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Relating forest structural characteristics to bat and bird diversity in the Italian Alps

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ABSTRACT

The global decline of biodiversity has affected European forests, involving many tree species and forest-dwelling threatened animals. An integrated approach linking forest structure and multi-taxon diversity is increasingly needed to maintain the multifunctionality of forest ecosystems. We investigated the relationship between forest structure, deadwood elements, canopy attributes, and tree-related microhabitats on bat and bird communities in the north-eastern Italian Alps. We collected forest attributes, bats, and bird data on 40 forest plots encompassing the diversity of forest types. To assess the different contributions of each forest attribute variables we performed a two-step statistical analysis using generalised and linear models, including bat and bird taxonomical and functional diversity indices as response variables. Our findings reveal that bats and birds respond differently to variation in forest structural characteristics. Specifically, bat species richness was higher in forests with both higher standing tree and lying deadwood volume. The Shannon diversity index for bird community was higher in forests with high volumes of coarse lying deadwood and stumps. Moreover, plots with mature trees, gaps, and heterogeneous diameter distribution fostered the presence of generalist species of bats and birds, while the abundance of tree-related microhabitats was not significant for these two taxa. This study demonstrates that the optimal habitat conditions for bats and birds in Alpine forests are multifaceted. Promoting distinctive elements within forest stands and a complex forest structure through adaptations in forest management interventions would enhance the conservation of multi-taxon forest biodiversity.

1. Introduction

Biodiversity is an essential property of any ecosystem. It is widely recognized that a taxonomically, ecologically, and functionally diverse ecosystem has a higher resilience and adaptive capacity to cope with environmental pressures. Forest ecosystems are essential elements in our landscapes and provide habitat to many taxonomic groups threatened with extinction in numerous regions of the world (Muys et al., 2022; Wende et al., 2018). Moreover, forests with diverse structure (e.g., multi-layered and composed by varying ages) and composition provide multiple ecosystem services, among them timber and non-timber products, carbon sequestration, erosion control, and water retention (Ishii

et al., 2004; Thompson et al., 2011). However, past anthropogenic activities such as logging have significantly modified forest ecosystems with the aim of maximising one or few goods and services (i.e., timber), often simplifying their forest structure and altering species composition, with direct consequences on biodiversity (Brockerhoff et al., 2017; Pereira et al., 2012). The European Forest Strategy and the European Biodiversity Strategy have recently recognised the crucial role of sustainable forest management for biodiversity (European Commission, 2021). Implementing such practices, however, requires a good understanding of the relationship between forest structural attributes (e.g., tree species composition, deadwood, vertical structure) and the abundance and richness of forest-dwelling taxa (Muys et al., 2022;

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Thompson, 2009).

While the effects of forest management on multi-taxon biodiversity is not sufficiently known, the links between indicators of biodiversity and sustainable management is increasingly receiving attention (Burrascano et al., 2023). In this line, monitoring and assessing the relationship between forest structure and forest organisms become important to shape forest management practices to combating biodiversity loss (Angelstam and Dönz-Breuss, 2004).

Among the many species relying on forests, bats and birds are common inhabitants of woodlands, playing a key role in these ecosystems, acting as pest control. For example, some insectivorous bats and birds have a specialised diet on pine processionary moths (Barbaro and Battisti, 2011; Charbonnier et al., 2014) and bark beetle larvae (Fayt et al., 2005). The abundance and richness of bat and bird populations are influenced by the horizontal and vertical structure of the forest canopies and by the presence of multiple elements within forest stands (Bouvet et al., 2016; Lisón et al., 2022). For example, old living trees naturally develop structures that bats and birds use to forage and nest, called tree-related microhabitats (Larrieu et al., 2022; Martin et al., 2022), which in some cases can also develop following a natural or anthropogenic disturbance (Marziliano et al., 2021). In other cases, cavities on the trunk or branches and bark pockets that form naturally on old trees provide the space for these taxa to nest (Kraus et al., 2016). Deadwood elements also play a crucial role, as they provide shelter, and nesting for several species (Bujoczek et al., 2021; Rondeux and Sanchez, 2010), but also food sources, such as arachnids and insects, during the decay process (Aszalós et al., 2020). Deadwood is naturally present in forests, but its amount and diversity in its elements are typically much lower in managed forests, where silvicultural interventions often do not allow a forest to reach late development stages typically rich in large deadwood elements (Martin et al., 2022). Additionally, bats and birds are also affected by the forest's arrangement of trees and canopies (Bouvet et al., 2016; Ishii et al., 2004) as these affect the behaviour and nesting habits of different species (Erasmy et al., 2021). Being canopy-dwelling organisms, a complex canopy structure within a forest stand results in various canopy habitats, thus in potentially more ecological niches, contributing to a higher diversity of these organisms (Ishii et al., 2004). The structural heterogeneity of the canopy determines the light distribution within a forest and supports complex trophic interactions reaching the forest floor, which can positively or negatively affect these two taxa (Depauw et al., 2021; Erasmy et al., 2021).

Several studies show the importance of deadwood, canopy and forest structure, and tree-related microhabitats on the abundance, diversity and dynamics of bats and bird communities. A heterogeneous vertical structure of the forest has been shown to favour bat and bird richness and other taxa (Heidrich et al., 2023), although certain bat species prefer a homogenous forest (Arlettaz, 1999). Russo and Ancillotto (2015) found that bats use deadwood for roosting, and the presence of deadwood was positively correlated with bat diversity. Similarly, Dufour-Pelletier et al. (2020) found that birds were more abundant in forests with higher levels of standing deadwood. Paillet et al. (2018) found that both bats and birds were more abundant in forests with a higher density of microhabitats, such as trees with cavities or hollows, while Cockle et al. (2012) showed that bird species richness was positively correlated with the number of tree cavities in forest fragments. Most of these studies, however, were carried out on a limited number of forest types, on monospecific stands or sampling plots distributed in a single study area (Mataji et al., 2014; Storch et al., 2023), making it hard to generalise implications for management and conservation across administrative regions. Moreover, as a measure of canopy structure, most studies use variables such as canopy openness (Schuldt et al., 2022), neglecting other canopy attributes expressing crown spatial patterns and heterogeneity (e.g., foliage clumping; Cui et al., 2021), which can be derived with indirect methods such as canopy photography (Chianucci, 2019).

on 2. Materials and methods

related microhabitats compared to birds.

multiple forest types in the Alps?

2.1. Study area

The study was conducted within the Autonomous Province of Bolzano/Bozen (South Tyrol) in north-eastern Italy. South Tyrol is a mountainous region in the Central Eastern Alps, with a large elevational range spanning from 204 to 3905 m a.s.l. at the highest mountain peaks. Almost half of South Tyrol's surface is covered by forests, with Norway spruce (*Picea abies*) being the most common tree species (Autonomous Province of Bolzano/Bozen, 2010). Due to a large elevational range, forests across the province vary from deciduous manna ash (*Fraxinus ornus*) with hop hornbeam (*Ostrya carpinifolia*) at low elevations to pure and mixed European beech (*Fagus sylvatica*) and oaks (*Quercus pubescens, Quercus petraea*) stands in the southernmost part. In the central and northern part we find mixed silver fir (*Abies alba*), beech and Norway spruce forests, but also pure montane spruce stands and European larch (*Larix decidua*) with Swiss stone pine (*Pinus cembra*) subalpine forests (Autonomous Province of Bolzano/Bozen, 2010).

2.2. Forest data

We gathered data on forest structure, deadwood elements, canopy characteristics, and tree-related microhabitats on 40 forest sampling plots within the entire study area (Fig. 1). Sampling plots were chosen using a stratified approach based on forest categories, and within each stratum, plots were randomly selected.

Data were collected during the summers of 2021 and 2022, covering



Fig. 1. The study area (province of South Tyrol, Italy) with the 40 randomly selected forest plots considered in this study.

attributes and their key elements, such as canopy structure, deadwood,

and tree-related microhabitats, on bat and bird abundance and diversity

(i.e., taxonomical diversity). Moreover, we are interested in explaining

the relationship between forest characteristics and roosting/nesting

behaviours or foraging of bats and birds (i.e., functional diversity). We

combined forest and biodiversity data from multiple forest types across a

large environmental gradient in the Italian Alps to explore the following

research questions: (1) What forest characteristics are related to the

diversity of bat and bird communities? (2) Is there a common pattern of

forest characteristics shaping both bat and bird communities across

related microhabitats, canopy and forest structure all have a significant

association with bats and birds, but that positive or negative relations

depend on the considered variable and its ecological meaning; (2)

abundance and diversity of both bats and birds are positively correlated

with deadwood volume and heterogenous canopy and forest structure.

Additionally, we expect a stronger correlation between bats and tree-

We hypothesised that: (1) forest attributes relate to deadwood, tree-

an elevation range between 256 and 2094 m a.s.l. and encompassing the diversity of forest types across the study area (Table S1). Following the approach suggested by Burrascano et al. (2021), within each forest site, we collected forest characteristics and structure data in two concentric plots (13-m and 4-m radius) typical of the Italian National Forest Inventory (Gasparini et al., 2022). We surveyed all trees with a minimum diameter of 9.5 cm and 4.5 cm on the two concentric plots, respectively. Tree diameter was measured for all the trees (dead and alive) within each plot. We also measured deadwood elements (complete trees, branches or stems lying on the ground, hereafter logs, and stumps), standing trees' diameter at breast height (DBH) and tree height on a selected number of trees in a 13-m radius plot. On each standing tree (both alive and dead), we visually assessed tree-related microhabitat (TreMs) presence following the catalogue proposed by Kraus et al. (2016). Additional information on our survey protocol can be found in section S1.2 of the Supplementary Material (see also Table S2 and Table S3 for an extensive list of collected variables).

Mean stand mensuration parameters (tree density, basal area, stand height) were then derived from individual tree inventory data. We also calculated the Gini index as a measure of tree size inequality of the forest stand (hereafter structural diversity), ranging from 0 (perfect equality of the individual tree's basal area) to 1 (maximum theoretical inequality; Bourdier et al., 2016). Standing volume for both living and dead trees was calculated with species-specific allometric equations following Scrinzi et al., (2010). Deadwood volume for stumps and logs was calculated by applying geometric formulas (truncated cone for the stumps and cylinder for the logs; Gasparini et al., 2022). TreMs richness was calculated as the number of unique TreMs types per forest site; roost/nest and feeding densities (see Section 2.4 below) were calculated as the number of trees bearing a TreMs that was useful for bats and birds to roost/nest and feed, respectively (Paillet et al., 2017).

Canopy openness (i.e., the proportion of sky that is not obscured by vegetation, viewed from a single point; Jennings, 1999) and clumping index (i.e., the foliage grouping within a distinct canopy; Cui et al., 2021) were assessed using hemispherical photos in each forest site during the summer of 2022. Photos were taken in a 5-point grid, one in the centre and four in the corners, 14.4 m from the centre (see Hilpold et al., 2023 for details of the canopy photography protocol). We used a camera (SONY A6000) and a full-frame fisheye lens (Walimex Pro 8 mm f/2.8 UMC Fisheye II E) mounted on a 1-m height tripod facing upwards. For the best contrast between sky and crowns, the shoot occurred close to sunrise/sunset or during completely overcast days. Photos were processed with the 'hemispheR' package (Chianucci and Macek, 2023). The blue channel of the image was classified using the 'Otsu' thresholding (Otsu, 1979). The hemisphere was then divided into seven zenith rings and eight azimuth sectors to calculate the foliage clumping index and openness from the angular distribution of gap fraction. Plot-level estimates were then derived by averaging canopy attributes across multiple images.

To account for a larger spatial extent than our sampling plots, we calculated forest cover on a buffer of a 250-m radius around the centre of the sampling plot. To do so, we used the tree cover density map (0–100%) from the High-Resolution Layer (HRL) of the Copernicus programme (EEA, 2018) and averaged the 10-m pixel within the buffer. Lastly, to account for changes in tree species composition across our plots, we calculated a broadleaf-conifer ratio based on the basal area of surveyed species (0: 100% broadleaf; 1: 100% conifer).

2.3. Bat and bird data

Bat activity was recorded in the same forest plots between 2019 and 2022 with the detector "BATLOGGER A+" (Elekon AG, Switzerland). The logger was installed at the centre of the forest sampling site, on a tree at 1.5 m height when possible, and was maintained active for three consecutive nights (from sunset to sunrise) between May and October. The selected three-day interval was chosen to mitigate the effect of

adverse weather conditions on individual nights, during which bat activity is significantly lower due to lower numbers of insects, and simultaneously maximize the detection probability of bat diversity (Skalak et al., 2012). Therefore, nights with no precipitation, no strong winds (tree branches should not move forcefully) and with night temperatures of not less than 8/10 °C were preferred. To identify bat echolocation calls to the species, we used the software BatExplorer (version 2.2.3) to measure bat calls automatically. We identified the echolocation sequences manually following Barataud (2020), Russ (2021), and Middleton et al. (2014). When possible, echolocation calls were identified at the species level. However, some bat species, such as Myotis and Plecotus calls, were assessed at the genus level, except for the greater and lesser mouse-eared bat Myotis myotis and Myotis blythii that were distinguished at the group level (M. myotis/M. blythii). Moreover, Pipistrellus kuhlii and Pipistrellus nathusii, were considered a group (Pipistrellus kuhlii/nathusii) since identification at the species level cannot be achieved without social calls (Pfalzer, 2002).

Birds were surveyed in the forest plots using point counts following the project protocol of the Biodiversity Monitoring South Tyrol project (Hilpold et al., 2023). The survey was conducted from mid-April to mid-July from 2019 to 2022. Point counts were performed from the centre of each forest site by the same person (M.A.), and the survey started after sunrise until 11 a.m. and took ten minutes. The researcher used visual and acoustic signals to identify bird species and individuals within a 100-m radius. We performed three repetitions per plot and avoided surveying during strong wind, rain, or snow. Exclusive migrant bird species (Arbeitsgemeinschaft für Vogelkunde, 2010) within the area and individuals only overflying the plots were excluded from the analysis.

2.4. Bat and bird diversity indices

For bat and bird response variables, we calculated species richness and Shannon diversity from data collected in the field using the R package 'vegan' (Oksanen et al., 2007). We then calculated two Community Weighted Mean indices (CWM) to characterise bat and bird communities regarding their roost/nest and foraging preference (see section S1.3 in the Supplementary Materials). This was done using available literature information and computed with the R package 'FD' (Laliberté et al., 2014).

Bat species richness was calculated as the number of species or groups detected at each plot during three consecutive nights. For the bat Shannon diversity index, we used the number of passages recorded by the microphone of each species at each site. The number of passages was considered a proxy for bat activity (Runkel et al., 2021). Bat roosting preference index was calculated by grouping activities of each bat species or group into six categories based on their degree of dependence on trees as overground roost, ranging from the most selective tree-roosting bat species (roosting only in tree holes, cavities, or crevices) to the least ones (bats roosting in caves, cracks, or attics; Dietz and Kiefer, 2016; Table S4). Bat foraging preference was calculated by dividing the activity of each species or group into three groups aligned along an openness gradient of foraging habits: narrow space, edge space, and open space foragers (sensu Denzinger et al., 2016; Table S4 and Table S5).

Bird species richness was calculated from the total number of species observed at each site during all visits. For calculating the bird Shannon diversity index, we chose the observation with the highest number of individuals per species out of all visits at a given site to avoid double counts of the same individual during multiple visits (Anderle et al., 2022). Nest preference was calculated following Anderle et al. (2023) and Marcolin et al. (2021) by grouping nest locations in four categories-aligned along a vertical gradient of forest vegetation development and assigning each bird species to one category (Table S6): rock and building nesters, ground-understory nesters (nesting directly on or close to the ground), mid-story and canopy nesters (closed and open arboreal), and

tree cavity nesters (Storchová and Hořák, 2018). For foraging preference, foraging strata were grouped into seven categories, also along a vertical gradient of forest vegetation development: foraging below the water surface, around the water surface, on the ground, in the understory, at mid-height, in the canopy, aerial (Wilman et al., 2014, Table S6). The mean value was taken when a species had more than one foraging preference.

Once each bat and bird species were characterised by their functional trait and assigned to a category regarding roost/nest and foraging preference, we calculated two CWM indices after constraining all trait values between 0 and 1 to account for the different number of categories (De Bello et al., 2021). For bats, the CWM-foraging preference index ranges from 0, corresponding to a community of narrow-space foragers, to 1 (with only open-space foragers). The CWM-roost preference index ranges from 0 to 1. Low values correspond to a community composed of cavity/crevice tree-roosting bats. For birds, the CWM-foraging preference index varies from 0 to 1 (high values correspond to a community composed mainly of aerial foragers). At the same time, the CWM-nest preference index varies from 0 (community composed mainly of ground nesters) to 1 (community composed mainly of tree cavity nesters).

2.5. Statistical modelling

We first explored the raw data by descriptive statistics (e.g., density plots as shown in Fig. S2 in the Supplementary Material). After standardising all the variables to harmonise their scale, we checked for multicollinearity with the variance inflation function (VIF < 4; Zuur et al., 2013), which confirmed no high correlation among them. The final list of explanatory variables (Table 1) included those related to deadwood (e.g., standing deadwood, lying logs), canopy structure and cover (e.g., openness, clumpiness), TreMs (e.g., richness, TreMs related to feeding or roosting/nesting), forest structure (structural diversity, basal area) and forest composition (broadleaf-conifer ratio based on the basal area).

We performed the statistical analysis in two steps, which allowed us to assess the different contributions of each variable group, and subsequently find the most important variables overall (Harrell, 2015), reducing the number of predictors step by step to avoid overfitting (Zuur et al., 2009). We built generalised linear models for species richness using a Poisson error distribution (count data) and linear models for Shannon diversity and the CWM indices, as they are continuous data (Zuur et al., 2013). In the first step, for each response variable (Table 1), using the *dredge* function, we first built separate models for each variable group: deadwood, canopy structure, tree-related microhabitats, and forest structure (Fig. 2). We selected the most supported models based on the Akaike's information criterion corrected for small sample size; all models with Δ AICc < 4 were considered because models with Δ AICc > 4 have considerably less support (Burnham et al., 2002) and averaged

Table 1

Variables used for the statistical models fitted by the variable group. Here, divided by type. Additionally, here we reported each variable's name, unit, and scale (i.e., sampling plot radius or buffer around the plot).

Туре	Variables	Unit	Scale (m)
Deadwood	Standing deadwood volume	m ³ /ha	13
	Logs volume	m ³ /ha	
	Stumps volume	m ³ /ha	
Canopy structure	Canopy openness	%	13
	Clumping index	-	13
	Forest cover	%	250
Tree-related	TreMs richness	-	13
microhabitats	Feeding density	-	
	Roost/nest density	-	
Forest structure	Structural diversity (Gini index)	-	13
	Basal area	m²/ha	
Forest composition	Conifer/Broadleaf ratio	-	13

to calculate the final estimates.

In the second step, we selected all the variables from each sub-model that were left in the most supported models fitted by group, added the variable accounting for the broadleaf-conifer ratio, and re-ran the same procedure for each response variable. The second step included the broadleaf-conifer ratio to streamline the process and avoid testing it several times for each model by the variable group. We initially tested mixed-effect models using forest category as a random effect. The small sample size of our observations per categories gave no better model results (higher values of AICc), thus we finally introduced the continuous variable (broadleaf/conifer ratio) instead of a random effect per forest type.

Lastly, we obtained four final models (one for each response variable), fitted separately for bats and birds, for a total of eight final models. All analyses were conducted with R 4.2.1 (R Core Team, 2022). For statistical analysis and modelling, we used R packages 'car' (Fox et al., 2012), 'MuMIn' (Barton, 2023), and 'tidyverse' (Wickham et al., 2019) for data processing and visualisation.

3. Results

We recorded 8518 bat echolocation sequences of 17 species or groups across all the forest plots (Table S7). The most abundant group, which accounted for 31% of all sequences, were Mouse-eared bat *Myotis* spp., while the less frequent were Greater noctule bat *Nyctalus lasiopte-rus,* Serotine bat *Eptesicus serotinus,* Long-eared bats *Plecotus spp.,* Geoffroy's bat *Myotis emarginatus* (< 1%). Moreover, we recorded 940 single birds of 57 species (Table S7). The most abundant species, which accounted for 32% of all individuals, were the Common chaffinch *Fringilla coelebs,* Coal tit *Periparus ater,* Common blackbird *Turdus merula,* and European robin *Erithacus rubecula.* On the other hand, three species were only recorded once with one individual (Northern goshawk *Accipiter gentilis,* Eurasian sparrowhawk *Accipiter nisus,* Marsh warbler *Acrocephalus palustris,* Table S7).

3.1. Modelling the relationship between different groups of variables and bats and birds

Overall, bats responded more significantly to the forest variables than birds. Fig. 3 shows the estimates for the linear and generalised linear models by the variable group for bat or bird response indices (see Table S8 and Table S9 for the values of the estimated coefficients and details on the goodness of fit for each model fitted by the variable group). In the sections below, we report the results all the variables included in the model, including the ones that were not fully significant.

The correlation between deadwood variables and the taxonomic and functional diversity of bat and bird was more evident, with more significant variables identified compared to the other three groups of variables (Fig. 3). Standing deadwood volume had a positive association with bat species richness but a negative relationship with bat foraging preference, while this variable was not significant for birds. The volume of logs was negatively correlated with bat species richness but positively related to bat roost/nest preference; this variable was also positively correlated with bird Shannon diversity. Finally, stump volume showed a significant negative association with the bat's roost/nest preference, while it exhibited a slightly positive correlation with the bird roost/nest preference.

Canopy variables showed less significant correlations with bat and bird taxonomic and functional diversity (Fig. 3). Forest cover had only a slight positive relation to bat richness and Shannon diversity (although not fully significant for both). Still, it did not show significant correlations for birds (see also Table S9). Only a slight negative relationship is shown between canopy openness and the bird roost/nest preference, while the clumping index, expressing canopy heterogeneity, did not turn out to be significant for either bats or birds.

Tree-related microhabitats variables only showed some correlation



Fig. 2. Statistical framework used in the study. Sub-models were run for bats and birds for each variable group separately for taxonomical diversity indices and functional diversity indices. Only variables that showed importance from the sub-models were then considered in the final models.



Fig. 3. Estimates of the linear and generalised linear models run in the first step of the analysis. Legend for response variables (vertical axis): S = species richness, H = Shannon diversity, R/N = roost/nest preference, and F = foraging preference. Legend for explanatory variables (horizontal axis): STA = standing deadwood volume, LO = logs volume, STU = stumps volume, CI = clumping index, CO = canopy openness, FC = forest cover, TR = tree-related microhabitats richness, RND = roost/nest tree-related microhabitats density, FD = feeding tree-related microhabitats density, BA = basal area, GI = structural diversity (Gini index). TreMs = Tree-related microhabitat. For forest variables details, please refer to Tables S7 and S8. Darker colours represent stronger associations (blue negative correlations, red positive ones). P-values significance levels: * ** p < 0.001, ** p < 0.5, (*) p < 0.1, n.s.: non-significant. White boxes mean that this variable was not selected in the model. Estimate scales differ between bats and birds.

with bat indices but not for birds (Fig. 3). For example, density of treerelated microhabitats related to feeding resources showed a slight correlation with bat species richness. The richness of TreMs was negatively associated with foraging preference for bats, whereas TreMs related to feed or roost/nest had a negative relation to bat species richness, although this result did not turn out to be significant. Lastly, forest structure variables showed significant association with both bat and bird diversity indices. For instance, the basal area of trees exhibited high significance and negative correlation with bat species richness but also displayed slight negative correlation with bat Shannon diversity. On the contrary, this variable showed a significant positive association with bird roost/nest preference. In contrast, the structural diversity (i.e., the Gini index), instead, had only a slight negative relation to bird roost/ nest preference and foraging preference.

3.2. Final models

Most of the variables selected in the models fitted by variable group also turned out to be significant when pooled together in the final models. The broadleaf/conifer ratio, added only in the final models, was not significant, thus not selected among the final variables. Moreover, AICs values from the final models were lower than the ones from the models fitted by the variable group, suggesting that the models built in the second step were more robust (see also Table S12 and S13 in Supplementary Material).

Concerning bats (Fig. 4a), our results showed a positive correlation between standing deadwood volume and forest cover and species richness. In contrast, volume of deadwood logs and basal area of trees revealed a negative correlation with species richness of bats. TreMs variables were not selected anymore in the final model for species richness. In fact, TreMs richness was discarded in the final model for bats. No explanatory variables were retained for bird species richness in the models fitted by variable groups, so no final model was built for birds. Regarding Shannon diversity (Fig. 4b), all the previously selected variables were maintained in the final models for bats and birds (see also Table S10 and Table S11). For birds, only deadwood log volume was slightly positively correlated with Shannon diversity, while for bats, forest cover and basal area showed opposite associations, which were positive and negative, respectively. Concerning roost preference, bats were negatively related by stumps volume, while coarse lying deadwood were positively correlated with this indicator (Fig. 4c). For birds, forest

variables such as the structural diversity, canopy openness, and basal area of trees showed the same trend as in the models fitted by variable group. The first two variables showed a slight negative association, while the third demonstrated a significant positive relationship. Stumps volume was discarded as explanatory variable in the final model for birds (see also Table S11). Finally, the final model for foraging preference (Fig. 4d) revealed negative associations between standing deadwood volume and bats, along with slight negative relationship of the structural diversity on birds, as previously shown in the models fitted by variable group.

4. Discussion

This study aimed to understand how forest attributes, as structural characteristics, and their key elements such as deadwood and treemicrohabitat, are related to the richness and diversity of bat and bird communities in forests of the Italian Alps. Moreover, we investigated whether bats and birds had a common response pattern to forest characteristics. Despite their ecological importance, this is one of the few works that examine the correlation between bats and forest structural attributes (Zeller et al., 2023). Overall, our outcomes showed that deadwood elements and forest structure significantly shape communities of bats and birds. At the same time, canopy attributes and tree-related microhabitats had little relationship on their abundance and richness. In addition, our results demonstrated that bats and birds are differently related to forest stand characteristics, with bat communities being generally more influenced by the presence of deadwood elements and structural characteristics than birds.

4.1. Influence of forest characteristics on bat and bird communities

In line with our first hypothesis, we found that some forest characteristics can significantly influence the taxonomic and functional diversity of bat and bird communities. However, sometimes the results were divergent, depending on the response and the explanatory variable considered. Deadwood had a positive correlation with both bats and birds, but the outcome differed depending on the deadwood type (whether standing deadwood, lying logs, or stumps), the chosen response variable (e.g., species richness vs Shannon diversity) and the taxon (i.e., bats or birds). The amount of standing deadwood influenced bats only; specifically, our outcomes showed that an increasing volume



Fig. 4. Coefficient estimates from model averaging results of the final models for the four response variables: a) Species richness, b) Shannon diversity, c) Roost/nest preference, and d) Foraging preference. The plot shows the regression coefficient estimates and their confidence intervals at 95%.

of snags within the forest stand resulted in more bat species entering the forest and hunting in clearer aerial space. This result aligns with Tillon et al. (2016) and Bouvet et al. (2016), suggesting that standing dead trees with different decay stages in the forest allow more bat species to benefit from it for foraging. Bouvet et al. (2016) also found that the presence of lying deadwood volume positively influenced the number of bat species. However, our outcomes revealed the opposite, showing that the bat community consisted mainly of bat species that typically had a low dependence on tree as overground roosts. Only a few bat species hunt in the understorey vegetation and use lying deadwood as a foraging source (e.g., M. myotis or M. blythii hunt beetles that live in the logs; Arlettaz, 1999; Dietz and Kiefer, 2016), thus it is plausible that with higher amounts of lying deadwood, there are more bat species that are specialised in foraging at lower strata feeding on it (Langridge et al., 2019). In addition, our results showed that the species detected in forests with large amount of log deadwood were generalists, and the community is mostly composed of non-tree-roosting species; typically, the presence of coarse lying deadwood in the forest is the result of small-scale disturbance events (e.g., windthrows, heavy snow damages, or human activity; Ferenčík et al., 2022), creating heterogeneity within forest stands and allowing generalist bat species, like Pipistrellus pipistrellus, and open-space bats to take advantage of gaps (Heim et al., 2017; Nicholls and Racey, 2006).

Regarding birds, we could see that the community was more diverse with higher volumes of coarse lying deadwood (i.e., with minimum diameter > 9.5 cm as per our sampling protocol), suggesting that more generalist and diverse species take advantage of the forest gaps and decaying logs on the forest floor, which is in line with results by Bujoczek et al. (2021). Finally, stump volume relates to both bats and birds, but eventually, we found this variable to be highly significant only for bat roost preference. This result suggests that, with more stump volume present, the bat community was more characterised by forest-related species that roost in the forest (e.g., *Barbastella barbastellus*). In our case, this can be an indirect result since forests with a larger presence of stumps, due to past management, usually are more productive, adult or mature stands characterised by lower tree density and trees with larger diameters, which in turn provide roost spaces to specialised bats (Larrieu et al., 2022).

Differences in canopy structure did not show relationship to the taxonomic and functional diversity of bat and bird communities, except for canopy openness on bird nesting behaviour. In this case, high levels of canopy openness mainly are connected to forest stands with gaps or large openings, which are ideal habitats for bird species that nest on the forest floor (e.g., *Erithacus rubecola* or *Phylloscopus collybita*). This result is partially in line with Bakermans et al. (2012), where species that nest on the forest floor or in the canopy were positively correlated with canopy openness. Our outcomes also indicate that the continuity of forest cover, which in our case was assessed at a spatial scale of 250-m radius, was positively correlated with the number of bat species and their community diversity. In our situation, the continuity of the forest was interrupted by small gaps that allowed more species and more diverse bat communities to be present when the cover was high (as reported by Hendel et al., 2023).

Regarding forest structure, we found that less diverse bat communities – with generalist species (e.g., *Pipistrellus pipistrellus*) or species that hunt on the forest floor (e.g., *Myotis myotis*) – were more typical of forest stands with a high value of tree basal area (i.e., in our case, mature stands or with the presence of large individuals). Unexpectedly, we did not detect forest-specific bat species in forest stands with these characteristics. Mature, single-storied forests typically have enough free space on the forest floor and in the mid-height layer for bat species to feed on and for generalist species to enter the forest (Dodd et al., 2012; Langridge et al., 2019). In these types of forests, the bird community was instead characterised by bird species that nest in tree cavities (e.g., *Certhia familiaris, Periparus ater, Poecile montanus*); trees with large diameters can develop branches big enough for a bird to nest on, but also cavities high in the crown for nesting (Paillet et al., 2017) – a large share of the latter ones might not have been detected in our field survey of tree-microhabitats (see below). Moreover, birds' communities tended to nest and forage at lower levels when tree size distribution was more heterogeneous; in fact, heterogeneity can create more niches and gaps, allowing more generalist bird species to enter the forest (Franklin et al., 2002; Reif et al., 2022).

Although there have been numerous studies examining the response of forest-dwelling taxa on microhabitats presence (Basile et al., 2020; Martin et al., 2022; Paillet et al., 2018; Regnery et al., 2013), our research did not reveal significant patterns on the presence of these features on bat and bird communities. This might be because the type of microhabitat mainly influencing bats – but particularly birds –are those that are found on crowns or at the intersection of branches at a specific height (e.g., bark shelters, breeding cavities), which were difficult to survey, resulting in a false absence of these particular TreMs (Paillet et al., 2015). Moreover, our survey could not specifically target certain forest-dwelling bird families, such as woodpeckers (see further below), known to take advantage of such TreMs structures on snags and to actively built nest inside trees that can benefit other cavity nesters as overmentioned species (Pakkala et al., 2018).

4.2. Differences between bat and bird responses

Contrary to our second hypothesis, where we assumed that both investigated taxa would benefit from deadwood elements and a heterogeneous forest structure, bat and bird communities reacted differently to forest characteristics. For example, in the case of deadwood, bats were related to all deadwood types, but bird communities were only associated with coarse lying deadwood. Furthermore, while standing deadwood was found to be positively significant for bats, our results revealed no discernible relationship with birds, despite Drapeau et al., (2002) and Beatty et al. (2022) reported the positive role of standing deadwood on bird communities. The reason, however, could be related to our above-mentioned survey method, which was not focused on the reproductive period of some key forest-dwelling bird families, such as woodpeckers (Picideae), as well as nocturnal birds (e.g., Strigiformes; Aszalós et al., 2020; Barbaro et al., 2016). Moreover, in our case, plots with large lying logs indicated more heterogeneous sites. Here, bat communities were composed of fewer species but were more generalist regarding feeding habits, while bird communities were more diverse (i. e., high value of Shannon diversity). The basal area of trees also exhibited opposite correlations with both taxa: it is negatively related to taxonomical diversity only for bats, while functional diversity was related only to birds. Forest stands with a higher basal area was connected to less diverse bat communities composed by more generalist species, but also provided habitats for bird communities characterised by forest specialist that nest on tree branches and in tree cavities. The mature structure allowed birds to find a nesting space on big branches or in tree cavities (Bouvet et al., 2016), while generalist bat species found more free space inside the forest (Allegrini et al., 2022). In contrast to our initial hypothesis, no observed association emerged between canopy characteristics and the taxonomic and functional diversity of either bats or birds. The fact that no significant relationships were detected with this variable might be due to the spatial scale of our investigation using canopy photography, which was likely too small to capture responses of bats and birds. These animals are highly mobile (Jaberg and Guisan, 2001), and small-scale changes in canopy structure are probably not relevant enough for capture patterns on these two communities. Our canopy photography methodology could have likely benefited from additional points for hemispherical photographs, so a larger portion of the forest would have been covered. In addition to this, combining canopy photography with other close-range remote sensing technologies (e.g., aerial and/or terrestrial laser scanning, drone-based multispectral imagery) could have better captured the complex phenomena of interaction between bats and birds and the forest environment on a larger

scale (Clawges et al., 2008; Froidevaux et al., 2016). In our case, only canopy openness somewhat demonstrated an association with bird communities, suggesting that a more heterogeneous forest structure can allow specific bird species to nest on the forest floor (Minias and Janiszewski, 2023).

Partly in line with our second hypothesis, bats responded more to the presence of tree-related microhabitats than birds, at least in the first step of the analysis. The fact that TreMs did not turn out to be strongly significant in our results was likely because the type of TreMs surveyed was of minor importance for birds (Basile et al., 2020). Even if our analysis was carried out across multiple forest types to deliver some management implications that can be generalised for a region, the presence and the type of tree microhabitats strongly depend on the tree species (Vuidot et al., 2011). In our case, we could not differentiate among forest types as we did not have enough replicates; therefore, a possible pattern between microhabitat types could have been obscured.

4.3. Implications for forest management and future developments

Despite the variability in correlations between forest structural attributes and bat and bird diversity, our findings can help derive some practical recommendations on forest management interventions that promote biodiversity conservation in the Alps.

Since our results highlighted the key role of standing deadwood elements for bat and bird communities, preserving a sufficient amount of dead and decaying snags with large diameters can promote the conservation of these species that can take advantage of these structural elements for feeding and nesting or roosting. For example, during silvicultural interventions within forest stands, large snags could be marked in the field, and their presence recorded together with their features (e.g., species, diameter, coordinates, and decay stage) to preserve them in the long term. Similarly, forests with coarse lying deadwood positively influence the diversity of bird communities and contribute to a more diverse bat community by providing habitats for more generalist species. Leaving behind coarse lying deadwood on the forest floor is primarily important for saproxylic taxa (e.g., saproxylic beetles; Parisi et al., 2023, or saproxylic heteropterans; Seibold et al., 2014), which are a food source for bats and birds (Knuff et al., 2020; Rothacher et al., 2023). According to the Third Italian National Forest Inventory (Gasparini et al., 2022), the amount of lying deadwood in South Tyrolean forests is on average 10 m³/ha, which is somewhat higher than the Italian average (5.7 m³/ha in 2015). However, in temperate primary forests the average lying deadwood is described to range between 120–150 m³/ha (Commarmot et al., 2013), but also in forest patches that are left unmanaged for at least 50 years the amount of deadwood can be considerable (Motta et al., 2015). Given the importance of lying deadwood under different decomposition stages for feeding purposes of multiple taxa, among them bats and birds, an increase of this crucial element is desirable to improve ecosystem functioning and biodiversity conservation (Löfroth et al., 2023), pending that this does not conflict with an increased risk of pest outbreaks such as European spruce bark beetle (Ips typographus) in spruce stands (Hlásny et al., 2021; Kärvemo et al., 2017). A feasible option to foster biodiversity in the Alps could be to designate some set-aside areas such as natural forest reserves (i.e., old-growth forest islands) featuring higher amount of deadwood and other structural characteristics (Motta et al., 2022). These interventions could be integrated in large scale and long-term management strategies in mountain regions of the Alps.

Regarding forest and canopy structure, our findings showed that a heterogeneous diameter distribution and the presence of gaps in the forest cover resulted in more diverse bat and bird communities, with generalist species entering the forest; however, our analysis also indicated that a mature forest with large trees was the preferred habitat for forest-specific birds. In the case of a threatened species in need of conservation efforts (for example, *Dryocopus martius* listed in annex I of the Bird Directive (79/409/CEE) requiring mature big trees for nesting and

feeding, mainly on ants (Rolstad et al., 2000; Saporetti et al., 2016)) such knowledge would allow forest managers to plan for specific silvicultural interventions in a target area, and promote certain forest characteristics that align best with the species' habits. Alternatively, fostering a complex and heterogeneous forest structure in an area designated for biodiversity conservation (e.g., a regional park), with both gaps and some large trees, would allow generalist species to enter the forest but also forest-specific species to be present as already reported from other taxa by Heidrich et al. (2023).

Despite delivering novel outcomes and recommendations, we also acknowledge some limitations in our approach that could be overcome with future research. For instance, although we could cover the diversity of forest types across an administrative region, the data surveyed in the field for bat and bird communities and forest structural attributes were only available for 40 plots. Data from more forest sites (e.g., more repetition per forest category) and from larger sampling plots (e.g., for better capturing forest stand heterogeneity) will allow exploring additional structural variables and interactions among them, achieving more robust correlations that could be better generalised for Alpine forests. In addition, monitoring through automated acoustic detectors might provide detection of a wide range of forest bird species (e.g., woodpeckers and owls) and significant responses with the modelled variables, as highlighted by Pérez-Granados and Traba (2021).

Concerning bats, the study's constraints are tied to consecutive recording nights, which were not uniformly distributed across the entire reproductive season. The implementation of our study should consider to incorporating acoustic surveys in various microhabitats, as variations have been observed in both guild composition and species abundance, as already reported by Froidevaux et al. (2014) and Müller et al. (2013).

5. Conclusions

Our study demonstrates that forest structural attributes influence the taxonomic and functional diversity of bat and bird communities in forests of the Alps. Deadwood elements play a key role in promoting bat and bird habitats. Species richness, diversity and roost/nest or foraging preference of these taxa are influenced by the type and amount of deadwood in the forest (standing deadwood, lying logs or stumps). Our analysis also highlighted important differences between the habitat preferences of bat and bird communities: bats were generally more related to deadwood elements and structural characteristics than birds, which were mainly associated with forest stand variables such as canopy openness, basal area and partly by stand heterogeneity.

Forest management can integrate this knowledge into practical implementation by promoting the presence of specific deadwood elements or structural attributes with small-scale interventions and adaptations of silvicultural practices in Alpine forests. Since biodiversity is a key supporting ecosystem service and a crucial component of ecological resilience, ensuring species-rich forest ecosystems via biodiversityfriendly forestry can be considered a win-win strategy for maintaining multifunctional forests under global change.

CRediT authorship contribution statement

Mina Marco: Conceptualization, Funding acquisition, Supervision, Writing – review & editing. Chianucci Francesco: Conceptualization, Investigation, Writing – review & editing. Anderle Matteo: Conceptualization, Formal analysis, Investigation, Writing – review & editing. Paniccia Chiara: Conceptualization, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing. Rigo Francesca: Conceptualization, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing. Tappeiner Ulrike: Conceptualization, Funding acquisition, Writing – review & editing. Obojes Nikolaus: Conceptualization, Investigation, Writing – review & editing. Hilpold Andreas: Conceptualization, Funding acquisition, Writing – review & editing.

Declaration of Competing Interest

The 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.

Data Availability

The data sets supporting the results of this article are available in the Zenodo repository, https://doi.org/10.5281/zenodo.10473817.

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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.2023.121673.

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