

1 **Latitudinal gradient in avian insectivory: complementary** 2 **effects of climate, habitat and bird diversity**

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103

104 **Abstract**

105 **Aim**

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

112 **Location**

113 Europe.

114 **Taxon**

115 Insectivorous birds and pedunculate oaks.

116 **Methods**

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

121 **Results**

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

127 **Main conclusions**

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

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

133 **Introduction**

134 The general increase in terrestrial and marine biodiversity from high to low latitudes is one of the most
135 consistent patterns in biogeography (MacArthur, 1984; Schemske, Mittelbach, Cornell, Sobel & Roy,
136 2009). Of the numerous hypotheses that have been proposed to explain this ubiquitous pattern, the
137 Latitudinal Biotic Interactions Hypothesis (LBIH) states that biotic interactions are more intense and
138 are the main driver of biotic evolution under milder climates, at low latitudes (Dobzhansky, 1950).
139 Whereas LBIH received partial support from numerous studies on plant-herbivore interactions
140 (Anstett, Chen & Johnson, 2016; Kozlov, Lanta, Zverev & Zvereva, 2015), much less is known about
141 biotic interactions involving higher trophic levels. Given the importance of top-down factors in the
142 control of herbivory, this omission represents a critical gap in knowledge that needs to be addressed.
143 Latitudinal clines in predation rates have received much less attention than latitudinal clines in
144 herbivory, and remains inconclusive (see Zvereva & Kozlov, 2021 for a review). Some authors have

145 documented an increase in predation by arthropods toward the equator (Roslin et al., 2017; Zvereva
146 et al., 2019), but neutral (Lövei & Ferrante, 2017; Roslin et al., 2017; Valdés-Correcher et al., 2021) or
147 even opposite (Zvereva et al., 2019) patterns have been found for predation by birds. Local variation
148 in resources drives the diversity and foraging activity of predators, with cascading effects on predation
149 intensity. By controlling for these factors we can further test our understanding of the effect of
150 latitudinal clines on prey-predator interactions.

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

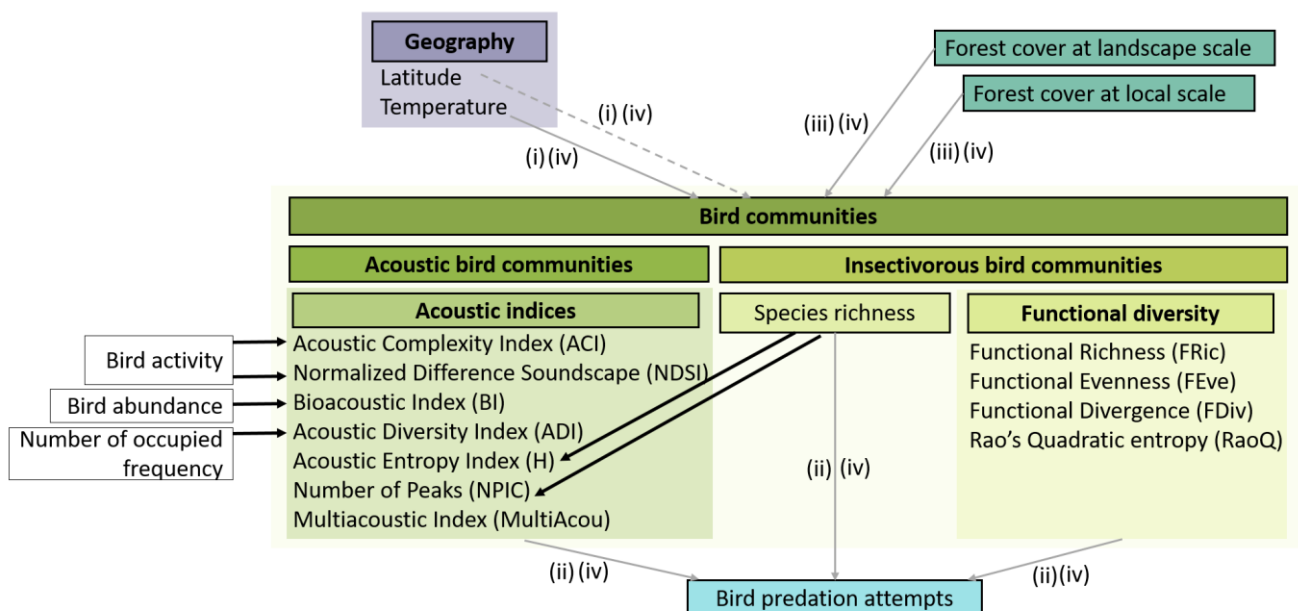
166 Biological communities are shaped by a combination of biotic and abiotic factors acting at multiple,
167 nested scales (Charbonnier et al., 2016; Ikin et al., 2014; Kissling, Sekercioglu & Jetz, 2012). Thus, also
168 local factors can alter macroecological patterns by filtering the regional species pool (De la Mora,
169 García-Ballinas & Philpott, 2015; Kleijn, Rundlöf, Scheper, Smith & Tschardtke, 2011). Forest cover

170 proved to be a good predictor of biodiversity, including acoustic diversity, likely due to the complex
171 architecture of trees and diversity of resources and trophic interactions between trees, insect
172 herbivores and their natural enemies (Barbaro et al., 2022; Long & Frank, 2020). Birds are particularly
173 sensitive to forest cover at different scales, which influences both the amount of available prey and
174 nesting sites (Lee, Fahrig, Freemark & Currie, 2002; Mazerolle & Villard, 1999; Rega-Brodsky & Nilon,
175 2017). As a result, modeling the response of forest bird communities to large-scale bioclimatic drivers
176 benefits from using a combination of habitat variables and biotic predictors such as food amount and
177 availability (Barbaro et al., 2019; Speakman et al., 2000). At the local scale, bird foraging activity is
178 ultimately determined by the vertical and horizontal heterogeneity of the habitat, which influences
179 both where prey can be found, and where foraging birds can hide from predators (Vickery & Arlettaz,
180 2012). However, cross-continental studies exploring the relationship between latitude and the
181 strength of biotic interactions generally ignore local factors, which may partly explain inconsistencies
182 in their findings (but see Just, Dale, Long & Frank, 2019).

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

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

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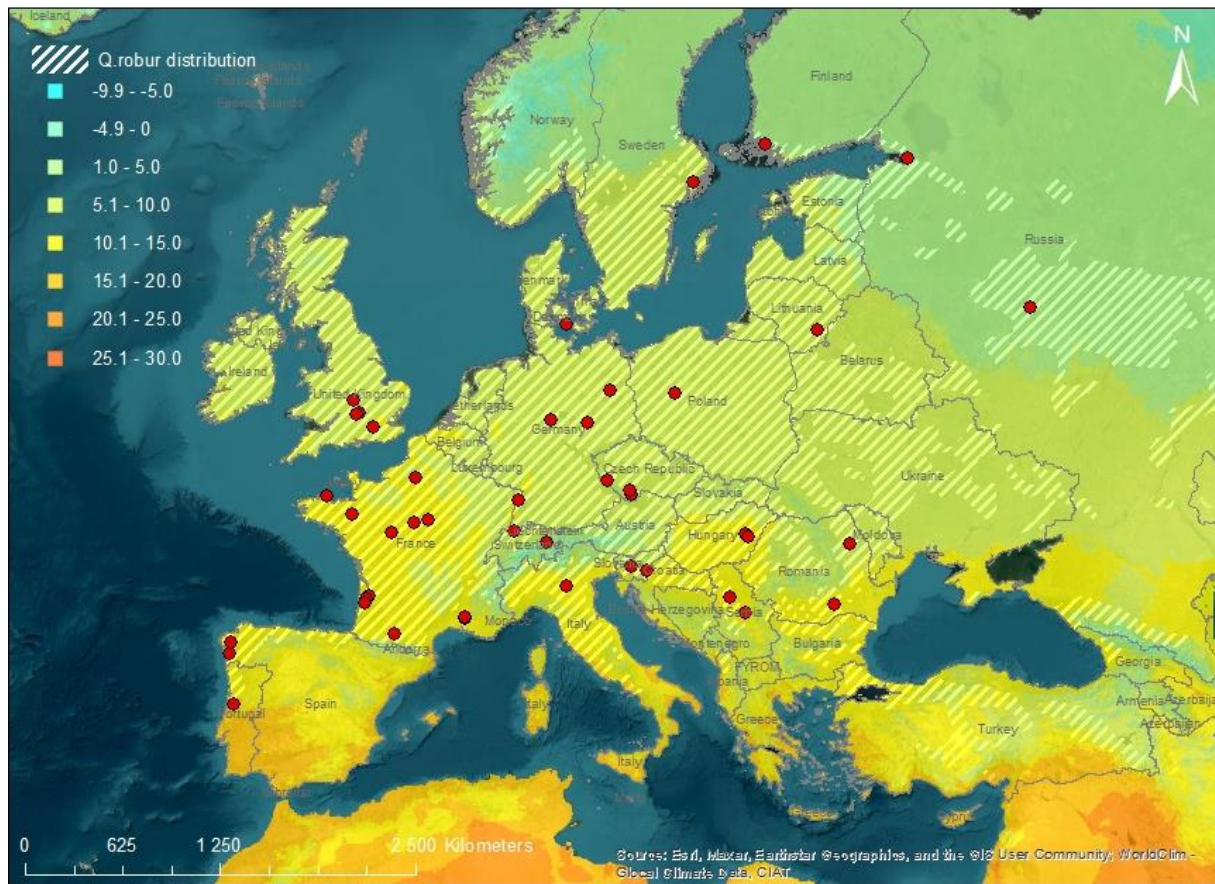
208 **Figure 1:** Conceptual diagram of the predictions of this study and the relationships already established in the literature. Boxed
 209 elements written in bold correspond to the main categories of variables tested, they are not variables as such. Variables used
 210 in models are shown in regular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

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

216 Materials and methods

217 Study area

218 We focused on the pedunculate oak, *Quercus robur*, which is one of the keystone deciduous tree
219 species in temperate European forests, where it is of high ecological, economic and symbolic
220 importance (Eaton, Caudullo, Oliveira & de Rigo, 2016). The species occurs from central Spain (39°N)
221 to southern Fennoscandia (62°N) and thus experiences a huge gradient of climatic conditions (Petit et
222 al., 2002). A widely diverse community of specialist and generalist herbivorous insects is associated
223 with this species throughout its distributional range (Southwood, Wint, Kennedy & Greenwood, 2005).
224 Between May and July 2021, we studied 138 trees in 47 sites across 17 European countries covering
225 most of the pedunculate oak geographic range (Fig. 2). The sites were chosen with the minimal
226 constraint of being located in a wooded area of at least 1ha (Valdés-Correcher et al., 2021). We
227 haphazardly selected three mature oaks per site, with the exception of six sites (three sites with one
228 tree, one site with two trees and two sites with five trees, see Table S1.1 in Appendix S1 in Supporting
229 Information).



230

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

233

234 Bird predation attempts

235 We measured bird predation attempts in the field by exposing a total of 40 plasticine caterpillars (20
236 plasticine caterpillars twice) on each individual oak. We made plasticine caterpillars of green plasticine,
237 mimicking common lepidopteran larvae (3 cm long, 0.5 cm diameter, see Low, Sam, McArthur, Posa &
238 Hochuli, 2014). We secured them on twigs with a 0.3 mm metallic wire. We attached five plasticine
239 caterpillars to each of four branches facing opposite directions (i.e., 20 caterpillars per tree) at about
240 2 m from the ground.

241 We installed the plasticine caterpillars six weeks after budburst in each study area, thus synchronizing
242 the study with local oak phenology. We removed the plasticine caterpillars after 15 days and installed

243 another set of 20 artificial caterpillars per tree for another 15 days. At the end of each exposure period
244 (which varied from 10 to 20 (mean \pm SD: 14.5 \pm 1.23) days due to weather conditions, we carefully
245 removed the plasticine caterpillars from branches, placed them into plastic vials and shipped them to
246 the project coordinator. Plasticine caterpillars from six sites were either lost or altered during shipping,
247 preventing the extraction of relevant data.

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

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

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

264 [Acoustic monitoring and related variables](#)

265 We used passive acoustic monitoring to characterize both the overall acoustic diversity (i.e., the
266 soundscape surrounding target oaks) and the bird species richness and functional diversity associated

267 with oaks, targeting the canopy insectivores that are expected to play a functional predation role on
268 oak herbivores (Fig. 2). In each site, we randomly chose one oak among those used to measure bird
269 predation rates in which we installed an AudioMoth device (Hill et al., 2018) to record audible sounds
270 for 30 min every hour. Automated recording started the day we installed the first set of 20 plasticine
271 caterpillars in trees and lasted until batteries stopped providing enough energy. The recording settings
272 are the following: Recording period: 00.00-24.00 (UTC); Sample rate: 48 kHz; Gain: Medium; Sleep
273 duration: 1800 s, Recording duration: 1800 s.

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

278 We processed acoustic samples with functions in the *soundecology* (Villanueva-Rivera & Pijanowski,
279 2018) and *seewave* libraries (Sueur, Aubin & Simonis, 2008) in the R environment (R Core Team, 2020),
280 and a wrap-up function made available by A. Gasc in GitHub ([https://github.com/agasc/Soundscape-](https://github.com/agasc/Soundscape-analysis-with-R)
281 [analysis-with-R](https://github.com/agasc/Soundscape-analysis-with-R)). To summarize information on the acoustic diversity of each site, we first divided every
282 acoustic sample (regardless of its length) into non-overlapping 1 min samples. Then, we calculated six
283 common acoustic diversity indices for each 1 min sample: the Acoustic Complexity Index (ACI), the
284 Acoustic Diversity Index (ADI), the Bioacoustic Index (BI), the total acoustic entropy (H), the Normalized
285 Difference Sound Index (NDSI), and the Number of frequency Peaks NPIC (Bradfer-Lawrence et al.,
286 2019; Sueur et al., 2014). We further aggregated these indices into a multiacoustic index (MultiAcou)
287 as proposed by Barbaro et al. (2022). We calculated the median of each acoustic index per day and
288 then averaged median values across days for each site separately. We proceeded like this because 24
289 h cycles summarize the acoustic activity and account for all possible sounds of a given day.
290 Furthermore, other studies have previously shown that median values of acoustic indices for a given
291 day are more representative than mean values of the acoustic activity because they are less sensitive

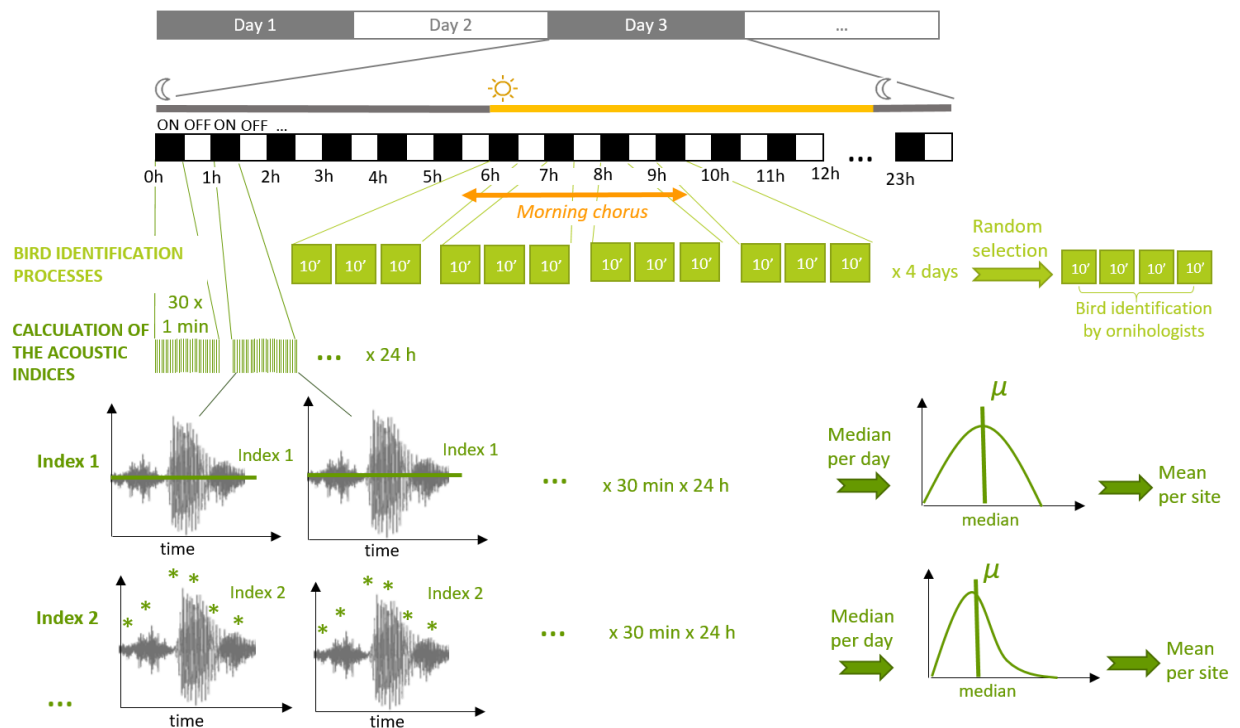
292 to extreme values (Barbaro et al., 2022; Dröge et al., 2021). This procedure resulted in one single value
293 of each acoustic diversity index per site. It is important to note that being calculated over 24 h, these
294 indices do not represent bird-related variables only, but are rather seen as an integrative component
295 of the surrounding habitat around target oaks.

296

297 Bird species richness and functional diversity

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

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



314

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

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

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

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

335 We derived acoustic traits calculations from the work of Krishnan & Tamma (2016). We first extracted
336 five pure recordings without sonic background for each of the 25 candidate insectivore species from
337 the online database Xeno-canto.org (Vellinga & Planque, 2015). We then calculated the *number of*
338 *peaks* (i.e., NPIC) in the audio signal (see § Acoustic diversity, above) as well as the *frequency of the*
339 *maximum amplitude peaks* for each vocal element using the *seewave* library (Sueur, Aubin & Simonis,
340 2008) and averaged these frequencies for each species. Being based on song and call frequency and
341 complexity, these indices inform on the adaptation of the vocal repertoire of these species to their
342 environment.

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

352 Environmental data

353 Environmental data refer to local temperature and forest cover. We used the high 10-m resolution GIS
354 layers from the Copernicus open platform (Cover, 2018) to calculate forest cover for all European sites.
355 We manually calculated the percentage of forest cover for the two sites located outside Europe using
356 the "World imagery" layer of Arcgis ver. 10.2.3552. We calculated both the percentage of forest cover
357 in a 20-m (henceforth called *local* forest cover) and 200-m (*landscape* forest cover) buffer around the
358 sampled oaks. We chose two nested buffer sizes to better capture the complexity of habitat structure
359 on the diversity and acoustic activity of birds. Local forest cover is particularly important for estimating
360 bird occurrence probability (Melles, Glenn & Martin, 2003), whereas landscape forest cover is an
361 important predictor of bird community composition in urban areas (Rega-Brodsky & Nilon, 2017).
362 Moreover, both local and landscape habitat factors shape insect prey distribution (Barr, van Dijk,
363 Hylander & Tack, 2021). Preliminary analyses revealed that results were qualitatively the same using
364 10-, 20- or 50-m buffers as predictors of local forest cover and 200- or 500-m buffers as predictors of
365 landscape forest cover (see Table S5.5 in Appendix S5). Because other variables were defined at the
366 site level, we averaged the percentage of forest cover for the sampled trees per site and per buffer
367 size.

368 We extracted the mean annual temperature at each site from the WorldClim database (the spatial
369 resolution is $\sim 86 \text{ km}^2$, Hijmans et al., 2005).

370 Statistical analyses

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

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

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):

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

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).

398

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

406

407 When several models competed with the best model (i.e., when multiple models were such that their
408 $\Delta\text{AICc} < 2$), we applied a procedure of multimodel inference, building a consensus model including the
409 variables in the set of best models. We then averaged their effect sizes across all the models in the set
410 of best models, using the variable weight as a weighting parameter (i.e., model averaging). We
411 considered that a given predictor had a statistically significant effect on the response variable when its
412 confidence interval excluded zero.

413

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

424

425 We run all analyses in the R language environment (R Core Team, 2020) with libraries *MuMIn* (Bartoń,
426 2020), *lme4* (Bates, Mächler, Bolker & Walker, 2015), and *piecewiseSEM* (Lefcheck, 2020).

427

428 Results

429 Bird acoustic diversity

430 Of the seven acoustic diversity indices (see Fig. S6.2 in Appendix S6 for correlation between indices),
431 only Acoustic Diversity Index (ADI) and acoustic entropy (H) were significantly associated with any of
432 the predictors tested, i.e., temperature or latitude, local forest cover and landscape forest cover (Table
433 S3.2 in Appendix S3). ADI and H both increased with local forest cover (i.e., percentage of forest cover
434 in a 20-m buffer around recorders). Landscape-scale forest cover (i.e., percentage of forest cover in a
435 200-m buffer around recorders) was the only other predictor retained in the set of competing models
436 in a range of $\Delta AICc < 2$ to explain acoustic entropy variation, but this predictor had little importance
437 ($RVI < 0.5$) and its effect was not statistically significant (Fig. 5b; Table S3.2 in Appendix S3).

438

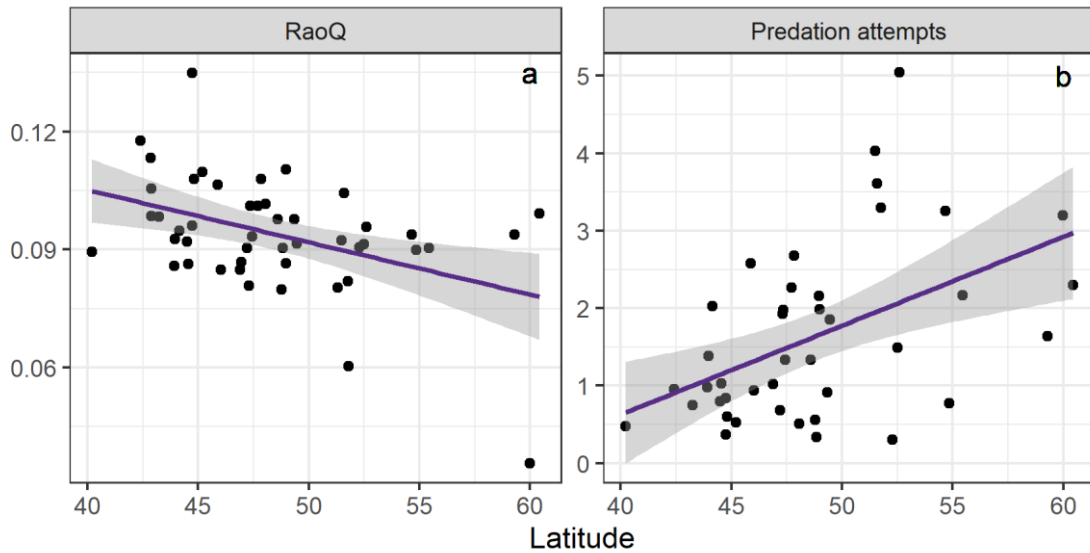
439 Bird species richness and functional diversity

440 We identified a total of 87 bird species, among which 25 were classified as candidate functional
441 insectivores. Bird species richness varied from 8 to 23 species per recording site (mean \pm SD: $15.2 \pm$
442 3.7 , $n = 47$ sites) and richness of candidate insectivores from 2 to 9 species (5.7 ± 1.5). The null model
443 was among models competing in a range of $\Delta AICc < 2$ for both total species richness and candidate
444 insectivores (Table S3.2 in Appendix S3).

445 Among the five bird functional diversity and species richness indices, only functional quadratic entropy
446 (Rao's Q) characterizing species dispersion from the functional centroid was significantly influenced by
447 the predictors tested (temperature or latitude, local and landscape forest cover, Table S3.2 in Appendix
448 S3). Specifically, Rao's Q decreased towards higher latitudes (Fig. 4a and Fig. 5c). Other predictors

449 retained in the set of competing models in a range of $\Delta AICc < 2$ had little importance ($RVI < 0.5$) and
450 were not significant (Fig. 5c; Table S3.2 in Appendix S3).

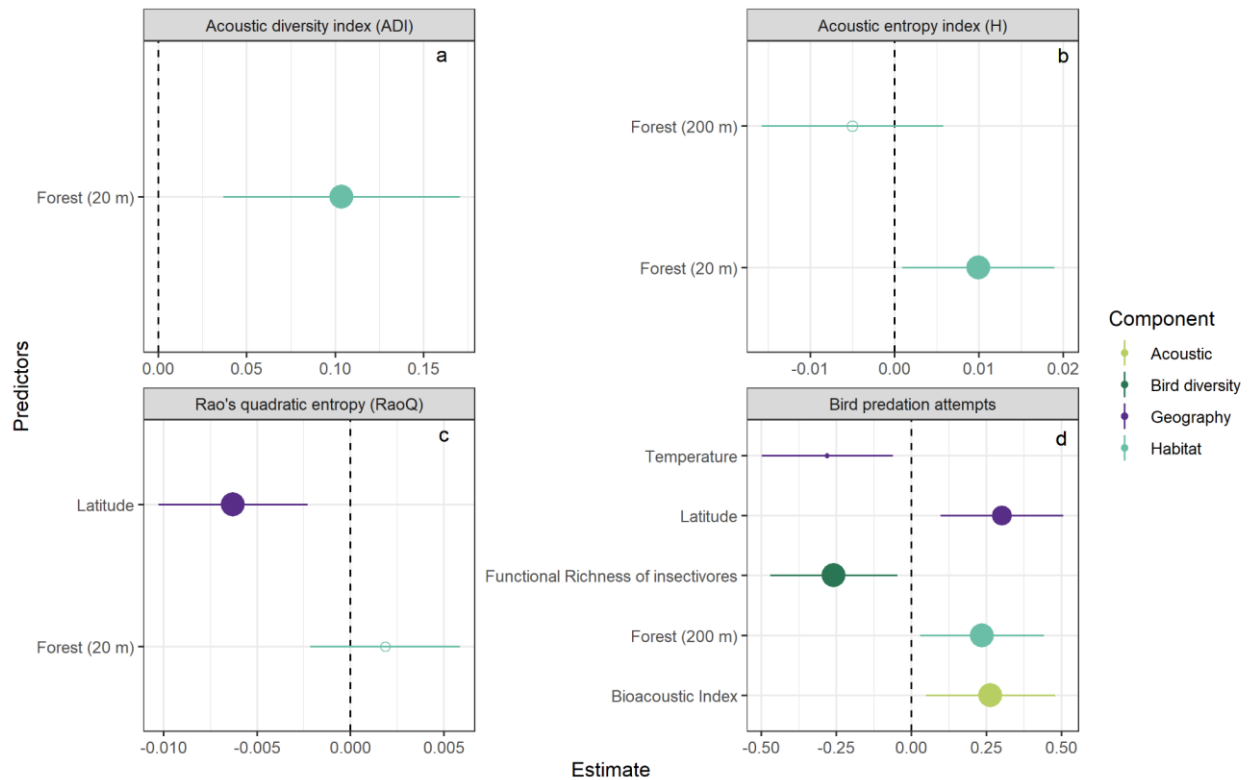
451



452

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

455



456

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

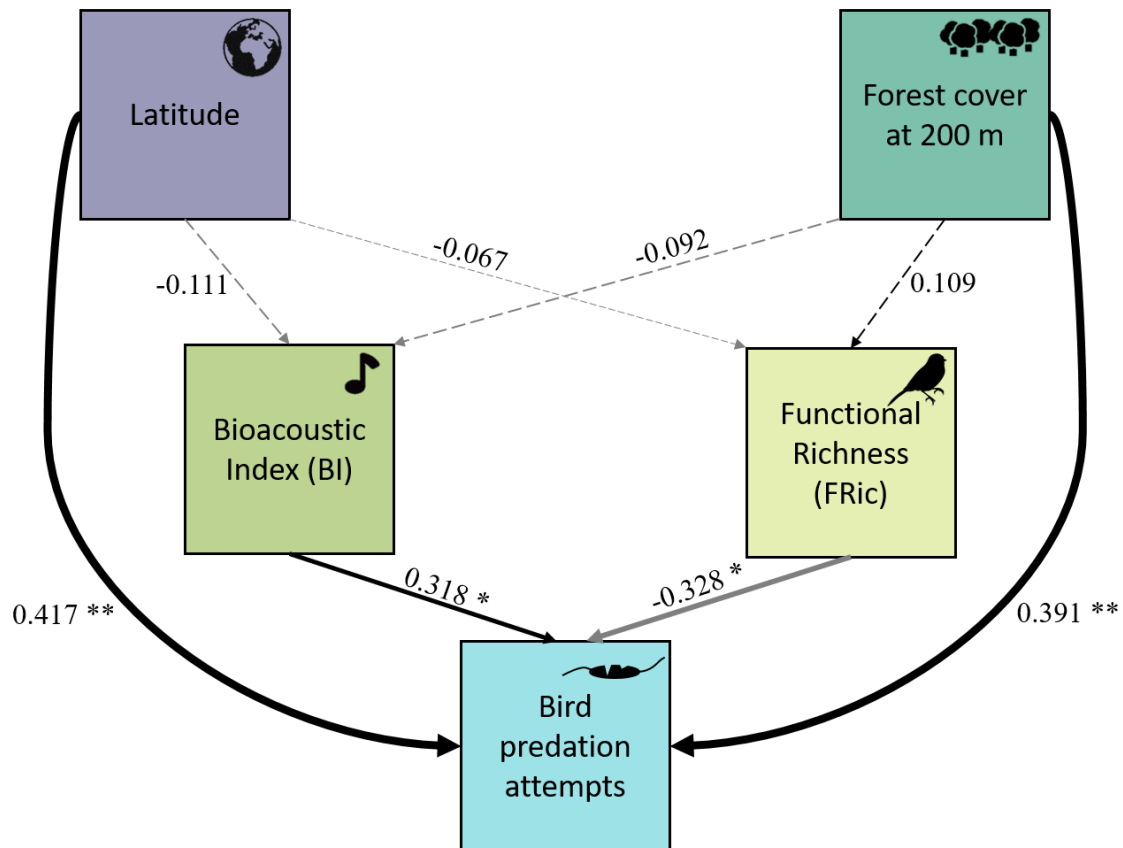
464 Bird predation attempts

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

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

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

478 A first SEM was set up by specifying direct links between environmental variables (latitude and
479 landscape forest cover) and bird diversity variables (FRic and BI) on the one hand and between bird
480 diversity variables and predation attempts on the other. The model was however misspecified ($C = 27$,
481 $P < 0.001$, $AIC = 51$). We ran a second model also including the direct paths between latitude, landscape
482 forest cover and bird predation attempts. Model AIC dropped dramatically ($\Delta AIC = 19$), indicating that
483 the full model with direct paths between latitude, forest cover and bird predation attempts had a
484 better fit ($C = 4$, $P = 0.131$, $AIC = 32$). Latitude, landscape forest cover and bioacoustic index had a
485 significant positive effect on bird predation attempts whereas FRic had a significant negative effect on
486 bird predation attempts. Altogether, these results indicate that latitude and forest cover had direct
487 effects on bird predation attempts that were not mediated by local changes in bird diversity (Fig. 6).



488

489 **Figure 6.** Structural equation model. The thickness of the arrows is proportional to coefficient parameter estimate.

490 Standardized estimates for each response variable are indicated next to each arrow. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

491 Continuous and dashed arrows represent significant ($P < 0.05$) and non-significant ($P > 0.05$) relationships respectively.

492 Black and gray arrows represent positive and negative relationships respectively. FRic refers to the functional richness of candidate

493 insectivorous birds.

494 Discussion

495

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

497 The Latitudinal Biotic Interactions Hypothesis (Dobzhansky, 1950) is a controversial idea, particularly

498 for biotic interactions between herbivores and higher trophic levels (Lövei & Ferrante, 2017; Zvereva

499 & Kozlov, 2021). Against this hypothesis and contrarily with our prediction ((i), Fig. 1), we found that

500 latitude was positively related to bird predation attempts. More bird predation attempts at higher

501 latitudes could be due to longer daylight duration in spring northwards, leading insectivorous birds to

502 have more time per day to find their prey and thus allowing high coexistence of predators during a

503 period of unlimited resource availability (Speakman et al., 2000). Alternatively, birds needing more
504 energy in colder temperatures to thermoregulate may need to feed more to maintain their metabolic
505 activity (Caraco et al., 1990; Kendeigh, 1969; Steen, 1958; Wansink & Tinbergen, 1994). Consistently
506 with this explanation, we found a negative relationship between temperature and bird predation
507 attempts. Moreover, temperature remained an important, significant predictor of bird predation
508 attempts when we controlled for the duration of daylight (Table S3.2 in Appendix S3), which further
509 supports this explanation. However, we cannot exclude the possibility that the lower predation rates
510 at lower latitudes was due to lower prey detectability.

511

512 In agreement with our prediction (i, Fig. 1), we provide evidence for a significant negative relationship
513 between latitude and the functional diversity of insectivorous birds. Despite substantial differences
514 among functional diversity indices, this suggests that more functionally diverse assemblages of
515 insectivorous birds are able to coexist locally in oak woods towards the south of Europe (Currie et al.,
516 2004; Hillebrand, 2004; Willig et al., 2003). Of the multiple functional diversity indices commonly used
517 to describe ecological communities, it is noticeable that only the quadratic entropy index responded
518 negatively to latitude, for it is a synthetic index which simultaneously takes into account the richness,
519 evenness, and divergence components of functional diversity (Mouillot et al., 2013).

520

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

522 We predicted that bird predation attempts would increase with bird functional diversity (ii, Fig. 1), but
523 found no or opposite effects, depending on the functional index considered. Only functional
524 insectivore richness was negatively correlated to predation rates. Negative relationships between
525 predation and predator functional diversity can arise from a combination of both intraguild predation
526 --- predators preying upon predators (Mooney et al., 2010) --- and intraguild competition (Houska
527 Tahadlova et al., 2022), although we can hardly tease them apart in the present study. An important
528 step forward would consist in testing whether predation patterns revealed with artificial prey are

529 representative of predation intensity as a whole (Zvereva & Kozlov, 2021). For example, functional
530 richness may be a proxy for dietary specialization such that functionally more diverse predator
531 communities would seek more prey of which they are specialists and thus predate less on artificial
532 caterpillars. It is possible that a higher diversity of insectivorous birds in warmer regions was linked to
533 higher diversity and abundance of arthropod prey (Kissling et al., 2012) and therefore to greater prey
534 availability (Charbonnier et al., 2016). If so, then the pattern we observed may merely be
535 representative of the 'dilution' of bird attacks on artificial prey among more abundant and diverse real
536 prey (Zeuss, Brunzel & Brandl, 2017; Zvereva et al., 2019). A follow-up of the present study should
537 therefore pay special attention on the real prey density pre-existing in each sampling site where
538 artificial prey are to be deployed as a standardized measure of predation rates across sites.

539

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

551

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

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

564

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

573

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

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

579

580 Latitude may directly drive both bird activity and abundance according to available resources
581 (Pennings & Silliman, 2005). Even changes in the abundance of a single, particularly active, predator
582 species along the latitudinal gradient to explain the observed pattern (Maas et al., 2015; Philpott et
583 al., 2009). For example, the blue tit *Cyanistes caeruleus* and the great tit *Parus major* are typical and
584 widespread canopy insectivores of European oak forests and are particularly prone to predate
585 herbivorous caterpillars while showing considerable adaptive behaviour to prey availability (Mols &
586 Visser, 2002; Naef-Daenzer & Keller, 1999). If the predation attempts on the plasticine caterpillars were
587 to be predominantly due to these species, then it would be their abundance and activity that would
588 play a role in predation attempts rather than the overall diversity of insectivores (Maas et al., 2015).
589 Here, we based our assessment of functional bird composition on candidate insectivore occurrences
590 obtained from standardized acoustic surveys, which on the one hand insures that we have no observer,
591 site, or phenological biases on species occurrences, but on the other hand also makes it difficult to
592 precisely account for each species' abundance. Other complementary methods to assess the relative
593 roles of each individual bird species on predation rates should be deployed further to better account
594 for actual predatory bird abundance and activity, including DNA sampling (Garfinkel, Minor & Whelan,
595 2022), camera traps (Martínez-Núñez et al., 2021) or species-specific bird surveys involving tape calls
596 or capture methods.

597

598 **Conclusion**

599 We found a negative association between latitude and bird functional diversity, but at the same time,
600 a positive relationship between latitude and avian predation. Our study therefore provides partial
601 support for the latitudinal clines in biodiversity hypothesis, but clearly conflicts with the Latitudinal
602 Biotic Interaction Hypothesis (Dobzhansky, 1950). As cross-continental studies exploring the large-
603 scale relationship between latitude and the strength of biotic interactions generally ignore local
604 factors, we argue that characterizing the contrasting habitats of the study sites is a good way to
605 circumvent some inconsistencies in the results. We identify pre-existing real prey density and single

606 key bird species abundances as two particularly important variables deserving further attention.
607 Furthermore, predicting ecosystem services — here, potential pest regulation service — on a large
608 scale by standardized proxies such as acoustic ecology for predator diversity and plasticine caterpillars
609 for predation function seem to be good ways to reduce methodological biases and strengthen our
610 understanding of the macro-ecology of biotic interactions.

611 [Data availability statement](#)

612

613 For the moment there is an embargo on data and codes which will be lifted after open acceptance.
614 Schille et al., 2023, « Data and codes for the article "Latitudinal gradient in avian insectivory:
615 complementary effects of climate, habitat and bird diversity" », <https://doi.org/10.57745/OE0JEA>,
616 Recherche Data Gouv.

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618

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623

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907 Biosketch

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

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

911 Author contribution: B.C., L.B. and E.V.C. conceptualized the study and developed the methodology.

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916 processed audio recordings for bird species identification. L.S. processed and analyzed the data with
917 guidance from B.C. and L.B. L.S., B.C., L.B. led the writing and all authors contributed critically to the
918 revisions.