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Latitudinal gradient in avian insectivory: complementary effects of climate, habitat and bird diversity

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Abstract

Aim

According to the Latitudinal Biotic Interaction Hypothesis (LBIH), the general increase in biodiversity towards lower latitudes can be partially explained by an increase in the intensity of biotic interactions. While LBIH received some support for plant-herbivores interactions, much less is known about how higher trophic levels may contribute to shape biotic interactions across latitudinal gradients. We hypothesized that the diversity of insectivorous birds increases towards lower latitude, leading to higher predation rates on insect herbivores.

Location

Europe.

Taxon

Insectivorous birds and pedunculate oaks.

Methods

We deployed plasticine caterpillars in 138 oak trees in 47 sites along a 19° latitudinal gradient in Europe to quantify bird insectivory through predation attempts. In addition, we used passive acoustic monitoring to (i) characterize the acoustic diversity of surrounding soundscapes; and (ii) infer both taxonomic and functional diversity of insectivorous birds from recordings.

Results

The functional diversity of insectivorous birds increased towards lower latitude. Bird predation increased with latitude, forest cover and bird acoustic diversity but decreased with mean annual temperature and functional richness of insectivorous birds. Contrary to our predictions, latitudinal clines in bird predation attempts were not directly mediated by changes in insectivorous bird diversity or acoustic diversity, but latitude and habitat still had independent effects on predation attempts.

Main conclusions

Our study does not fully support the predictions of the LBIH of more biotic interactions southwards and advocates for better accounting for activity and abundance of insectivorous birds when studying the large-scale variation in insect-tree interactions.

Keywords: Acoustic diversity, Functional diversity, Insectivorous birds, Latitudinal gradient, Plasticine caterpillars, Predation function

Introduction

The general increase in terrestrial and marine biodiversity from high to low latitudes is one of the most consistent patterns in biogeography (MacArthur, 1984; Schemske, Mittelbach, Cornell, Sobel & Roy, 2009). Of the numerous hypotheses that have been proposed to explain this ubiquitous pattern, the Latitudinal Biotic Interactions Hypothesis (LBIH) states that biotic interactions are more intense and are the main driver of biotic evolution under milder climates, at low latitudes (Dobzhansky, 1950). Whereas LBIH received partial support from numerous studies on plant-herbivore interactions (Anstett, Chen & Johnson, 2016; Kozlov, Lanta, Zverev & Zvereva, 2015), much less is known about biotic interactions involving higher trophic levels. Given the importance of top-down factors in the control of herbivory, this omission represents a critical gap in knowledge that needs to be addressed.

Latitudinal clines in predation rates have received much less attention than latitudinal clines in herbivory, and remains inconclusive (see Zvereva & Kozlov, 2021 for a review). Some authors have documented an increase in predation by arthropods toward the equator (Roslin et al., 2017; Zvereva et al., 2019), but neutral (Lövei & Ferrante, 2017; Roslin et al., 2017; Valdés-Correcher et al., 2021) or even opposite (Zvereva et al., 2019) patterns have been found for predation by birds. Local variation in resources drives the diversity and foraging activity of predators, with cascading effects on predation intensity. By controlling for these factors we can further test our understanding of the effect of latitudinal clines on prey-predator interactions.

Current theory predicts a positive relationship between biodiversity and ecosystem functioning regulation (Loreau et al., 2001), suggesting that greater predator diversity may, to some extent, lead to greater predation (van Bael et al., 2008; Otto, Berlow, Rank, Smiley & Brose, 2008; Sinclair, Mduma & Brashares, 2003). Beyond taxonomic diversity, functional diversity – that is the diversity, distribution and complementarity of predator traits involved in predation – is a key driver of predation rates (Barbaro et al., 2014; Greenop, Woodcock, Wilby, Cook & Pywell, 2018; Philpott et al., 2009). Birds are among predators contributing the most to the control of insect herbivores in terrestrial ecosystems (van Bael et al., 2008; Sekercioglu, 2006). Niche opportunities increase towards lower latitudes due to climatic conditions that allow higher habitat heterogeneity and increased species coexistence, leading to higher bird species richness and greater functional diversity (Blackburn & Gaston, 1996; Willig, Kaufman & Stevens, 2003). Bird predation should in turn follow the same pattern as bird diversity (Zvereva & Kozlov, 2021). However, whether the diversity-predation relationship ultimately contributes to increased predation upon herbivores, and whether it cascades down to the primary producer level, is still controversial (Mooney et al., 2010), partly due to bird predation on predatory arthropods (i.e., intraguild predation).

Biological communities are shaped by a combination of biotic and abiotic factors acting at multiple, nested scales (Charbonnier et al., 2016; Ikin et al., 2014; Kissling, Sekercioglu & Jetz, 2012). Thus, also local factors can alter macroecological patterns by filtering the regional species pool (De la Mora, García-Ballinas & Philpott, 2015; Kleijn, Rundlöf, Scheper, Smith & Tscharntke, 2011). Forest cover proved to be a good predictor of biodiversity, including acoustic diversity, likely due to the complex architecture of trees and diversity of resources and trophic interactions between trees, insect herbivores and their natural enemies (Barbaro et al., 2022; Long & Frank, 2020). Birds are particularly sensitive to forest cover at different scales, which influences both the amount of available prey and nesting sites (Lee, Fahrig, Freemark & Currie, 2002; Mazerolle & Villard, 1999; Rega-Brodsky & Nilon, 2017). As a result, modeling the response of forest bird communities to large-scale bioclimatic drivers benefits from using a combination of habitat variables and biotic predictors such as food amount and availability (Barbaro et al., 2019; Speakman et al., 2000). At the local scale, bird foraging activity is ultimately determined by the vertical and horizontal heterogeneity of the habitat, which influences both where prey can be found, and where foraging birds can hide from predators (Vickery & Arlettaz, 2012). However, cross-continental studies exploring the relationship between latitude and the strength of biotic interactions generally ignore local factors, which may partly explain inconsistencies in their findings (but see Just, Dale, Long & Frank, 2019).

A major challenge to analyze latitudinal patterns in biotic interactions consists in simultaneously characterizing changes in predator biodiversity and experimentally assessing the strength of predation, while considering the effect of contrasting habitats. However, the recent development of passive acoustic monitoring provides a standardized, low-cost and non-invasive approach for ecological studies and biodiversity monitoring (Gibb, Browning, Glover-Kapfer, Jones & Börger, 2019). Acoustic monitoring of a habitat firstly allows the identification of bird species. Secondly, through the calculation of acoustic diversity indices, it allows to characterize the activity of the community as a whole while also accounting for the importance of human disturbances (Gasc et al., 2013; Sueur, Farina, Gasc, Pieretti & Pavoine, 2014). Should such indices consistently correlate with macro-scales biotic interactions, ecoacoustics would be a promising complementary approach to existing methods in macroecology and in functional ecology.

Here, we addressed the LBIH through the lens of predation by simultaneously characterizing changes in insectivorous bird community diversity, bird predation, and the biodiversity-function relationship while controlling for local factors throughout the European distribution range of the pedunculate oak (*Quercus robur* L., 1753), a major forest tree species. Specifically, we predict the following (Fig. 1): (i) bird diversity (including bird acoustic diversity, insectivorous bird species richness and functional diversity) and predation rates increase toward lower latitudes; (ii) bird predation rates increase with bird acoustic activity, species richness and greater functional diversity of insectivorous birds; (iii) bird diversity, acoustic activity and bird predation rates increase with increasing forest cover at both local (neighborhood) and larger spatial scales; (iv) large-scale variability in bird predation rates is primarily driven by local changes in the diversity and activity of birds. To test these predictions, we quantified bird predation attempts on plasticine caterpillars and estimated bird species richness, functional diversity and activity through simultaneous passive acoustic monitoring. We eventually tested the respective responses of these variables and their relationships at the pan-European scale.

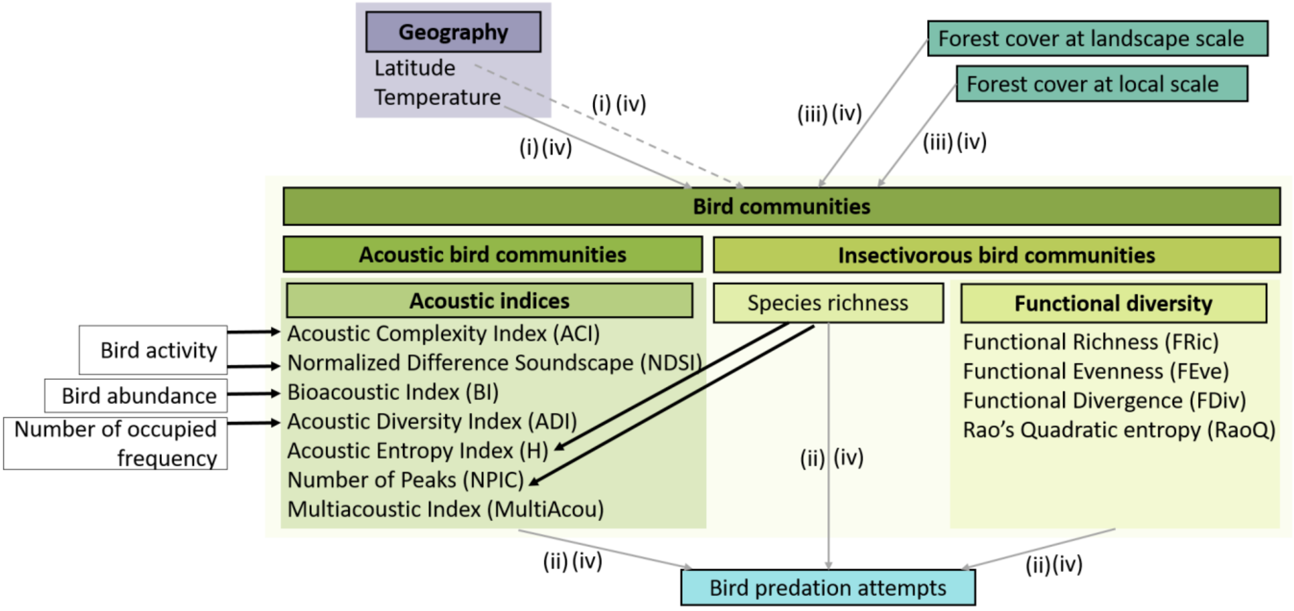

Figure 1*: Conceptual diagram of the predictions of this study and the relationships already established in the literature. Boxed elements written in bold correspond to the main categories of variables tested, they are not variables as such. Variables used in models are shown in regular font. Where several variables described the same category (e.g. ACI, NDSI, BI, ADI, H, NPIC,*

MultiAcou, all describing acoustic indices), we used multi-model comparisons to identify the best variable. Items framed in black on a white background represent untested variables. Black arrows indicate relationships well supported by the literature (see Fig.2 Sánchez-Giraldo, Correa Ayram & Daza, 2021). Our specific predictions are represented with grey arrows, solid and dashed lines representing positive and negative (predicted) relationships. Numbers refer to predictions as stated in the main text.

Materials and methods

Study area

We focused on the pedunculate oak, *Quercus robur,* which is one of the keystone deciduous tree species in temperate European forests, where it is of high ecological, economic and symbolic importance (Eaton, Caudullo, Oliveira & de Rigo, 2016). The species occurs from central Spain (39°N) to southern Fennoscandia (62°N) and thus experiences a huge gradient of climatic conditions (Petit et al., 2002). A widely diverse community of specialist and generalist herbivorous insects is associated with this species throughout its distributional range (Southwood, Wint, Kennedy & Greenwood, 2005).

Between May and July 2021, we studied 138 trees in 47 sites across 17 European countries covering most of the pedunculate oak geographic range (Fig. 2). The sites were chosen with the minimal constraint of being located in a wooded area of at least 1ha (Valdés-Correcher et al., 2021). We haphazardly selected three mature oaks per site, with the exception of six sites (three sites with one tree, one site with two trees and two sites with five trees, see Table S1.1 in Appendix S1 in Supporting Information).

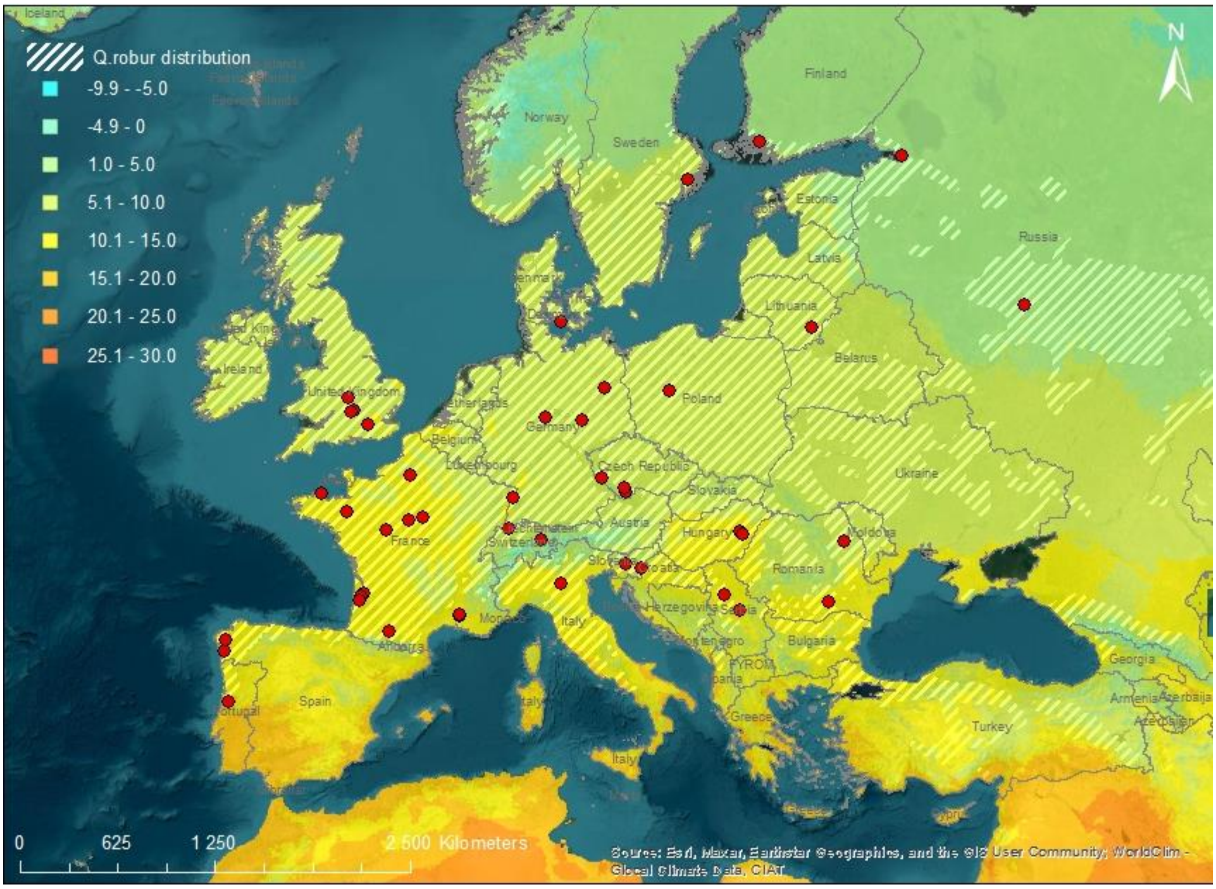

Figure 2 *Locations of the 47 sites sampled in spring 2021. Average annual temperature (color scale) according to WorldClim (Hijmans, Cameron, Parra, Jones & Jarvis, 2005) and Quercus robur distribution range are indicated.*

Bird predation attempts

We measured bird predation attempts in the field by exposing a total of 40 plasticine caterpillars (20 plasticine caterpillars twice) on each individual oak. We made plasticine caterpillars of green plasticine, mimicking common lepidopteran larvae (3 cm long, 0.5 cm diameter, see Low, Sam, McArthur, Posa & Hochuli, 2014). We secured them on twigs with a 0.3 mm metallic wire. We attached five plasticine caterpillars to each of four branches facing opposite directions (i.e., 20 caterpillars per tree) at about 2 m from the ground.

We installed the plasticine caterpillars six weeks after budburst in each study area, thus synchronizing the study with local oak phenology. We removed the plasticine caterpillars after 15 days and installed another set of 20 artificial caterpillars per tree for another 15 days. At the end of each exposure period (which varied from 10 to 20 (mean ± SD: 14.5 ± 1.23) days due to weather conditions, we carefully removed the plasticine caterpillars from branches, placed them into plastic vials and shipped them to the project coordinator. Plasticine caterpillars from six sites were either lost or altered during shipping, preventing the extraction of relevant data.

A single trained observer (EVC) screened the surface of plasticine caterpillars with a magnifying lens to search for the presence of bill marks on clay surface (Low et al., 2014). As we were ultimately interested in linking bird diversity with bird predation rates, we did not consider marks left by arthropods and mammals.

We defined *bird predation attempts index* as p / d, where p is the proportion of plasticine caterpillars with at least one sign of attempted predation by birds and d is the number of days plasticine caterpillars were exposed to predators in the field. We only considered as attacked those caterpillars that we retrieved; missing caterpillars were not accounted for in the calculation of p. We calculated bird predation attempts for each tree and survey period separately. Because other variables were defined at site level (see below), we averaged bird predation attempts across trees and surveys in each site (total: $n = 41$).

To assess the effect of temperature independently of other variables that could covary with latitude, we also calculated a second bird predation attempts index by standardizing the predation attempts by daylight duration in every site (see Fig. S2.1 in Appendix S2 for the calculation of this index). We run the statistical models in exactly the same way as for the non-standardized bird predation attempts and the results are presented in Table S3.2 in Appendix S3.

Acoustic monitoring and related variables

We used passive acoustic monitoring to characterize both the overall acoustic diversity (i.e., the soundscape surrounding target oaks) and the bird species richness and functional diversity associated with oaks, targeting the canopy insectivores that are expected to play a functional predation role on oak herbivores (Fig. 2). In each site, we randomly chose one oak among those used to measure bird predation rates in which we installed an AudioMoth device (Hill et al., 2018) to record audible sounds for 30 min every hour. Automated recording started the day we installed the first set of 20 plasticine caterpillars in trees and lasted until batteries stopped providing enough energy. The recording settings are the following: Recording period: *00.00-24.00 (UTC); Sample rate: 48 kHZ; Gain: Medium; Sleep duration: 1800 s, Recording duration: 1800 s.*

In all 47 sites, Audiomoths were active on average (± S.D.) for 9 ± 3 days (range: 1-24), which corresponded to 5920 h of recordings in total and from 70 to 335 (246 ± 65) 30 min continuous acoustic samples per site. When Audiomoths ran out of battery, the recordings lasted less than 30 min (between 1 and 56 recordings per site were affected).

We processed acoustic samples with functions in the *soundecology* (Villanueva-Rivera & Pijanowski, 2018) and *seewave* libraries (Sueur, Aubin & Simonis, 2008) in the R environment (R Core Team, 2020), and a wrap-up function made available by A. Gasc in GitHub (https://github.com/agasc/Soundscape-analysis-with-R). To summarize information on the acoustic diversity of each site, we first divided every acoustic sample (regardless of its length) into non-overlapping 1 min samples. Then, we calculated six common acoustic diversity indices for each 1 min sample: the Acoustic Complexity Index (ACI), the Acoustic Diversity Index (ADI), the Bioacoustic Index (BI), the total acoustic entropy (H), the Normalized Difference Sound Index (NDSI), and the Number of frequency Peaks NPIC (Bradfer-Lawrence et al., 2019; Sueur et al., 2014). We further aggregated these indices into a multiacoustic index (MultiAcou) as proposed by Barbaro et al. (2022). We calculated the median of each acoustic index per day and then averaged median values across days for each site separately. We proceeded like this because 24 h cycles summarize the acoustic activity and account for all possible sounds of a given day. Furthermore, other studies have previously shown that median values of acoustic indices for a given day are more representative than mean values of the acoustic activity because they are less sensitive to extreme values (Barbaro et al., 2022; Dröge et al., 2021). This procedure resulted in one single value of each acoustic diversity index per site. It is important to note that being calculated over 24 h, these indices do not represent bird-related variables only, but are rather seen as an integrative component of the surrounding habitat around target oaks.

Bird species richness and functional diversity

We used acoustic samples to identify birds based on their vocalizations (songs and calls) at the species level, from which we further computed functional diversity indices (Fig. 3).

Data processing – For each site, we subsampled the 30 min samples corresponding to the songbird morning chorus (*i.e.,* the period of maximum singing activity), which incidentally also corresponds to the time of the day when anthropic sounds were of the lowest intensity. Specifically, we selected sounds recorded within a period running from 30 min before sunrise to 3 h 30 min after sunrise. We then split each 30 min sample into up to three 10 min sequences, from which we only retained those recorded on Tuesday, Thursday, Saturday, and Sunday. We chose these days on purpose to balance the differences in anthropogenic noises between working days and weekends. For each sound sample, we displayed the corresponding spectrogram with the '*seewave*' library in the *R* environment (Sueur, Aubin & Simonis, 2008). We visually sorted sound samples thanks to spectrograms and discarded samples with noise from anthropogenic sources, rain, or wind, which can be recognized as very low frequency noise on the spectrogram. We also discarded samples with noise of very high frequency corresponding to cicada chirps. We then randomly selected one sound sample per site and per day, with the exception of four sites for which the four samples only covered two to three days. In total, we selected 188 samples of 10 min (i.e., 4 samples per site).

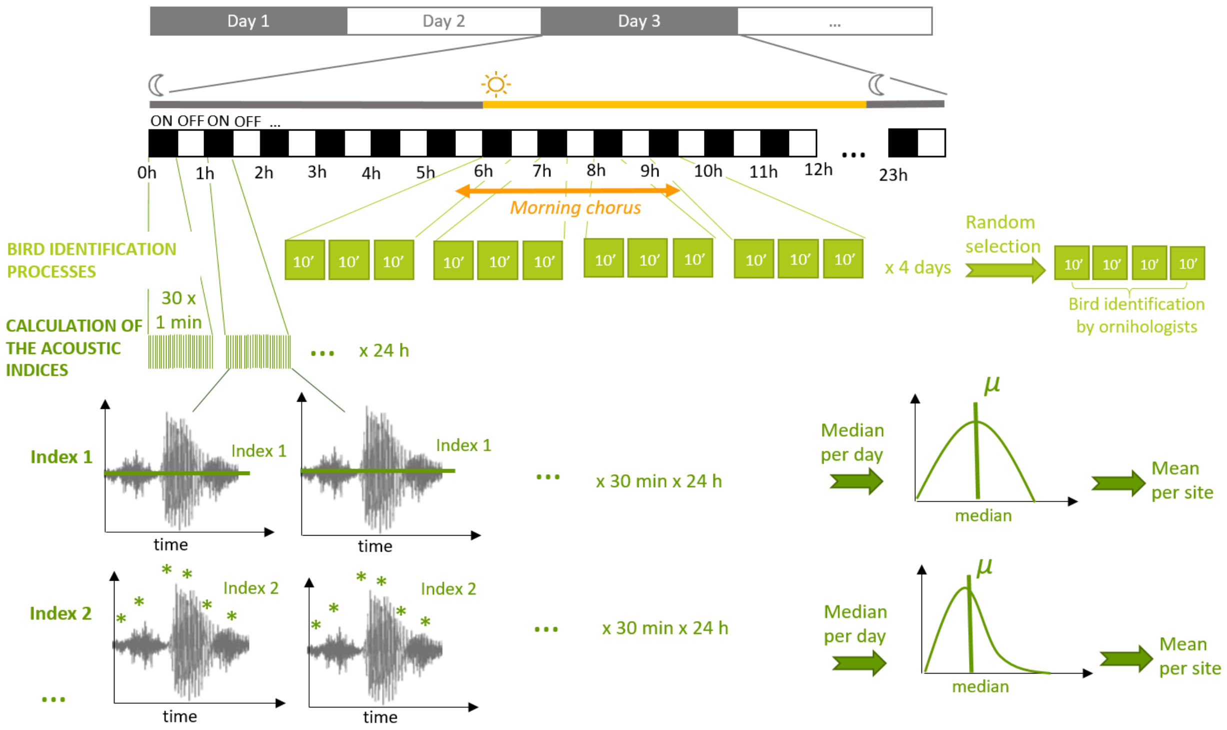

Figure 3*: Methodological pathway used to identify bird species (in light green) and calculate acoustic indices (in dark green) from automated recordings (see text for details)*

Bird species identification – We distributed the samples among 21 expert ornithologists. Each expert performing aural bird species identifications from 4 (one site) to 52 samples (13 sites), primarily from her/his region of residence, for auditory acoustic detection of bird species. We established a presence/absence Site × Species matrix, from which we calculated species richness and functional diversity. Note that bird species abundance can not be reliably assessed with this approach.

Functional diversity – We defined 25 bird species as candidate insectivores for attacking plasticine caterpillars (Table S4.3 in Appendix S4) with those bird species meeting the following criteria: be insectivorous during the breeding season or likely to feed their offspring with insects, forage primarily in forested habitats, and are likely to use substrates such as lower branches or lower leaves of trees where caterpillars were attached to find their prey (Barbaro et al., 2021; Brambilla & Gatti, 2022). We calculated the functional diversity of these candidate insectivores by combining morphological, reproductive, behavioral and acoustic traits.

With the exception of acoustic traits, we extracted functional traits from different published sources, listed in Table S4.4 in Appendix S4. Specifically, we used three continuous traits: *body mass*, *mean clutch size* and *bill culmen length* (see Fig. 2 in Tobias et al., 2022) combined with four categorical traits: *foraging method* (predominantly understory gleaner, ground gleaner, canopy gleaner), *diet* (insectivores or mixed diet), *nest type* (open in shrub, open on ground, cavity or open in tree) and *migration* (short migration, long migration or resident).

We derived acoustic traits calculations from the work of Krishnan & Tamma (2016). We first extracted five pure recordings without sonic background for each of the 25 candidate insectivore species from the online database Xeno-canto.org (Vellinga & Planque, 2015). We then calculated the *number of peaks* (i.e., NPIC) in the audio signal (see § Acoustic diversity, above) as well as the *frequency of the maximum amplitude peaks* for each vocal element using the *seewave* library (Sueur, Aubin & Simonis, 2008) and averaged these frequencies for each species. Being based on song and call frequency and complexity, these indices inform on the adaptation of the vocal repertoire of these species to their environment.

We summarized the information conveyed by the 9 traits categories into five indices representing complementary dimensions of the functional diversity (FD) of a community (Mouillot, Graham, Villéger, Mason & Bellwood, 2013): functional richness (FRic, i.e., convex hull volume of the functional trait space summarized by a principal coordinates analysis), functional evenness (FEve, i.e., minimum spanning tree measuring the regularity of trait abundance distribution within the functional space), and functional divergence (FDiv, i.e., trait abundance distribution within the functional trait space volume) (Villéger, Mason & Mouillot, 2008), as well as Rao's quadratic entropy (RaoQ, i.e., species dispersion from the functional centroïd) (Botta-Dukát, 2005). These were calculated for each site with the *dbFD* function of the *FD* library (Laliberté, Legendre & Shipley, 2014) in the R environment.

Environmental data

Environmental data refer to local temperature and forest cover. We used the high 10-m resolution GIS layers from the Copernicus open platform (Cover, 2018) to calculate forest cover for all European sites. We manually calculated the percentage of forest cover for the two sites located outside Europe using the "World imagery" layer of Arcgis ver. 10.2.3552. We calculated both the percentage of forest cover in a 20-m (henceforth called *local* forest cover) and 200-m (*landscape* forest cover) buffer around the sampled oaks. We chose two nested buffer sizes to better capture the complexity of habitat structure on the diversity and acoustic activity of birds. Local forest cover is particularly important for estimating bird occurrence probability (Melles, Glenn & Martin, 2003), whereas landscape forest cover is an important predictor of bird community composition in urban areas (Rega-Brodsky & Nilon, 2017). Moreover, both local and landscape habitat factors shape insect prey distribution (Barr, van Dijk, Hylander & Tack, 2021). Preliminary analyses revealed that results were qualitatively the same using 10-, 20- or 50-m buffers as predictors of local forest cover and 200- or 500-m buffers as predictors of landscape forest cover (see Table S5.5 in Appendix S5). Because other variables were defined at the site level, we averaged the percentage of forest cover for the sampled trees per site and per buffer size.

We extracted the mean annual temperature at each site from the WorldClim database (the spatial resolution is ~86 km^2, Hijmans et al., 2005).

Statistical analyses

We analyzed 14 response variables in separate linear models (LMs) (Table S3.2 in Appendix S3): bird predation attempts, species richness of the entire bird community and that of candidate insectivores, functional diversity (each of the 4 indices) and acoustic diversity (each of the 7 indices). For each response variable, we first built a full model including a minimum of two components: geography and habitat. The general model equation was (Eq. 1):

$$Y_i = \beta_0 + \beta_1 \times Forest_{20,\,i} + \beta_2 \times Forest_{200,\,i} + \beta_3 \times Geography_i + \varepsilon_i \qquad (1)$$

where Y is the response variable, β_0 the model intercept, β_{is} model coefficient parameters, $Forest_{20}$ and $Forest_{200}$ the effects of the local and landscape forest cover respectively, *Geography* the effect of mean annual temperature or latitude (since the two variables are correlated, they were never tested together in the same models) and ε the residuals.

When modeling the response of bird predation attempts (Eq. 2), we added two more variables to the model, being any of the seven acoustic diversity indices (*Acoustic diversity*, Eq. 2) and the species richness or any of the four indices describing the functional diversity of candidate insectivores (*Bird diversity*, Eq. 2):

$$Y_i = \beta_0 + \beta_1 \times Forest_{20,i} + \beta_2 \times Forest_{200,i} + \beta_3 \times Geography_i + \beta_4 \times Bird\ diversity_i + \beta_5 \times Acoustic\ diversity_i + \varepsilon_i \qquad (2)$$

We used logarithmic transformations (for bird predation attempts and acoustic entropy (H) models) or square rooted transformation (for species richness of the complete bird community) of some response variables where appropriate to satisfy model assumptions. We scaled and centered every continuous predictor prior to modeling to facilitate comparisons of their effect sizes, and made sure that none of the explanatory variables were strongly correlated using the variance inflation factor (VIF) (all VIFs < 5, the usual cutoff values used to check for multicollinearity issues (Miles, 2014)).

For each response variable, we ran the full model as well as every model nested within the full model and then used Akaike's Information Criterion corrected for small sample size (AICc) to identify the most parsimonious model(s) fitting the data the best. We simultaneously selected the best variable describing the geography, habitat, diversity and acoustic component (variable selection) and the best set of variables describing the variability of the response variable (model selection).

First, we ranked each model according to the difference in AICc between the given model and the model with the lowest AICc (ΔAICc). Models within 2 ΔAICc units of the best model (i.e., the model with the lowest AICc) are generally considered as likely (Burnham & Anderson, 2002). We computed AICc weights for each model (w_i). w_i is interpreted as the probability of a given model being the best model among the set of candidate models. Eventually, we calculated the relative variable importance (RVI) as the sum of w_i of every model including this variable, which corresponds to the probability a variable is included in the best model.

When several models competed with the best model (i.e., when multiple models were such that their ΔAICc < 2), we applied a procedure of multimodel inference, building a consensus model including the variables in the set of best models. We then averaged their effect sizes across all the models in the set of best models, using the variable weight as a weighting parameter (i.e., model averaging). We considered that a given predictor had a statistically significant effect on the response variable when its confidence interval excluded zero.

Finally, we used confirmatory structural equation modeling (SEM) (Lefcheck, 2016) to infer direct and indirect causality links between predictors and response variables. We first built a theoretical model linking the temperature and forest cover with bird acoustic and functional diversity, and the latter with bird predation attempts. We then ran a second model also including the direct paths between temperature, landscape forest cover and bird predation attempts and compared models with *vs* without direct paths between temperature or landscape forest cover and bird predation attempts. To avoid model over-parameterization, we used the results of the model selection procedure described above to identify which variable should represent the habitat, diversity and acoustic components. We tested independence claims between temperature or forest cover and avian predation rates with *d*-separation, and we evaluated the overall goodness of fit of the model with Fisher's C statistic.

We run all analyses in the R language environment (R Core Team, 2020) with libraries *MuMIn* (Bartoń, 2020), *lme4* (Bates, Mächler, Bolker & Walker, 2015), and *piecewiseSEM* (Lefcheck, 2020).

Results

Bird acoustic diversity

Of the seven acoustic diversity indices (see Fig. S6.2 in Appendix S6 for correlation between indices), only Acoustic Diversity Index (ADI) and acoustic entropy (H) were significantly associated with any of the predictors tested, i.e., temperature or latitude, local forest cover and landscape forest cover (Table S3.2 in Appendix S3). ADI and H both increased with local forest cover (i.e., percentage of forest cover in a 20-m buffer around recorders). Landscape-scale forest cover (i.e., percentage of forest cover in a 200-m buffer around recorders) was the only other predictor retained in the set of competing models in a range of ΔAICc < 2 to explain acoustic entropy variation, but this predictor had little importance (RVI < 0.5) and its effect was not statistically significant (Fig. 5b; Table S3.2 in Appendix S3).

Bird species richness and functional diversity

We identified a total of 87 bird species, among which 25 were classified as candidate functional insectivores. Bird species richness varied from 8 to 23 species per recording site (mean ± SD: 15.2 ± 3.7, n = 47 sites) and richness of candidate insectivores from 2 to 9 species (5.7 ± 1.5). The null model was among models competing in a range of ΔAICc < 2 for both total species richness and candidate insectivores (Table S3.2 in Appendix S3).

Among the five bird functional diversity and species richness indices, only functional quadratic entropy (Rao's Q) characterizing species dispersion from the functional centroid was significantly influenced by the predictors tested (temperature or latitude, local and landscape forest cover, Table S3.2 in Appendix S3). Specifically, Rao's Q decreased towards higher latitudes (Fig. 4a and Fig. 5c). Other predictors retained in the set of competing models in a range of ΔAICc < 2 had little importance (RVI < 0.5) and were not significant (Fig. 5c; Table S3.2 in Appendix S3).

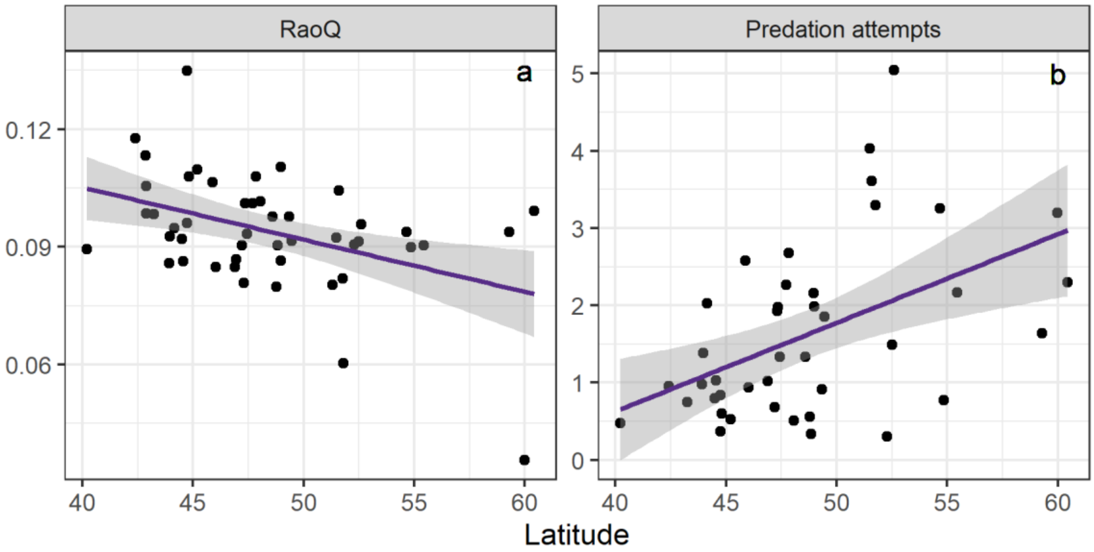

Figure 4*: Scatter diagrams showing changes in (a) Rao's Q and (b) predation attempts with latitude. These relationships were identified as significant in the linear models tested*

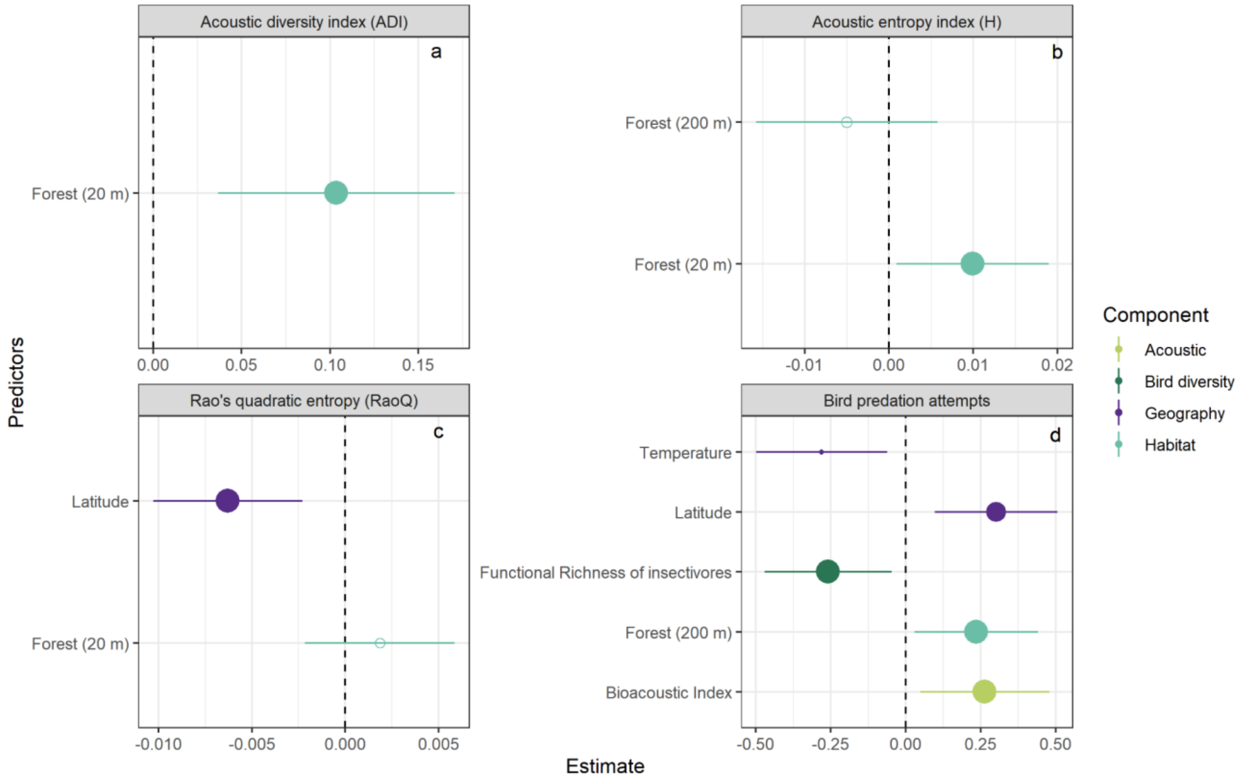

***Figure 5**: Effects of geography (temperature or latitude) and habitat (percentage of forest cover at 20 or 200 m) on Acoustic Diversity Index (ADI) (a), Acoustic Entropy Index (H) (b), Rao's quadratic entropy (RaoQ) (c) and bird predation attempts (d) and effects of acoustic (Bioacoustic Index), bird diversity (Functional Richness) on bird predation attempts (d). Circles and error bars represent standardized parameter estimates and corresponding 95% confidence intervals (CI), respectively. The vertical dashed line centered on zero represents the null hypothesis. Full and empty circles represent significant and non-significant effect sizes, respectively. Circle size is proportional to RVI. The colors correspond to the different components tested (acoustic, bird diversity, geography and habitat).*

Bird predation attempts

Of the 4,860 exposed dummy caterpillars, 22.8% (*n* = 1,108) had bird bill marks. Model selection retained two models in the set of competing models in a range of ΔAICc < 2 (Table S3.2 in Appendix S3). Landscape forest cover (RVI = 1.00), bird functional richness (FRic) (RVI = 1.00) and bioacoustic index (BI) (RVI = 1.00) were selected in all models. Latitude (RVI = 0.73) and temperature (RVI = 0.27) were also each selected in one of the two best models.

Bird predation attempts increased towards higher latitudes and consistently decreased with increasing mean annual temperature. Bird predation attempts further increased with bioacoustic index (BI), but decreased with bird functional richness (FRic) (Fig. 4b and Fig. 5d).

The results were comparable when we incorporated latitudinal changes in diel phenology in the calculation of predation attempts through the standardization with the daylight duration (see Table S3.2 in Appendix S3). The only noticeable difference was that the importance of temperature as a predictor was higher (RVI=1.00, compared with RVI = 0.27 for the first model with unstandardized rates of predation attempts).

A first SEM was set up by specifying direct links between environmental variables (latitude and landscape forest cover) and bird diversity variables (FRic and BI) on the one hand and between bird diversity variables and predation attempts on the other. The model was however misspecified (C = 27, P < 0.001, AIC = 51). We ran a second model also including the direct paths between latitude, landscape forest cover and bird predation attempts. Model AIC dropped dramatically (ΔAIC = 19), indicating that the full model with direct paths between latitude, forest cover and bird predation attempts had a better fit (C = 4, P = 0.131, AIC = 32). Latitude, landscape forest cover and bioacoustic index had a significant positive effect on bird predation attempts whereas FRic had a significant negative effect on bird predation attempts. Altogether, these results indicate that latitude and forest cover had direct effects on bird predation attempts that were not mediated by local changes in bird diversity (Fig. 6).

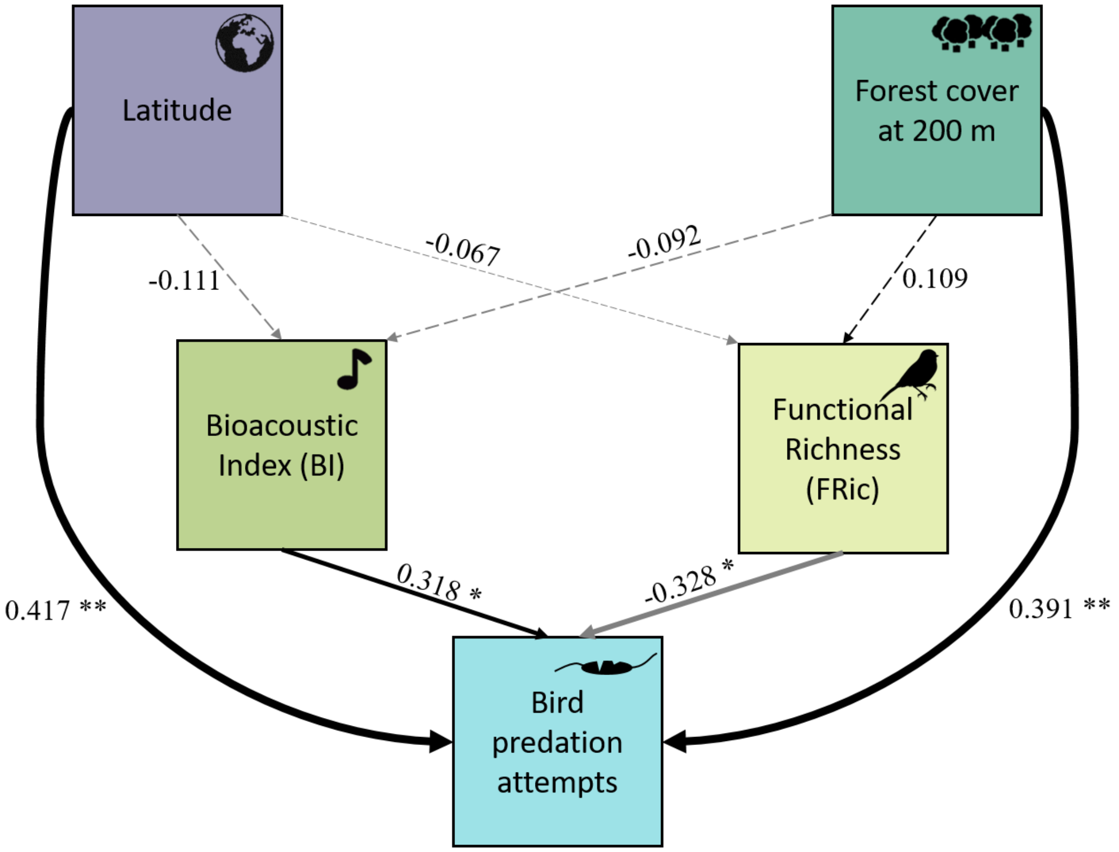

*__Figure 6.__ Structural equation model. The thickness of the arrows is proportional to coefficient parameter estimate. Standardized estimates for each response variable are indicated next to each arrow. *P < 0.05, **P < 0.01, ***P < 0.001. Continuous and dashed arrows represent significant (P < 0.05) and non-significant (P > 0.05) relationships respectively. Black and gray arrows represent positive and negative relationships respectively. FRic refers to the functional richness of candidate insectivorous birds.*

Discussion

Bird predation and functional diversity of bird insectivores are both influenced by latitude

The Latitudinal Biotic Interactions Hypothesis (Dobzhansky, 1950) is a controversial idea, particularly for biotic interactions between herbivores and higher trophic levels (Lövei & Ferrante, 2017; Zvereva & Kozlov, 2021). Against this hypothesis and contrarily with our prediction ((i), Fig. 1), we found that latitude was positively related to bird predation attempts. More bird predation attempts at higher latitudes could be due to longer daylight duration in spring northwards, leading insectivorous birds to have more time per day to find their prey and thus allowing high coexistence of predators during a period of unlimited resource availability (Speakman et al., 2000). Alternatively, birds needing more energy in colder temperatures to thermoregulate may need to feed more to maintain their metabolic activity (Caraco et al., 1990; Kendeigh, 1969; Steen, 1958; Wansink & Tinbergen, 1994). Consistently with this explanation, we found a negative relationship between temperature and bird predation attempts. Moreover, temperature remained an important, significant predictor of bird predation attempts when we controlled for the duration of daylight (Table S3.2 in Appendix S3), which further supports this explanation. However, we cannot exclude the possibility that the lower predation rates at lower latitudes was due to lower prey detectability.

In agreement with our prediction (i, Fig. 1), we provide evidence for a significant negative relationship between latitude and the functional diversity of insectivorous birds. Despite substantial differences among functional diversity indices, this suggests that more functionally diverse assemblages of insectivorous birds are able to coexist locally in oak woods towards the south of Europe (Currie et al., 2004; Hillebrand, 2004; Willig et al., 2003). Of the multiple functional diversity indices commonly used to describe ecological communities, it is noticeable that only the quadratic entropy index responded negatively to latitude, for it is a synthetic index which simultaneously takes into account the richness, evenness, and divergence components of functional diversity (Mouillot et al., 2013).

Bird predation attempts are partly predicted by bird functional and acoustic diversity

We predicted that bird predation attempts would increase with bird functional diversity (ii, Fig. 1), but found no or opposite effects, depending on the functional index considered. Only functional insectivore richness was negatively correlated to predation rates. Negative relationships between predation and predator functional diversity can arise from a combination of both intraguild predation --- predators preying upon predators (Mooney et al., 2010) --- and intraguild competition (Houska Tahadlova et al., 2022), although we can hardly tease them apart in the present study. An important step forward would consist in testing whether predation patterns revealed with artificial prey are representative of predation intensity as a whole (Zvereva & Kozlov, 2021). For example, functional richness may be a proxy for dietary specialization such that functionally more diverse predator communities would seek more prey of which they are specialists and thus predate less on artificial caterpillars. It is possible that a higher diversity of insectivorous birds in warmer regions was linked to higher diversity and abundance of arthropod prey (Kissling et al., 2012) and therefore to greater prey availability (Charbonnier et al., 2016). If so, then the pattern we observed may merely be representative of the 'dilution' of bird attacks on artificial prey among more abundant and diverse real prey (Zeuss, Brunzel & Brandl, 2017; Zvereva et al., 2019). A follow-up of the present study should therefore pay special attention on the real prey density pre-existing in each sampling site where artificial prey are to be deployed as a standardized measure of predation rates across sites.

Bird predation attempts increased with the Bioacoustic Index (BI), which is regarded as a good proxy for bird abundance (Sueur et al., 2014). This finding is thus consistent with previous studies having reported positive relationships between bird abundance and predation attempts on artificial prey (Roels, Porter & Lindell, 2018; Sam, Koane & Novotny, 2015). Acoustic diversity indices are complementary to functional diversity indices and reflect both the composition of the avian community and the nature of the habitat (Gasc, Francomano, Dunning & Pijanowski, 2017; Sugai, Silva, Ribeiro & Llusia, 2019). We further show that the acoustic monitoring of the habitat could yield proxies for the intensity of bird predation on invertebrates. In addition, our study is to our knowledge among the first to detect significant relationships between acoustic indices and an ecosystem function measured independently (Gasc et al., 2013), thus opening pathways for new research on the link between functional and acoustic ecology.

Local forest cover predicts bird acoustic activity, whereas landscape forest cover increases bird predation

Acoustic diversity increased with closeness of canopy cover in the immediate neighborhood (20m radius) of sampled trees (iii, Fig. 1). The most responsive indices were the acoustic diversity (ADI) and the acoustic entropy (H). Both are especially suitable at predicting acoustic diversity across different habitats under various ambient sound conditions (Fuller, Axel, Tucker & Gage, 2015; Machado, Aguiar & Jones, 2017). The former is related to a greater regularity of the soundscape and the latter is related to the amplitude between frequency bands and time. They therefore correspond to soundscapes containing multiple vocalizing species (Sueur et al., 2008; Villanueva-Rivera, Pijanowski, Doucette & Pekin, 2011). Acoustic entropy is also known to respond significantly to local forest habitat (Barbaro et al., 2022), which is generally a good predictor of bird occupancy probability (Morante-Filho, Benchimol & Faria, 2021).

Bird predation attempts were best predicted by forest cover at the landscape level (Prediction (iii), Fig. 1). Indeed, it is likely that forest cover at the landscape level provides structural complexity with a dense understorey and habitat heterogeneity that is both a source of food and niches for predatory birds to exploit (Poch & Simonetti, 2013). As a result, forest cover at the landscape scale is often a key predictor of avian insectivory in various study areas (Barbaro et al., 2014; González-Gómez et al., 2006; Valdés-Correcher et al., 2021). This is also consistent with the results of Rega-Brodsky & Nilon, (2017) who found greater abundance of insectivorous birds in mosaic urban or rural landscapes including a significant part of semi-natural wooded habitats, such as those we studied here.

Latitudinal variation in avian predation is independent from large-scale changes in the diversity and acoustic activity of birds

We found no evidence that the relationship between latitude and bird predation attempts was mediated by changes in bird diversity or activity (iv, Fig. 1). On the contrary, geography and bird diversity had independent and complementary effects on predation.

Latitude may directly drive both bird activity and abundance according to available resources (Pennings & Silliman, 2005). Even changes in the abundance of a single, particularly active, predator species along the latitudinal gradient to explain the observed pattern (Maas et al., 2015; Philpott et al., 2009). For example, the blue tit *Cyanistes caeruleus* and the great tit *Parus major* are typical and widespread canopy insectivores of European oak forests and are particularly prone to predate herbivorous caterpillars while showing considerable adaptive behaviour to prey availability (Mols & Visser, 2002; Naef-Daenzer & Keller, 1999). If the predation attempts on the plasticine caterpillars were to be predominantly due to these species, then it would be their abundance and activity that would play a role in predation attempts rather than the overall diversity of insectivores (Maas et al., 2015). Here, we based our assessment of functional bird composition on candidate insectivore occurrences obtained from standardized acoustic surveys, which on the one hand insures that we have no observer, site, or phenological biases on species occurrences, but on the other hand also makes it difficult to precisely account for each species' abundance. Other complementary methods to assess the relative roles of each individual bird species on predation rates should be deployed further to better account for actual predatory bird abundance and activity, including DNA sampling (Garfinkel, Minor & Whelan, 2022), camera traps (Martínez-Núñez et al., 2021) or species-specific bird surveys involving tape calls or capture methods.

Conclusion

We found a negative association between latitude and bird functional diversity, but at the same time, a positive relationship between latitude and avian predation. Our study therefore provides partial support for the latitudinal clines in biodiversity hypothesis, but clearly conflicts with the Latitudinal Biotic Interaction Hypothesis (Dobzhansky, 1950). As cross-continental studies exploring the large-scale relationship between latitude and the strength of biotic interactions generally ignore local factors, we argue that characterizing the contrasting habitats of the study sites is a good way to circumvent some inconsistencies in the results. We identify pre-existing real prey density and single key bird species abundances as two particularly important variables deserving further attention. Furthermore, predicting ecosystem services — here, potential pest regulation service — on a large scale by standardized proxies such as acoustic ecology for predator diversity and plasticine caterpillars for predation function seem to be good ways to reduce methodological biases and strengthen our understanding of the macro-ecology of biotic interactions.

Data availability statement

For the moment there is an embargo on data and codes which will be lifted after open acceptance. Schille et al., 2023, « Data and codes for the article "Latitudinal gradient in avian insectivory: complementary effects of climate, habitat and bird diversity" », https://doi.org/10.57745/0E0JEA, Recherche Data Gouv.

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Biosketch

Laura Schillé is a PhD candidate interested in the functional ecology of bird communities, which she studies at different scales. She also has an interest in acoustic ecology.

Co-authors are ornithologists and/or have interests in community ecology and functional ecology.

Author contribution: B.C., L.B. and E.V.C. conceptualized the study and developed the methodology. E.V.C., F.B., M.C.B, M.Bo., M.Br., T.D., M.dG., J.D., ML.D., AM.D., S.G., CB.E., M.F., P.F.C., E.F., A.G., MM.G., S.G., J.H., D.H., R.H., R.I., A.K., MV.K, V.L., B.L.T., C.L.V, S.M., E.M., S.M., X.M., A.M., DL.M., A.P., AV.P., A.P., A.S., K.S., T.S., A.T., R.T., D.T., G.V., I.V.H., Z.V., L.B. & B.C. collected the data. A.H., M.dG., T.B., A.P., V.L., L.P., F.A., D.F., T.P., M.M., N.S., L.B., V.M., E.M., J.G., K.T., L.G., A.M., M.C.B. & R.B. processed audio recordings for bird species identification. L.S. processed and analyzed the data with guidance from B.C. and L.B. L.S., B.C., L.B. led the writing and all authors contributed critically to the revisions.