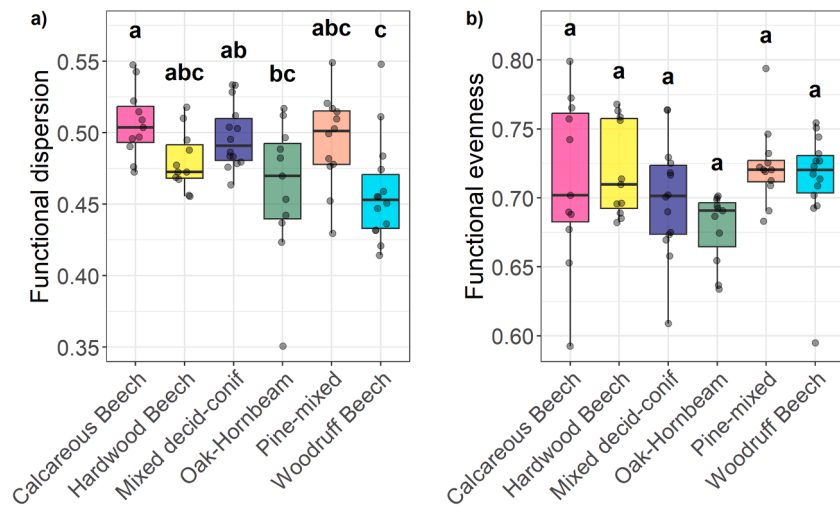


Fig. 7. Functional diversity of bird communities in different forest types, (a) Functional dispersion, (b) Functional evenness. Boxplots display the median (black line), first and third quartiles (box hinges), and whiskers extending to 1.5 x the interquartile range. Group differences were assessed using ANOVA followed by Tukey post hoc comparisons (significance level 0.05).

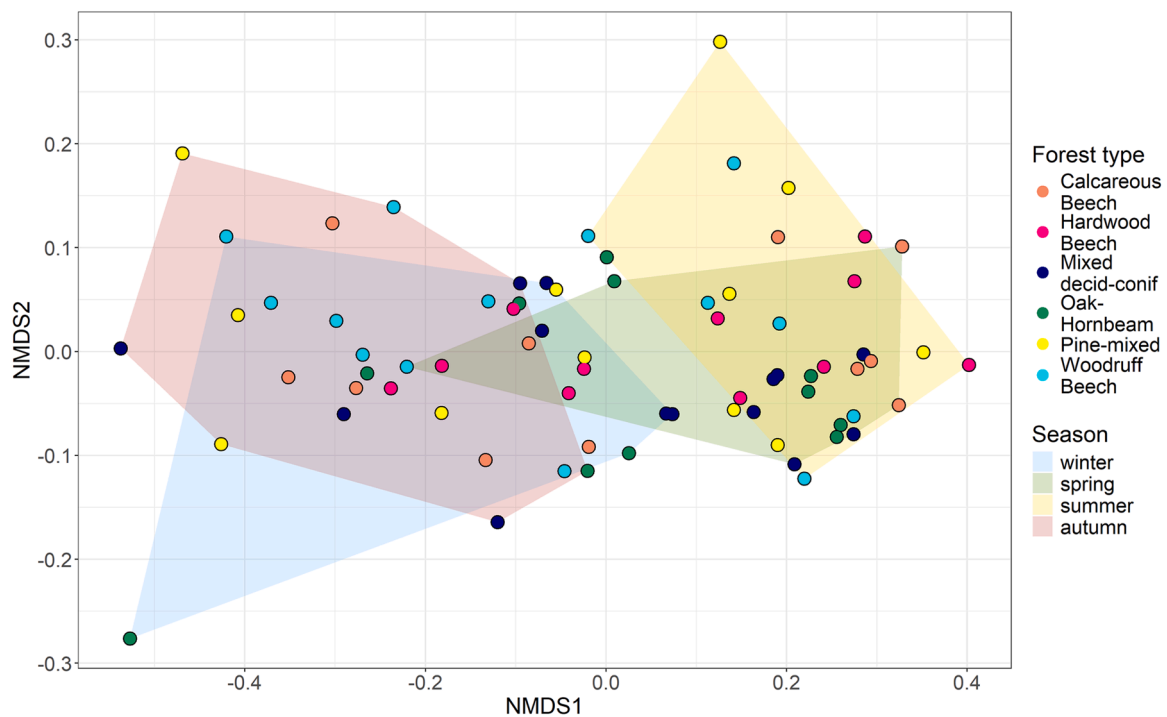


Fig. 8. Functional dissimilarity ordination of bird communities across all sites and seasons using non-metric multidimensional scaling (NMDS) based on Jaccard distance with two dimensions. Each point represents the functional trait composition of a single site-season combination, and the distance between two points illustrates their functional similarity or dissimilarity. The ordination stress value of 0.09 indicates a good fit.

but had departed before our autumn sampling in November. A total of 58 species were included in our analysis, of which 52 were detected during the spring period. This species richness is comparable to that reported in point-count studies of temperate European forests during spring (Augustynczyk et al., 2019; Batáry et al., 2014; Renner et al., 2018; Sommer and Fichtner, 2023). Only *Apus apus*, *Falco tinnunculus*, *Pernis apivorus*, *Pica pica*, and *Turdus iliacus* and *T. pilaris* were recorded outside, but not during, spring.

Richness peaked in spring and summer, likely because migrants left before autumn and winter (Barbe et al., 2018). Effective numbers of common and dominant species (Hill numbers with $q = 1, 2$) showed the same seasonal pattern, with higher values in spring and summer,

reflecting both higher richness and greater evenness. This suggests seasonal diversity differences are shaped not only by rare but also common species, and that winter and autumn communities are less even and dominated by fewer species.

Our analysis revealed no significant differences in species richness among forest types. While previous research has linked higher proportions of coniferous trees to reduced bird species richness (Zeller et al., 2023), we found that the proportion of basal area covered by deciduous trees – which was strongly negatively correlated with conifer cover – did not predict richness in our study. This aligns with other studies reporting no significant effect of dominant tree species on bird species richness (Charbonnier et al., 2016; Hanzelka and Reif, 2016; Schuldt et al.,

2022). One explanation for this is that although different forest types might harbour distinct communities (see below), bird species richness can still be comparable across them. Furthermore, the high mobility of birds possibly enables conifer specialists to occur in deciduous forests and vice versa. Additionally, our aggregation of species richness over 30-day periods may have obscured site-specific specialisation by individual species.

The only forest-related predictor to emerge as significant in our seasonal models was shrub species richness in autumn, which was positively associated with avian richness. This relationship likely reflects the importance of fruit-bearing shrubs as an autumn food source for birds (Suthers et al., 2000), particularly during migration or pre-winter periods. However, the observed association could also indicate a positive effect of shrubs as structural refuges (Moudrý et al., 2021).

Taken together, these results indicate that all forest types in our study support comparable levels of bird species diversity. In turn, bird species richness does not appear to be a suitable indicator of varying forest types and management intensities, and thus of evaluating nature conservation efforts (Boch et al., 2013).

4.2. Community composition

The ordination of community composition revealed distinct seasonal patterns, most prominently between spring-summer and autumn-winter (Fig. 4). These differences are driven by differences in species dominance and the presence of unique assemblages, as autumn and winter species lists are mainly subsets of the spring and summer communities, reduced to resident species. Winter assemblages exhibited greater homogeneity than those in other seasons, likely due to lower species richness resulting from migration (Barbe et al., 2018). In contrast, summer communities showed the highest heterogeneity, with greater variation in species vocal activity and richness relative to spring.

Within seasons, bird communities clustered by forest type, forming a transparent gradient from deciduous to mixed to coniferous forest sites. Previous studies also found that such a gradient was most important in structuring bird communities (Barbe et al., 2018; Hanzelka and Reif, 2016; Rehling et al., 2023; Schuldt et al., 2022). This can be explained by differences in habitat preferences and resource requirements among species (Storchová and Horák, 2018). In our case, the deciduous-mixed-conifer gradient was most pronounced in spring and summer. During winter and autumn, the birds possibly moved more across forest types, being less restricted to their nesting sites and searching for food more opportunistically (Carrascal et al., 2016). Lower species diversity and reduced vocal activity during these colder seasons may have further obscured distinct community patterns.

The significant species in the ordination further supported the forest-type gradient from deciduous to coniferous forest sites. Coniferous sites were characterised by species such as *Lophophanes cristatus*, *Spinus spinus*, and *Regulus regulus*, which all prefer conifer habitats (Hamedani Raja et al., 2025; Storchová and Horák, 2018). These sites also exhibited higher shrub and herb species richness, likely due to reduced canopy cover, which allowed for a more diverse understory. In contrast, the lower end of the ordination plot was dominated by species common in deciduous forests, such as *Certhia brachydactyla*, *C. familiaris*, *Sitta europaea*, and woodpecker species. These species are cavity nesters (Storchová and Horák, 2018), and their association with these sites aligns with the higher abundance of tree microhabitats in sites with higher share of basal area by deciduous trees, particularly in sites with oaks. Oaks are known to support a greater number of microhabitats and are generally recognised as beneficial habitats for birds (Penone et al., 2019; Vuidot et al., 2011). Sites with higher share of basal area of deciduous trees also had higher tree cover and higher vegetation stratification, reflecting higher evenness in the cover values of the three vegetation layers. Microclimatic variables, however, did not emerge as drivers of species community composition, likely because similar microclimatic conditions were observed in autumn and spring, or

because differences in vegetation masked microclimatic differences between sites.

When looking at the ordination plots separately by season (Fig. 5), the patterns observed in the full-year ordination remained consistent. Notably, in spring, light was identified as a significant predictor, being particularly high at the Calcareous Beech forest sites, which were among the steepest sites and relatively open. This likely allowed for this higher understorey vegetation diversity around the beginning of the vegetation period. Overall, these findings highlight forest type, especially along the coniferous-mixed-deciduous gradient, as a primary driver of bird community structure within seasons. This aligns with previous studies, such as those by Sommer and Fichtner (2023), which documented differences in community composition between managed and unmanaged forest stands. Similarly, Schuldt et al. (2022) reported significant variations in community composition between pure beech and pure conifer stands, and Leidingner et al. (2021) found significant changes in bird community composition between deciduous or conifer monocultures and mixed stands.

The indicator species analysis further supported the seasonal differences, but not the forest-type gradient. Several species showed pronounced seasonal fidelity, serving as indicators of particular periods and confirming migration patterns. For instance, *Turdus pilaris* and *T. iliacus* were detected only in winter (and in autumn for the latter), reflecting their status as northern breeders that overwinter in Germany. Resident species such as *Parus major* and *Troglodytes troglodytes* acted as multi-season indicators, underscoring their year-round presence in the study region. Conversely, species like *Spinus spinus*, despite breeding locally and being known as winter visitors, did not show an increase in activity days during the colder seasons, which could, however, be due to seasonal differences in vocal activity and thus highlights that our data are not suitable for assessing abundance changes.

Although no species emerged as indicators of particular forest types, the PERMANOVA and post hoc tests revealed significant compositional differences among some forest types. The absence of forest-type-specific indicator species may be due to the small sample size per forest type, or to the fact that the ecological differences between the six forest types were too subtle to yield species uniquely associated with them. In any case, this underscores that the most ecologically meaningful pattern across seasons is not the distinction among the six predefined forest types, but rather the continuous coniferous-mixed-deciduous forest gradient that structures bird community composition.

4.3. Functional diversity

Functional dispersion (FDis) was highest in spring and summer and lowest in autumn and winter. This reflects greater variation from the central functional trait space during the warmer seasons and indicates that more species with rare or unique traits were present during these seasons. In contrast, the colder seasons appeared to be dominated by more generalist species with more common functional traits, a pattern confirmed by Martin and Fahrig (2018). Functional evenness (FEve) showed no significant seasonal differences, indicating that the regularity of trait distribution among species remained stable across seasons. However, despite the increases in FDis, the lack of differences in FEve implies that the pattern of trait distribution did not become more balanced. This suggests that species joining in the warmer seasons increased trait space (as reflected in the increase in FDis), but unevenly (since FEve did not change). In this context, we can consider the concept of ecological niches (MacArthur, 1965; Pigot et al., 2016). It investigates how niche and functional trait occupation change with increasing species richness, offering two patterns: one is niche expansion, where additional species add new functional traits and thus increase the volume of the trait space, and the other is niche packing, where the additional species cluster with the existing ones in the trait space, potentially leading to higher specialisation or higher overlap of niches. In our case, we observe mainly niche expansion in the warmer seasons compared to

the colder ones, as shown by the increase in FDis.

Significant differences in FDis were observed among forest types, with Calcareous Beech forests exhibiting the highest and Woodruff Beech forests the lowest values, while other forest types occupied intermediate positions. Notably, these results contrast with previous studies (e.g., Schuldt et al., 2022), which typically report lower species and functional diversity in conifer stands, both pure conifer and mixed conifer-beech. Our findings suggest context-dependent patterns in functional diversity, warranting further investigation. While FDis varied, FEve showed no significant differences between forest types. This indicates that, although the overall spread of traits in trait space (FDis) is sensitive to forest type – likely due to differences in dominant species, environmental filtering, or resource heterogeneity – the regularity of trait distribution (FEve) is not. The lack of difference in FEve aligns with Schuldt et al. (2022), who also found no variation in FEve between stand types, and contrasts with Charbonnier et al. (2016), who reported higher FEve in forests with more complex understorey structure. Similarly, Renner et al. (2018) found that bird functional groups respond to forest structure, reinforcing the idea that structural complexity can influence functional organisation. Our results suggest that, despite differences in the overall spread of traits, the fundamental patterns of trait uniqueness and distribution regularity are consistent across forest types, possibly due to functional constraints that operate regardless of forest type.

The seasonal convex hulls of functional dissimilarity exhibited greater overlap than observed in taxonomic community composition, yet still revealed distinct seasonal clustering (Fig. 8). This pattern provides evidence for functional temporal turnover. Still, the greater overlap suggests that functional redundancy within the community buffers against compositional changes (Tsianou et al., 2021). As species composition shifts seasonally, their functional roles are often filled by other taxa, maintaining overall ecosystem processes. This is further supported by the fact that the ordination did not reveal as much apparent clustering by forest type as did the ordination based on taxonomic identity, suggesting that similar functional roles are maintained across habitats regardless of species composition. The lack of significant environmental predictors in this analysis – and also in the season-specific analysis, where temperature in spring was the only significant predictor – indicates that patterns in functional dissimilarity are either driven by different environmental factors than those investigated here, or that they are primarily a consequence of seasonal taxonomic turnover (Tsianou et al., 2021; White et al., 2018). Together, these findings suggest that while bird communities undergo substantial changes in taxonomic composition across seasons and habitats, their functional roles remain more stable, with important implications for ecosystem resilience.

4.4. Limitations

Some methodological limitations should be mentioned. Our species richness estimates are conservative, as we excluded habitat-inappropriate species, those detected fewer than 50 times by BirdNET, and species for which logistic regression thresholds (based on validation) resulted in the exclusion of all detections (Schuster et al., 2024; Shaw et al., 2022). Our approach, thus, may have omitted some rare species. Still, the species accumulation curves (see Fig. A2 in the appendix) indicate that the sampling coverage was sufficient to capture most species in the ecosystem, and comparative studies found that passive acoustic monitoring may capture species richness comparable to that of point counts (Fairbairn et al., 2025; Kułaga and Budka, 2019). At the same time, false positive detections of species with vocalisations similar to those of other species (e.g., *Regulus regulus* vs. *R. ignicapilla*) led to higher detection thresholds and potentially lower final counts, i.e., activity days (Schuster et al., 2024). These effects may vary in magnitude between seasons, as vocal activity changes over the year (Ehnes et al., 2018; Gil and Llusia, 2020). It should also be noted that reliable abundance estimates, which are ideally needed for community analyses,

could not be obtained in this case (see Pérez-Granados and Traba, 2021). However, we presume that our method of calculating species activity days is appropriate, as this metric indicates a site's importance to a species while minimising species-specific behavioural differences in vocal activity. Additional factors – such as weather (Schäfer et al., 2017), vegetation density (Darras et al., 2016), and presence of neighbouring birds (Sánchez and Mennill, 2024) – may influence both avian vocal behaviour and what is captured by AudioMoths (A. P. Hill et al., 2018). The effective detection area of each recorder is also complex to define (Winiarska et al., 2024). In addition, a future study could, given the resources, expand the monitoring period to cover a full year without gaps, allowing for even finer-scale observations of bird community patterns. Despite the challenges of processing and storing large amounts of audio data, the advantages of PAM outweigh these limitations, making it a valuable tool for biodiversity assessments (Sugai et al., 2019). PAM allows for more standardised, continual, and time-extending monitoring than manual point counts.

4.5. Implications for forest management

Our study, one of the first to examine year-round acoustic bird assemblages, reveals that season has the most significant influence on species diversity, species composition, and functional diversity in Central European forests. Importantly, we also found that forest type – particularly when following the gradient from deciduous to coniferous stands – significantly shapes community composition across seasons. This underscores that management decisions influencing stand structure and tree species have significant and long-term effects on bird assemblages, as each forest type, including conifer-dominated stands, supports distinct and diverse bird communities throughout the year. These results advance our understanding of forest ecosystems by revealing how both seasonal dynamics and forest management interact to structure bird communities. Especially in light of the functional analyses, it becomes clear that the assessment of management consequences on ecosystem properties should focus on complete assemblages rather than just typical forest species. There have already been studies that found effects of warming temperatures due to climate change on bird species' phenology; for example, Samplonius et al. (2018) found that residential populations were more sensitive than migratory ones. In any case, it can be expected that climate change will alter bird communities, with implications for ecosystem function, underscoring the importance of conducting detailed passive acoustic monitoring to document these shifts.

For forest management, our findings highlight the value of maintaining a mosaic of forest types at small scales to promote year-round avian diversity. The presence of functional redundancy further suggests that these communities possess some resilience to habitat changes. Conducted entirely within the urban-adjacent forests of Jena, our study highlights the potential for managed, small-scale forests to support high biodiversity, even in human-modified landscapes.

CRedit authorship contribution statement

Markus Bernhardt-Römermann: Writing – review & editing, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization. **David Singer:** Writing – review & editing, Methodology, Conceptualization. **Esther Sophie Felgentreff:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Funding acquisition, Formal analysis, Data curation, Conceptualization.

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Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests. Esther Sophie Felgentreff reports financial support was provided by Federal Ministry of Education and Research Berlin Office. Esther Sophie Felgentreff reports financial support was provided by German Centre for Integrative Biodiversity Research Halle-Jena-Leipzig - iDiv. The other authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.foreco.2026.123617](https://doi.org/10.1016/j.foreco.2026.123617).

Data availability

The BirdNET-based species detections and environmental data used to conduct the analyses can be found under Felgentreff & Bernhardt-Römermann 2025 (<https://doi.org/10.71758/refodat.62>). The raw audio files are available upon request, please see Felgentreff & Bernhardt-Römermann 2026 (<https://doi.org/10.71758/refodat.73>). For a documentation of the AudioMoth and BirdNET workflow and corresponding scripts see <https://git.uni-jena.de/passive.acoustic.monitoring/forest.birds/audiomoths-birdnet>.

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