


# Soundscapes and airborne laser scanning identify vegetation density and its interaction with elevation as main driver of bird diversity and community composition

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## Abstract

**Aim:** Mountain ecosystems are hotspots of biodiversity due to their high variation in climate and habitats. Yet, above average rates of climate change and enhanced forest disturbance regimes alter local climatic conditions and vegetation structure, which should impact biodiversity. We here investigated the impact of vegetation and elevation as well as their interactions on bird communities to improve our ability to predict climate change effects on bird communities.

**Location:** European Alps, Germany.

**Methods:** We studied patterns and drivers of bird communities at 213 plots along gradients in vegetation density and elevation using autonomous sound recorders. Bird species were identified from soundscapes by Convolutional Neural Networks (BirdNET) and taxonomists.

**Results:** Bird diversity and community metrics were moderately to strongly correlated for data based on either identification by BirdNET or taxonomists (Pearson's  $r = .47-.94$ ), and ecological findings were overall similar for both datasets. Vegetation density 1–2 m and >2 m above ground strongly affected bird diversity and community composition and mediated effects of elevation. Community composition changed with elevation more strongly in habitats with low than high vegetation density >2 m. Species numbers decreased with elevation in habitats with low vegetation density 1–2 m and >2 m above ground, but increased in habitats with high vegetation density. Overall, functional and phylogenetic diversity increased with elevation indicating lower habitat filtering, but patterns were also mediated by vegetation density.

**Main Conclusions:** Our results indicate that bird communities in the German Alps are determined by strong interactive effects of elevation and vegetation, underlining the importance to consider variation in vegetation in studies of biodiversity patterns along elevational gradients and under climate change. Combining remote sensing data and biodiversity monitoring based on autonomous sampling

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and AI-based species identification opens new avenues for bird monitoring and research in remote areas.

#### KEYWORDS

altitude, bioacoustics, BirdNET, mountain, soundscape, succession

## 1 | INTRODUCTION

Mountain regions are hotspots of biodiversity, including endemic and threatened species. High biodiversity in mountain ecosystems is the result of high habitat heterogeneity due to climatic differences between elevations, topographic heterogeneity and natural dynamics initiating successional processes (Körner, 2002). In addition, human land use has modified parts of the landscape, further increasing habitat heterogeneity. However, mountain biodiversity is under pressure due to climate change in at least two ways. First, climatic conditions in mountain regions are changing at rates that are above the global average (Schmeller et al., 2022). Second, climate change is altering disturbance regimes, for example, forest disturbances are becoming more frequent and severe, leading to long-term changes in vegetation dynamics (Albrich et al., 2023; Thom & Seidl, 2021). On top of these climate induced changes, land use practices are changing, including both intensification and abandonment, which is further altering mountain ecosystems (Schmeller et al., 2022). As a response to climate and vegetation change, species have started to shift their ranges, but patterns are variable (Bässler et al., 2013; Vitasse et al., 2021). To predict trends and patterns of mountain biodiversity, a more detailed understanding of the interactions of climate and vegetation characteristics with species communities is needed.

Birds are an emblematic and functionally important taxon including many species of conservation concern. Consequently, patterns of bird communities along elevational gradients have been in focus of numerous studies (McCain, 2009; Quintero & Jetz, 2018; Terborgh, 1977). Different elevational patterns of bird species richness have been observed, such as monotonical decreasing and hump-shaped pattern, and heavily debated (Rahbek, 1995). One inherent problem is that several potential drivers change simultaneously with elevation (McCain, 2009). Vegetation characteristics determine habitat conditions and resource availability for many bird species (Blondel & Farré, 1988; MacArthur & MacArthur, 1961; Moning & Müller, 2008; Müller et al., 2009) and change strongly with elevation. Changes include elevational zones dominated by different tree species, as well as open habitats above the tree line. With increasing elevation, forests usually change in structure, for example, decrease in tree height and canopy cover (Stritih et al., 2023). In addition to these zonal changes in bird habitat characteristics, natural forest disturbances create patchy mosaics of different forest developmental stages, which are inhabited by different bird communities (Hilmers et al., 2018; Moning & Müller, 2008; Thorn et al., 2016).

Moreover, open habitats occur also below the timber line due to natural ecosystem dynamics, such as avalanches or landslides (Alba et al., 2023), and human land use, such as pasturing (Archaux, 2007; Laiolo et al., 2004). Depending on the type and range of habitats included in a study of bird diversity along elevational gradients, elevational patterns of bird diversity may thus differ.

Standardized bird surveys as suggested by Bibby et al. (2000) are methodologically challenging in mountain regions due to limited access for vehicles, steep terrain and quickly changing weather conditions. Under these conditions, it is often neither possible to visit remote sites early in the morning nor to randomize the order at which sites are visited, thus hampering the comparability between study sites. Autonomous bird sound recording has been successfully applied in challenging study systems (Burivalova et al., 2019; Ross et al., 2023; Sugai et al., 2018) and thus, this approach appears promising for mountain ecosystems (Lauha et al., 2022). Simultaneous recording allows to compare vocalizing bird communities from exactly the same time periods between sites and thus ensures the maximum level of standardization. Species can be identified from soundscapes by taxonomists or deep learning algorithms (Kahl et al., 2021; Lauha et al., 2022; Stowell et al., 2019). As mountain ecosystems are particularly under threat from climate change (Schmeller et al., 2022) and birds are important indicator species for global change in mountain environments (Fraixedas et al., 2020), bird monitoring methods that are suitable for mountain regions need to be further refined.

To study how elevation and vegetation interactively shape bird communities and to evaluate the potential of using sound recorders and automated bird sound identification for ecological research, we collected soundscapes at 213 sites in the German Alps. Sites were distributed along an elevational gradient of 1600m and – independent of elevation – along a vegetation gradient from anthropogenic and natural open habitats to open and to very dense forest. Species were identified from soundscapes by taxonomists as well as using the Convolutional Neural Network (CNN) BirdNET (Kahl et al., 2021). Specifically, we asked:

- (i) How strongly are Convolutional Neural Network (CNN)-based metrics of community composition and diversity correlated to data generated by taxonomists, and are metrics based on the two identification methods resulting in similar patterns along elevation and vegetation gradients?
- (ii) How do elevation and vegetation cover interactively shape characteristics of bird communities?

## 2 | METHODS

### 2.1 | Study area and design

This study was conducted at Berchtesgaden National Park, south-eastern Germany, located in the northern Front Range of the Alps (Figure S1). The area is characterized by a steep elevational gradient ranging from 603 m (Lake Königssee) to 2713 m above sea level (a.s.l.; Mt. Watzmann) and a high variation in vegetation cover and structure. Approximately 46% of the national park are covered by forest, with European beech (*Fagus sylvatica*) dominating the submontane zone (<850 m a.s.l.), mixed forests of European beech, Norway spruce (*Picea abies*) and Silver fir (*Abies alba*) in the montane zone (850–1400 m a.s.l.), and conifer forests of Norway spruce, European larch (*Larix decidua*) and Swiss stone pine (*Pinus cembra*) in the subalpine zone (1400–1900 m a.s.l.) (Thom & Seidl, 2021; Walentowski, 2004). Conventional forest management ceased on 75% of the area when the national park was founded in 1978, but due to historic land use, shares of Norway spruce are increased in the submontane and montane zone (Zierl, 2009). About 10% of the area are covered by shrub forest types dominated by dwarf mountain pine (*Pinus mugo*). Moreover, approximately 27% of the area are permanently open habitats including alpine grasslands above the timber line as well as natural open habitats below the timber line, for example, where frequent avalanches, rock slides or flooding prevent forest establishment. Approximately 5% of the area are anthropogenic grasslands managed as summer pastures.

In 2020, we selected 213 plots covering the full gradient in vegetation cover across the elevational gradient from 605 to 2255 m a.s.l. in a stratified sampling approach. We selected plots according to the vegetation that occurred within a radius of 12.6 m around the central point of the plot. In each of the three elevational zones below the tree line (i.e. submontane, montane and subalpine), we selected 10 plots in each of five forest development stages (gap, establishment, optimum, plenter and terminal/decay; (Zenner et al., 2016)) to cover the full gradient of vegetation cover in forests. Forest plots were selected from the 3759 permanent forest inventory plots of the national park based on the inventory period 2010–2012, as well as site visits to assure that plots still represent the respective forest development stage. We selected five plots in anthropogenic open habitats (pastures) in the submontane, montane and subalpine zone, respectively. Finally, we selected four replicate plots in either rock, grass or shrub dominated natural open habitats in each of the three elevational zones below the timber line and in the alpine zone above the timber line. Plots were distributed as evenly as possible over the national park, but for logistic reasons plots were often arranged along access roads and hiking trails resulting in moderate spatial clumping (Figure S1). The minimum distance between plot centres of adjacent plots was 150 m.

### 2.2 | Bird sampling

We used bioacoustic audio recorders (BAR, Frontier Labs, Salisbury, Australia; standard settings) to capture soundscapes in 2021.

Recorders had to be moved between plots and could not be installed permanently due to the limited availability of recorders. On each plot, recording took place on 4–5 days distributed evenly between late winter (mid March) and late summer (mid August) in the submontane, montane and subalpine zones. In the subalpine and alpine zone, only three to four recordings were conducted between late April and mid August due to snow cover restricting access in spring. For an overview of the recording times, see Table S1. Recording was limited to days with no or negligible rain and low wind speed. We placed recorders at approximately 1.8 m height close to the plot centre, either attached to a tree or wooden pole. Recorders were programmed to record for 2 min every 12 min from 2 h before to 4 h after sunrise and from 3 h before sunset to 3 h after sunset.

### 2.3 | Bird identification

For species identification by taxonomists, we selected the first 2 min of every hour of the morning recording, that is, 12 min per plot and sampling day. However, since owls typically sing early in the season (Südbeck et al., 2005), we omitted the recording from 2 h before sunrise from the second sampling on and only used the subsequent five recordings, that is, 10 min per plot and sampling day. Ten minutes per plot and sampling day is a frequently used sampling effort in classic point count surveys in which ornithologists record birds on a plot (Südbeck et al., 2005). Yet, an advantage of the recorders is that the 10 min of recording were evenly distributed over a period of 5 h (6 h on the first recording day) and recordings covered the same time periods for all plots. In some cases, recordings could not be used because of noise (e.g. running water, cowbells and airplanes) masking bird sounds. In such cases, we selected another recording as close in time as possible to the original one. Taxonomists (R.M., Lu.G. and others (see acknowledgments)) identified vocalizing species and documented each species as presence and absence for each recording. For further analyses, we excluded all species which are not breeding bird species of terrestrial habitats of the region to avoid spurious results due to species not associated with the environmental conditions of our plots.

For species identification with BirdNET (version 2.4), a Convolutional Neural Network (Kahl et al., 2021), we used all recordings, that is, 60 min around sunrise and sunset. Each recorded file was split into segments of 3 s before it was presented to the recognition algorithm (settings: overlap=0, sensitivity=1). All species that are not breeding bird species of terrestrial habitats of the region were then excluded. We validated 7399 classifications across 89 (out of 98 species identified by CNN) in order to identify species-specific confidence thresholds that maximize the separation between correct and incorrect identifications. R.M. reviewed 5527 3-s segments and categorized the BirdNET classifications either as true or false positive. We further used annotations of our recordings done by Lu.G. at the Bird Sounds Global platform (<https://bsg.laji.fi/>) of the LIFEPLAN research programme (<https://www.helsinki.fi/en/projects/lifepan>). The annotations were provided with a timestamp

which allowed us to match and categorize 1874 additional classifications. For all species with more than 30 true positive classifications, we fitted Conditional Inference Trees (function 'ctree' in package 'partykit' (Hothorn & Zeileis, 2015)) to identify species-specific confidence thresholds. For species with 5 to 30 true-positive classifications, we visually inspected the distribution of true and false positives along the confidence axis (Figure S2). If the distribution of true and false positives showed a discriminable pattern, we assigned them to one of three threshold classes (0.3, 0.5 and 0.8). If true and false positives were similarly distributed along the confidence axis or if less than 5 true-positive classifications were available, we used the highest threshold class (0.8). For the final list of species-specific confidence thresholds, see Table S2 and Figure S2.

## 2.4 | Trait data and phylogeny

We downloaded the bird megatree by Jin and Qian (2023) based on Jetz et al. (2012), which was pruned to the species identified by one of the two methods applied in our study. Moreover, we compiled information on 11 morphometric traits, two habitat-related traits, migratory behaviour and trophic level from the AVONET database (Tobias et al., 2022). Morphometric traits were corrected for their relationship with body size by taking residuals from linear models with respective traits as response (log-scale) and body mass (log-scale) as predictor (Hagge et al., 2021). Based on correlations among morphometric traits we selected the continuous traits body mass, hand wing index, beak length, beak width, tail length and tarsus length for further analyses. In addition, analyses included preferred habitat (ordinal: 1=dense, 2=semi-open, 3=open), migratory behaviour (ordinal: 1=sedentary, 2=partially migratory, 3=migratory) and trophic level (categorical: herbivore, carnivore and omnivore). The trait trophic level was converted into two binary traits herbivore (0/1) and carnivore (0/1), whereas omnivores were binned 1 in both binary traits.

## 2.5 | Environmental data

We measured the coordinates and elevation of each plot centre using a Trimble r12i GNSS receiver. To characterize vegetation at each plot, we used a high-resolution LiDAR dataset acquired in September 2021 during leaf-on conditions using a helicopter-mounted Riegel VQ-780i sensor with average point density of ~50 points m<sup>2</sup> (Mandl et al., 2023). Vegetation parameters were calculated within a 25m radius around the plot centre by clipping the point cloud to the plot area and normalizing it using an existing ground classification. Vegetation density >2m above ground and 1–2m above ground were calculated as the proportion of returns within these height layers, and the variation in vegetation height was characterized as the standard deviation of LiDAR returns. In addition, we used data on herb layer cover (<1m above ground) and shrub layer cover (1–5m above ground) from ground-based vegetation surveys conducted on one 4m x 4m vegetation survey area per

plot (Braziunas et al., 2024). We tested for collinearities between vegetation characteristics calculating pairwise Pearson's correlation coefficients and by conducting a principal component analysis. Based on these results (Figure S3), we selected LiDAR-based vegetation density >2m above ground and vegetation density 1–2m above ground as predictors for bird analyses since they represent different vegetation layers, were not correlated strongly and reflected a larger area around the plot centre than the parameters derived from the vegetation surveys.

## 2.6 | Statistical analyses

All statistical analyses were conducted in R version 4.3.2 (R Core Team, 2021).

All bird metrics were calculated per plot separately for taxonomists' and CNN data. The number of bird species per plot was calculated as the total number of species observed per plot across all recordings. Community composition was derived using Non-metric Multidimensional Scaling (NMDS) based on Bray–Curtis distances for abundance data using the function 'metaMDS' in the package 'vegan' (Oksanen et al., 2016) with two dimensions (stress values <0.2). We extracted the first and second axes as measures of community composition in all further analyses. To obtain a standardized measure of species diversity accounting for differences in sampling effort, we used the function 'estimated' from the 'iNEXT' package to compute species diversity by considering Hill numbers for a sample coverage of 80% (Hsieh et al., 2016). Results for standardized species diversity are only shown in Table S3, as they were similar to the raw species number.

Phylogenetic and functional diversity were calculated as standardized effect sizes of the mean pairwise distance between co-occurring species for each sample based on either the branch lengths of the phylogenetic tree or a Gower distance of the selected functional traits. Phylogenetic distances were calculated as cophenetic distance using the function 'cophenetic.phylo' in the package 'ape' (Paradis & Schliep, 2019). Functional distances were calculated using the function 'daisy' in the package 'cluster' accounting for categorical, ordinal and continuous variables (Gower, 1971). To obtain measures of functional and phylogenetic diversity that are independent from species number, we calculated standardized effect sizes by comparing the observed mean pairwise distance per plot with 999 artificial assemblages. This was achieved by using null models (function 'ses.mpd' in the package 'picante'; (Kembel et al., 2010)) created via randomly selecting species from the regional species pool (i.e. all species recorded by either one of the two identification methods).

To test how strongly CNN-based metrics match the same metric based on data generated by taxonomists, we calculated Pearson's correlation coefficients for species number, both NMDS axes, phylogenetic diversity and functional diversity based on taxonomists' and CNN data, respectively. In addition, we calculated  $R^2$  (functions 'rsq.glm' and 'rsq.lmm' in package 'rsq'; Zhang, 2022) of fixed effects from (generalized) linear mixed models with the metric based on taxonomists' data as response and the same metric based on CNN

data as predictor. A negative binomial error distribution was used for modelling species number (function 'glmer.nb', package 'lme4'; Bates et al., 2015) and a gaussian error (function "lmer") for both NMDS axes, phylogenetic diversity and functional diversity. Models included 'tour' as random effect to account for spatial clumping of plots along access roads and hiking trails.

To test how elevation and vegetation density interactively shape characteristics of bird communities, we fitted (generalized) linear mixed models for species number, standardized bird diversity ( $q=0, 1$  and  $2$ ), NMDS axis 1, NMDS axis 2, phylogenetic and functional diversity separately for taxonomists' and CNN data with negative binomial errors for species number and gaussian errors for all other metrics. All models included elevation, vegetation density  $>2$  m and vegetation density 1–2 m above ground as well as the interactions between elevation and each vegetation variable as fixed effects and 'tour' as random effect. Elevation and vegetation density variables were z-transformed (mean=0, SD=1).

### 3 | RESULTS

Taxonomists identified 76 breeding-bird species from a total of 8662 min of recording and CNN models identified 84 breeding-bird species with a confidence level above species-specific thresholds from a total of 105,648 min of recording (Table S2). A total of 71 species were identified by both approaches and five and 13 uniquely by taxonomists and CNN models, respectively, resulting in a total of 89 species across both datasets (Figure S4). All five species recorded only by taxonomists were also identified by CNN models but with confidence below the minimum thresholds (Table S2). Of the 13 species identified exclusively by CNN models, three species were confirmed by expert validation (*Anthus pratensis*, *Montifringilla nivalis* and *Delichon urbicum*), while for the others all validated records were false positives (note that the number of validated records was low in some species and that not all records were validated; Table S2).

Bird community metrics based on identification by taxonomists and CNN models showed intermediate to strong correlations (Pearson's  $r=.47-.94$ ) and CNN-based metrics explained between 19% and 88% of the variation in taxonomists' data (Figure 1). The strongest relationship was found for NMDS-axis 1, followed by NMDS-axis 2, species number, phylogenetic diversity and functional diversity. Patterns of bird species number, phylogenetic and functional diversity, and community composition along elevational and vegetation cover gradients were overall similar for data based on taxonomic identification and CNN models with only few differences (Table 1). Only for functional diversity, effects of elevation, vegetation density  $>2$  m and their interaction were weaker for CNN-based data (see below).

Bird species number for both identification methods increased with increasing vegetation density  $>2$  m (Figure 2; Table 1). A significant interaction between elevation and vegetation density  $>2$  m indicated that species numbers decreased with elevation in open habitats with low vegetation density  $>2$  m, but increased with elevation in forests with high vegetation density  $>2$  m, resulting in a non-significant main

effect of elevation (Figure 2; Table 1). Vegetation density 1–2 m above ground had no significant overall effect on bird species number but mediated effects of elevation, as indicated by a significant interaction, similarly to vegetation density  $>2$  m (Figure 2; Table 1). Results for standardized bird diversity for all values of  $q$  were similar to those of raw species number, except for a significant negative effect of vegetation density 1–2 m above ground (Table S3).

Phylogenetic diversity increased with elevation and decreased with vegetation density 1–2 m above ground for taxonomists' and CNN based data (Figure 2, Table 1). A significant interaction term indicated that phylogenetic diversity increased more strongly with elevation in habitats with a high vegetation density  $>2$  m, but only for CNN-based data (Figure 2, Table 1).

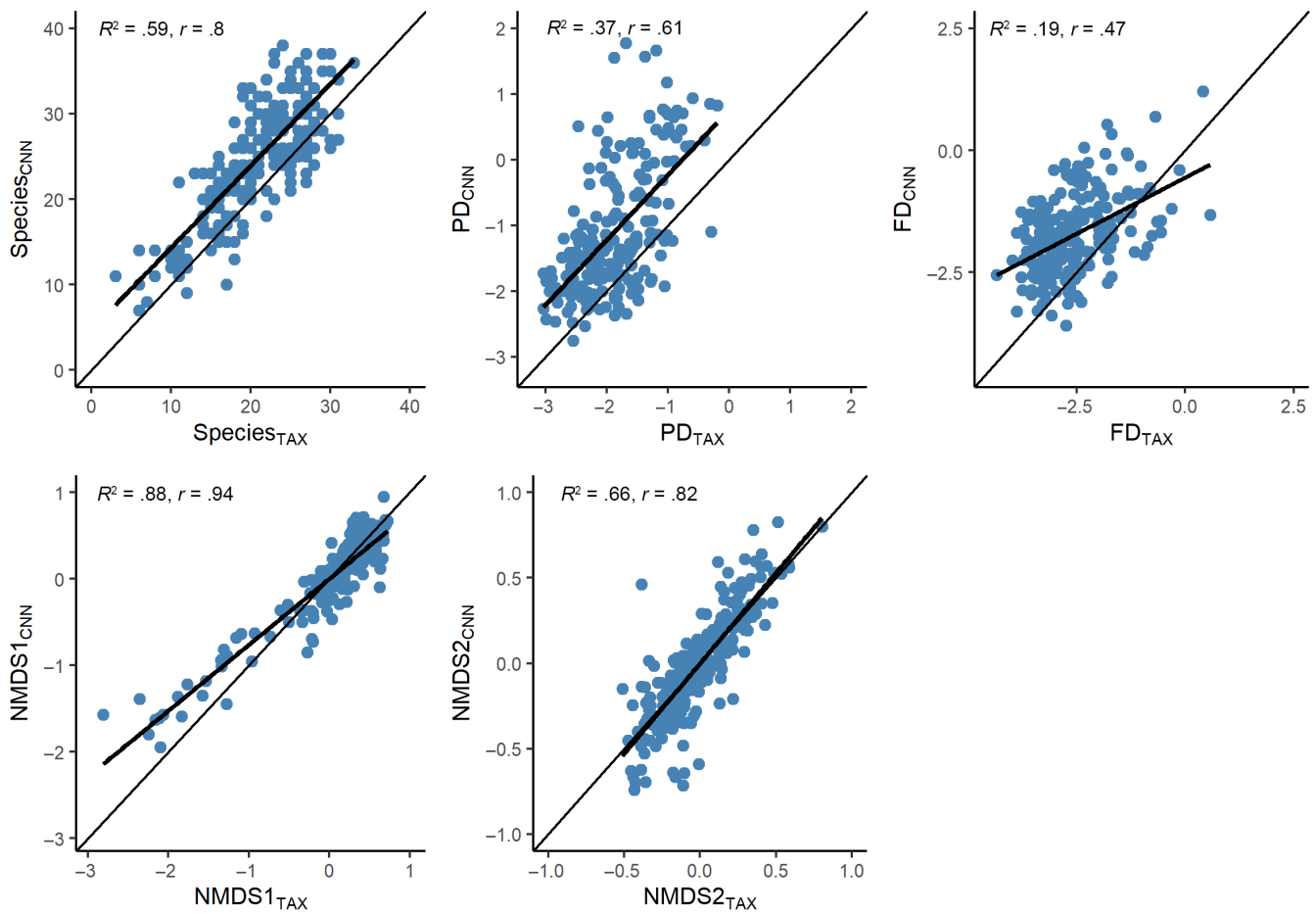
Functional diversity increased with elevation and decreased with increasing vegetation density  $>2$  m. A significant interaction indicated that the increase with elevation was stronger in open habitats with low vegetation density  $>2$  m (Figure 2, Table 1). Yet, these effects were only significant for taxonomists' data. Vegetation density 1–2 m above ground had no overall effect on functional diversity, but modified elevational pattern with stronger increases in habitats with high vegetation density (Figure 2, Table 1).

Bird community composition for taxonomists' and CNN data was similarly affected by elevation and vegetation density  $>2$  m and 1–2 m above ground for both identification methods (Figure S5, Table 1). Both elevation and vegetation density  $>2$  m inversely affected NMDS axis 1 (Figure 2 and S5, Table 1), reflecting that vegetation density decreased with elevation in forests. Effects of elevation on NMDS axis 1 were significantly stronger in open habitats with low vegetation density  $>2$  m than in forests with high vegetation density  $>2$  m, but note that the elevational gradient was longer for open habitats extending beyond the tree line. Vegetation 1–2 m above ground led to changes in community composition along NMDS axis 2 for both data sets and along NMDS axis 1 for CNN data (Table 1).

### 4 | DISCUSSION

Studying bird communities using audio recorders along elevation and vegetation gradients in the European Alps, we found that bird diversity and community metrics were moderately to strongly correlated for data based on identification by taxonomists and CNN and that ecological patterns along elevation and vegetation gradients were similar for both datasets (note that a few differences occurred; Table 1). Species number, phylogenetic diversity, functional diversity and composition of bird communities were driven by interactive effects of elevation and vegetation. In habitats with low density of vegetation  $>2$  m, that is, tall shrubs and trees, species numbers decreased with elevation and communities became functionally less clustered (i.e. less similar). In contrast, species numbers increased with elevation and remained functionally clustered in habitats with a high vegetation density  $>2$  m. In habitats with high vegetation density 1–2 m above ground, that is, herbs and shrubs, bird communities were phylogenetically more clustered (i.e. more closely related) than





**FIGURE 1** Relationships between bird community metrics based on species identification by taxonomists ('TAX') and CNN models including species number, standardized effect sizes of phylogenetic diversity (PD) and functional diversity (FD), and the two NMDS axes describing community composition.  $R^2$  result from (generalized) linear mixed models with the respective metric for taxonomists' data as response and CNN data as predictor.  $r$  shows Pearson's correlation coefficients. Simple regression lines (bold) and 1:1 lines shown for illustrative purposes.

in habitats with low vegetation density 1–2 m above ground. The composition of bird communities changed with increasing vegetation density >2 m and between 1 and 2 m above ground. Moreover, vegetation density >2 m mediated effects of elevation leading to stronger changes in community composition along elevation in habitats with low vegetation density >2 m than in those with high vegetation density >2 m.

#### 4.1 | Acoustic bird monitoring in mountain ecosystems

Bird monitoring in mountain ecosystem is inherently challenging, but this study shows that autonomous audio recorders combined with CNN-based species identification provide an operational solution. Technical and computational advances allowed for major improvements in the field of bioacoustics and species identification from soundscapes over the last years (Darras et al., 2019; Pavan et al., 2022). Direct comparison showed that autonomous bird sound recorders outperform point counts by human observers (Darras et al., 2019). Moreover,

audio recorders can operate autonomously for several months up to a full season, which makes them ideal for bird monitoring in remote and logistically challenging places, such as tropical rain forests (Burivalova et al., 2019) or mountain ecosystems (this study).

The high amounts of data generated by continuous monitoring, however, cannot be analysed by human taxonomists, which spurred the rapid development of methods to identify species automatically (Lauha et al., 2022). BirdNET, the current state-of-the-art CNN method, allows to identify a large number of bird species worldwide (Kahl et al., 2021). Here, we applied BirdNET-Analyzer v2.4, validated a subset of classifications, and compared the generated data to identification of birds from a subset of the same soundscapes by taxonomists. Our aim was not to evaluate the performance for single bird species detections but rather to assess whether bird community metrics derived from BirdNET data as well as ecological patterns of these metrics match those based on taxonomists' data. We found moderate to very strong correlations between metrics of the two datasets with strongest correlations for community composition, followed by species numbers and phylogenetic and functional diversity. Moreover, the ecological patterns of bird species

and community composition along elevation and vegetation gradients were very similar for both data sets. Patterns of phylogenetic and functional diversity were also similar but effect sizes differed. Overall, this indicates that BirdNET is well suited to be used for ecological bird monitoring in the European Alps.

Yet, the detection probability differs between species (Lauha et al., 2022) and thus, if certain focal species are to be monitored, the performance of the specific CNN model for these particular species should be assessed. To exclude identifications with a high chance of being false positives, we applied species-specific minimum confidence thresholds which can essentially improve CNN-based datasets (Singer et al., 2024). These thresholds were based on the validation of >7000 classifications and the distribution of true and false positives along a confidence gradient. This approach allowed to derive unambiguous thresholds for some species, such as the alpine accentor *Prunella collaris*, the pygmy owl *Glaucidium passerinum* and the ring ouzel *Turdus torquatus*. For other species, however, either the number of true positives was too low or a high rate of false positives occurred even at high levels of confidence and thus, we had to apply a generic high threshold of 0.8. Because of this, a few species, such as the wall creeper *Tichodroma muraria*, the golden eagle *Aquila chrysaetos* and the crag martin *Ptyonoprogne rupestris* – all three are alpine specialist species – were excluded from the final BirdNET dataset although they were identified by taxonomists and initially by BirdNET but at confidence levels below the minimum thresholds. Future research should thus aim at improving CNN models for species for which the model performance is still low and at detecting non-generic species-specific thresholds.

A major advantage of soundscape data is that it can be reanalysed anytime with improved algorithms, thus generating highly standardized time-series data (Kitzes & Schricker, 2019). In contrast to time series generated by taxonomists surveying birds in the field, soundscape time series are not sensitive to changes in personnel (Campbell & Francis, 2011; Farmer et al., 2014). Moreover, the use of automatic identification tools allows to analyse longer time periods than observer-based surveys could do, which increases the chance to detect rare species (Darras et al., 2019). In our study, for example, the snow finch *Montifringilla nivalis*, was only detected by BirdNET as it was not present in the fewer recordings analysed by taxonomists.

In this study, recorders could not be installed permanently at each plot due to the limited availability of recorders and the large number of plots and thus, recorders had to be moved between plots several times to record at each plot for at least three times between late winter and early summer. This approach was very labour intensive and, since recording took place only at a subset of plots at the same time, less standardized than simultaneous recording at all plots. Yet, we chose this approach to study spatial patterns of bird communities along environmental gradients with a sufficient samples size and environmental resolution. For long-term monitoring, we suggest to permanently equip all plots with autonomous audio recorders and if necessary, reduce the number of plots while still covering full environmental gradients. This does not only reduce efforts and increase the level of standardization, but also allows to analyse phenological patterns and changes therein.

## 4.2 | Patterns of bird communities along elevation and vegetation gradients

Globally, patterns of bird species number along elevational gradients differ strongly, particularly between climatic regions (McCain, 2009). Within a region, bird species patterns along elevational gradients are partly explained by differences in vegetation structure between elevational zones which typically include several different forest types and, in some studies, also open habitats above the tree line (Acharya et al., 2011; Kattan & Franco, 2004; Terborgh, 1977). In our study, vegetation changed both across and within elevational zones, including open habitat above the tree line as well as below, with the latter including natural permanently open habitats, forest gaps after natural disturbances, and anthropogenic pastures. This high habitat diversity is typical for many mountain regions (Körner, 2002; Schmeller et al., 2022) and enabled us to show that vegetation strongly mediates patterns of bird communities along elevation. In habitats with low density of vegetation taller than 2 m (i.e. pastures, natural open habitats, young canopy gaps) species number decreased with elevation, whereas the opposite pattern was found for forests with high density of tall shrubs and trees. Similar but weaker patterns were found also for lower vegetation 1–2 m above ground. This indicates that elevational patterns of bird species number differ not only between regions (McCain, 2009), but also between vegetation types within regions. This is consistent with the findings that relationships between bird species number and elevation in North America and the Himalayas are partly driven by habitat heterogeneity (Dillon & Conway, 2021; Ding et al., 2021). For studies on elevation patterns, this implies that focusing on certain vegetation types (e.g. the main zonal vegetation types, such as forests) may not reveal the full range of patterns and that, if various vegetation types are included in the data but not accounted for in the analyses, observed overall patterns may be a mix of various different underlying patterns. In our study, it is striking that without considering the interaction of elevation and vegetation density >2 m, the overall pattern of species number against elevation resembles a mid-elevation peak (Figure S6). In contrast, when considering different vegetation types separately, trends of species number with elevation are either monotonically increasing or decreasing (Figure 2).

Bird community composition changed strongly along elevation and vegetation gradients. The first NMDS axis represented a combined gradient of elevation and vegetation >2 m, which reflects that vegetation structure is changing with elevation (e.g. lower canopy cover in subalpine forests (Vandewiele et al., 2023)). The effect of elevation on community composition was strongly mediated by vegetation >2 m with stronger changes in open than in closed habitats. Our findings match results of Blondel and Farré (1988) who studied bird community composition along successional gradients in different climate regions across Europe and found that communities differ strongly between regions in early successional habitats but are highly similar in late successional habitats. While dissimilarity between early successional habitats across Europe may be partly explained by recolonization history after the last glaciation (Blondel & Farré, 1988), there are several potential

TABLE 1 Results from (generalized) linear mixed models testing effects of elevation, vegetation cover and their interaction on bird community metrics based on identification by taxonomists (TAX) or CNN models.

Response	Elevation		Vegetation density >2m		Vegetation density 1-2m		Elevation * vegetation density >2m		Elevation * vegetation density 1-2m	
	z-value	p-value	z-value	p-value	z-value	p-value	z-value	p-value	z-value	p-value
Species										
TAX	-1.48	.14	2.92	<.001	-1.23	.22	5.72	<.001	4.12	<.001
CNN	-.02	.99	4.83	<.001	.82	.41	7.13	<.001	2.47	.01
PD										
TAX	2.16	.03	1.50	.13	-3.05	<.001	-.43	.67	-1.74	.08
CNN	2.05	.04	.48	.63	-3.62	<.001	2.06	.04	1.73	.08
FD										
TAX	3.89	<.001	-4.03	<.001	.96	.34	-7.53	<.001	2.32	.02
CNN	1.16	.24	-1.93	.05	-1.24	.21	-.64	.52	2.03	.04
NMDS1										
TAX	-12.74	<.001	1.93	<.001	.13	.90	12.26	<.001	1.15	.25
CNN	-12.66	<.001	16.11	<.001	3.21	<.001	9.63	<.001	.53	.59
NMDS2										
TAX	-.39	.70	.21	.83	4.50	<.001	.70	.49	-1.67	.09
CNN	-1.69	.09	.68	.50	5.32	<.001	-.06	.95	-2.47	.01

Note: Significant effects are indicated by bold typesetting.

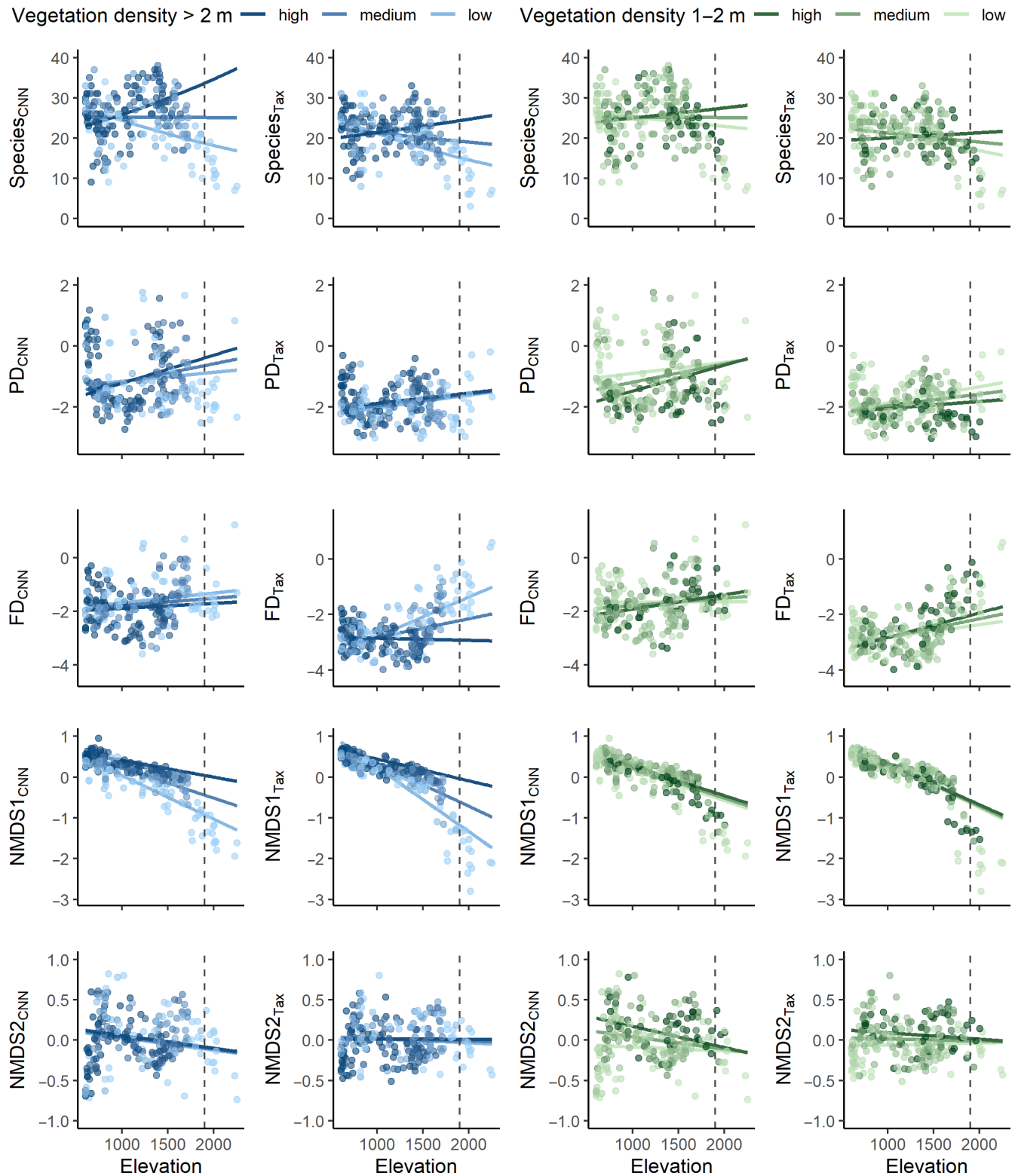
explanations why bird community composition changed more strongly with elevation in open than closed habitats in our study. First, dense vegetation and especially forests buffer microclimatic conditions (De Frenne et al., 2019) with cooler mean temperatures in forests than in open habitats at lower elevation, but even warmer mean temperatures in forests and tall shrubs than in open habitats in the subalpine zone (Vandewiele et al., 2023). Thus, stronger microclimatic differences between open habitats at different elevations than in forests may cause stronger differences in bird communities. Second, habitat structures in forests change with elevation (Holeksa et al., 2007; Stritih et al., 2023), but these changes may be less important for birds than elevational changes in habitat structure in open habitats. Open habitats at lower elevations are restricted to sites with low soil fertility or frequent disturbances that impede growth of forest vegetation, whereas open habitats at higher elevations are increasingly determined by climatic conditions. And third, with increasing elevation, land-cover composition shifts from forest-dominated to open-habitat-dominated above the tree line. Open-habitat patches at lower elevation may thus be too small for certain open-habitat species and favour forest-edge species due to the vicinity of forest habitats, whereas open-habitat patches at higher elevation host species that are specialized to high-alpine open habitats. In both forests and open habitats, the herb and shrub layer are an important foraging and nesting habitat for a large number of species (Alba et al., 2023; Moning & Müller, 2008; Thorn et al., 2016) explaining the strong effect of vegetation density 1–2m above ground – reflecting taller herbs and shrubs – on community composition as characterized by the second NMDS axis.

Overall, bird communities were clustered, that is, standardized effects sizes of functional and phylogenetic diversity were mostly

negative, indicating that species were functionally more similar or phylogenetically more closely related than expected from null-modelling. This pattern is regularly interpreted as the result of habitat filtering (Cadotte & Tucker, 2017; Pausas & Verdú, 2010). Although stronger clustering due to harsher environmental conditions, lower productivity and shorter seasons at high elevations may be expected, a global meta-analysis could not find consistent declines of functional or phylogenetic diversity with elevation (Montaño-Centellas et al., 2020). In our study, standardized effects sizes of functional diversity (although only significantly for taxonomists' data) and phylogenetic diversity increased with elevation, indicating weaker clustering at higher elevations. Stronger functional and phylogenetic clustering despite higher species number at low elevations may indicate higher specialization and higher niche-packing (Belmaker et al., 2012), in line with the altitudinal-niche-breadth hypothesis (Rasmann et al., 2014). However, further analyses of single traits and environmental variables are needed to address this hypothesis (Cadotte & Tucker, 2017).

Bird communities were phylogenetically more strongly clustered in habitats with a dense understorey vegetation (1–2m above ground) which could be explained by the occurrence of several closely related species among shrub-associated species, such as within the genus *Phylloscopus* (Moning & Müller, 2008). Stronger functional clustering was observed in forests with high vegetation density >2m compared to open habitats without a tree layer. This pattern could be due to traits associated with breeding, foraging and navigating in forest habitats (Campos-Silva & Piratelli, 2021; Newbold et al., 2013; Thorn et al., 2016), yet further analyses of single traits are needed to explore this. Moreover, vegetation density mediated effects of elevation on phylogenetic and functional diversity. Functional diversity increased





**FIGURE 2** Interactive effects of elevation and vegetation density higher than 2 m above ground (blue) and of elevation and vegetation density between 1 and 2 m above ground (green) on bird community metrics based on species identification by CNN models (columns 1 and 3) or taxonomists (columns 2 and 4). Community metrics (rows) include species number, phylogenetic (PD) and functional diversity (FD), and the first and second NMDS axes describing community composition. Regression lines were derived by (generalized) linear mixed models (Table 1). Effects of elevation are shown for low, medium and high vegetation density for both vegetation layers representing mean – SD, mean, and mean + SD, respectively. The upper end of the tree line ecotone is indicated by dashed lines at approximately 1900 m a.s.l.

with elevation in open habitats when vegetation density >2m was low, indicating weaker functional clustering, but did not change with elevation in closed forests. Vegetation density 1–2m above ground had the opposite effect leading to a stronger increase of functional clustering with elevation in habitats with a high vegetation density 1–2m above ground. The observed patterns indicate that stronger abiotic or habitat filtering selecting for certain functional traits occurs at higher elevations only in closed forests without dense understorey vegetation. Yet, despite being functionally more similar, these communities in high-elevation forests are less closely related than species within communities in open habitats at the same elevation. Variable patterns of functional and phylogenetic patterns along elevational gradients across studies globally (Montaño-Centellas et al., 2020) may thus be at least partly due to differences in vegetation types highlighting the need to account for vegetation in studies of elevation patterns.

## 5 | CONCLUSION

Our results indicate that bird communities in the German Alps are determined by strong interactive effects of gradients in elevation and vegetation. Patterns of bird species number, functional diversity and community composition along elevation are strongly mediated by vegetation indicating that vegetation should be more strongly considered in studies on the elevational patterns of birds, as it could explain differences observed between studies.

Birds are target species for conservation and indicators for environmental change and thus, typical focal species of monitoring. Considering the interactive effects of elevation and vegetation on bird communities, bird monitoring in mountain regions should not only cover different elevation zones, but also full vegetation gradients in each elevation zone. Such monitoring data would allow to assess, for example, whether effects of climate change on bird communities differ between elevational zones and/or between vegetation types, or how climate-change induced changes in vegetation, such as upslope shifts of vegetation zones or changes in natural forest dynamics (Seidl et al., 2017), affect bird communities.

The combination of autonomous sound recorders and identification of species by deep learning approaches, such as BirdNet, represents an operational solution for bird monitoring in mountain regions characterized by challenging terrain and remote locations. This opens new avenues for a next generation of highly standardized bird monitoring time series across large areas.

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[Correction added on 13th August 2024, after first online publication: Projekt DEAL funding statement has been added.]

## CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to report.

## PEER REVIEW

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## DATA AVAILABILITY STATEMENT

Raw audio data and processed data are publicly available from Dryad under DOI [10.5061/dryad.0000000br](https://doi.org/10.5061/dryad.0000000br).

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#### BIOSKETCH

The research team of Berchtesgaden National Park is conducting basic and applied research with a strong focus on the natural dynamics of ecosystems in space and time. This includes changes in biodiversity and species composition of taxa across trophic levels along elevation, microclimatic and vegetation gradients. In addition to conducting targeted research, the National Park also runs long-term monitoring programs. Together with their collaborators the National Park team aims at contributing to the development of new monitoring approaches and their implementation.

Author contributions: Conceptualization: SS, RS, JM. Investigation: TR, LiG, SS, CS, LuG, RM. Formal analysis: SS, TR. Software: OM, RM. Writing: SS, with inputs from all co-authors.

#### SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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