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1

2 **Decomposing drivers in avian insectivory: large-scale effects**

3 **of climate, habitat and bird diversity**

4

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103

104 **Abstract**

105 **Aim**

106 Climate is a major driver of large scale variability in biodiversity, as a likely result of more intense biotic
107 interactions under warmer conditions. This idea fuelled decades of research on plant-herbivore
108 interactions, but much less is known about higher-level trophic interactions. We addressed this
109 research gap by characterizing both bird diversity and avian predation along a climatic gradient at the
110 European scale.

111 **Location**

112 Europe.

113 **Taxon**

114 Insectivorous birds and pedunculate oaks.

115 **Methods**

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

121 **Results**

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

127 **Main conclusions**

128 Our study supports the hypothesis of an increase in the diversity of insectivorous birds towards warmer
129 climates, but refutes the idea that an increase in diversity would lead to more predation and advocates
130 for better accounting for activity and abundance of insectivorous birds when studying the large-scale
131 variation in insect-tree interactions.

132 **Keywords:** Acoustic diversity, Climatic gradient, Functional diversity, Insectivorous birds, Plasticine
133 caterpillars, Predation function

134

135 **Résumé**

136 **Objectif**

137 Le climat est l'un des principaux facteur structurant de la variabilité à grande échelle de la biodiversité,
138 possiblement en raison d'interactions biotiques plus intenses dans des conditions de température plus
139 élevées. Cette idée a alimenté des décennies de recherche sur les interactions plantes-herbivores, mais
140 on en sait beaucoup moins sur les interactions impliquant les niveaux trophiques supérieurs. Nous
141 avons comblé cette lacune en caractérisant à la fois la diversité des oiseaux et leur activité de prédation
142 le long d'un gradient climatique à l'échelle européenne.

143 **Localisation**

144 Europe.

145 **Taxon**

146 Oiseaux insectivores et chênes pédonculés.

147 **Méthodes**

148 Nous avons déployé des leurres en pâte à modeler mimant des chenilles sur 138 chênes dans 47 sites
149 le long d'un gradient latitudinal de 19° en Europe pour quantifier l'insectivorie avienne par le biais de
150 tentatives de prédation. De plus, nous avons utilisé la surveillance acoustique passive pour (i)
151 caractériser la diversité acoustique des paysages sonores environnants ; (ii) estimer l'abondance et
152 l'activité des oiseaux à travers des enregistrements acoustiques passifs et (iii) déduire à la fois la
153 diversité taxonomique et fonctionnelle des oiseaux insectivores à partir des enregistrements.

154 **Résultats**

155 Nous avons montré une augmentation de la diversité fonctionnelle des oiseaux insectivores avec la
156 température moyenne. La prédation avienne augmentait avec la couverture forestière et l'activité
157 acoustique des oiseaux, mais diminuait avec la température annuelle moyenne et la richesse
158 fonctionnelle des oiseaux insectivores. Contrairement à nos prédictions, la variation de la diversité des
159 oiseaux n'était pas le lien mécaniste entre le climat et la variation des tentatives de prédation sur les
160 leurres, laquelle était directement influencée par le climat et la couverture forestière.

161 **Conclusions principales**

162 Notre étude confirme l'hypothèse d'une augmentation de la diversité des oiseaux insectivores vers des
163 climats plus chauds, mais ne corrobore pas l'idée qu'une augmentation de la diversité conduirait à
164 davantage de prédation. Elle plaide en faveur d'une meilleure prise en compte de l'activité et de
165 l'abondance des oiseaux insectivores lors de l'étude de la variation à grande échelle des interactions
166 entre insectes et arbres.

167 **Mots-clés** : Diversité acoustique, Gradient climatique, Diversité fonctionnelle, Oiseaux insectivores,
168 Chenilles en pâte à modeler, Fonction de prédation.

169 Introduction

170

171 Climate is a key driver of biotic interactions (Dobzhansky, 1950). A long held view in ecology posits that
172 warmer and more stable climatic conditions intensify biotic interactions and accelerates speciation
173 (MacArthur, 1984; Schemske, Mittelbach, Cornell, Sobel & Roy, 2009), which should result in large
174 scale positive correlations between biodiversity and biotic interactions. However appealing this idea
175 is, the generality of large-scale climatic clines in biodiversity and biotic interactions as well as the
176 underlying causal links are still widely debated. Yet, insights into the controversy have been dominated
177 by studies on plant-insect interactions (Anstett, Chen & Johnson, 2016; Kozlov, Lanta, Zverev &
178 Zvereva, 2015). Biotic interactions involving higher trophic levels received much less attention. Yet,
179 insectivorous birds are among the predators contributing the most to the control of insect herbivores
180 in terrestrial ecosystems (van Bael et al., 2008; Sam, Jorge, Koane, Amick & Sivault, 2023; Sekercioglu,
181 2006) and therefore have consequences on both the assembly of ecological communities and the
182 functioning of ecosystems. The omission of predation in theories linking large-scale variability in
183 climate with biodiversity therefore represents a critical gap in knowledge that needs to be addressed.

184

185 Bird communities are highly responsive to climate, at both regional and continental scale. There is a
186 large body of literature demonstrating that several dimensions of bird diversity vary with climate,
187 including bird abundance, species richness, phylogenetic or functional diversity (Blackburn & Gaston,
188 1996; Symonds Christidis & Johnson, 2006; Willig, Kaufman & Stevens, 2003). A well substantiated
189 explanation is that niche opportunities increase with increasing habitat heterogeneity under milder
190 climatic conditions, which increases species coexistence and ultimately species richness through
191 functional complementarity (Hawkins, Diniz-Filho, Jaramillo & Soeller, 2006). The biodiversity and
192 ecosystem relationship theory predicts that both abundance and diversity of birds are crucial

193 predictors of the top-down control they exert upon insect prey (Bael et al., 2008; Nell, Abdala-Roberts,
194 Parra-Tabla & Mooney, 2018; Otto, Berlow, Rank, Smiley & Brose, 2008; Sinclair, Mduma & Brashares,
195 2003). Numerous studies supported this theory and demonstrated that bird functional diversity in
196 particular --- that is the diversity, distribution and complementarity of predator traits involved in
197 predation --- is a good predictor of predation (Barbaro, Giffard, Charbonnier, van Halder & Brockerhoff,
198 2014; Greenop, Woodcock, Wilby, Cook & Pywell, 2018; Philpott et al., 2009). It follows that variation
199 in bird diversity along climatic gradients should be mirrored by consistent variation in avian predation
200 rates.

201

202 Local factors can however alter macroecological patterns (Ikin et al., 2014; Kissling, Sekercioglu & Jetz,
203 2012), by filtering the regional species pool (De la Mora, García-Ballinas & Philpott, 2015; Kleijn,
204 Rundlöf, Scheper, Smith & Tscharntke, 2011) and by influencing the behavior of organisms. The
205 diversity and composition of bird communities heavily depends on local factors that provide niches
206 and food opportunities (Charbonnier et al., 2016). In this respect, multiscale forest cover proved to be
207 a particularly good predictor of composition of birds communities at different spatial scales, as bird
208 foraging activity is ultimately determined by vertical and horizontal habitat heterogeneity, which
209 influences both where prey can be found and caught, and where foraging birds can breed and hide
210 from predators (Vickery & Arlettaz, 2012). Thus, modeling the response of bird communities to large-
211 scale bioclimatic drivers as well as their role as predators would benefit from using a combination of
212 habitat variables and biotic predictors (Barbaro et al., 2019; Speakman et al., 2000). However, cross-
213 continental studies exploring the relationship between large scale climatic gradients and the strength
214 of biotic interactions generally ignore local factors, which may partly explain inconsistencies in their
215 findings (but see Just, Dale, Long & Frank, 2019).

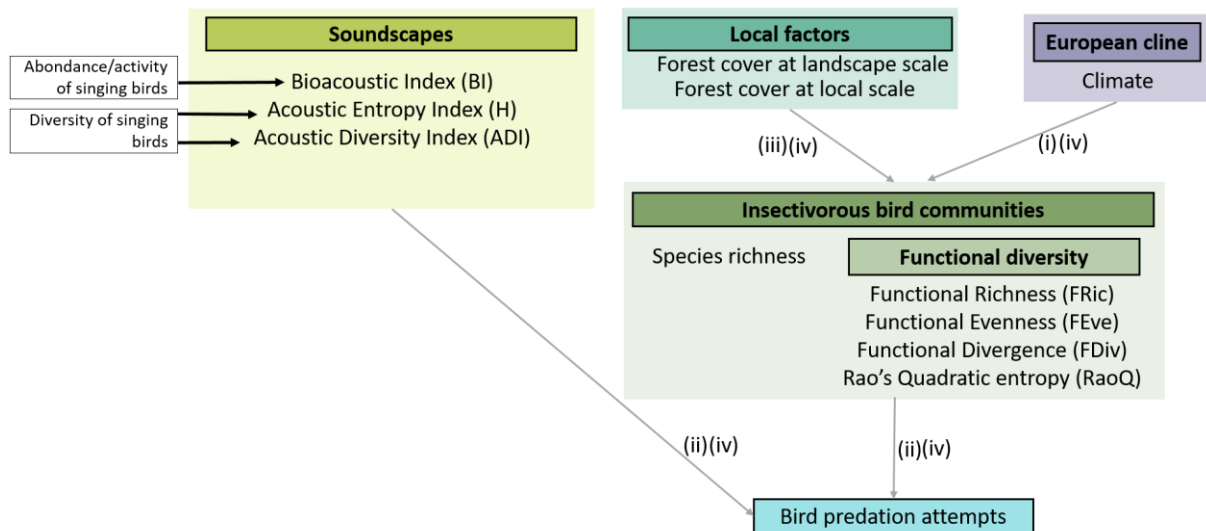
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217 A major challenge to analyze climatic clines in biotic interactions consists in simultaneously
218 characterizing changes in predator biodiversity and experimentally assessing the strength of predation,

219 while considering the effect of contrasting habitats. However, the recent development of passive
220 acoustic monitoring provides a standardized, low-cost and non-invasive approach for ecological
221 studies and biodiversity monitoring (Gibb, Browning, Glover-Kapfer, Jones & Börger, 2019). The
222 acoustic monitoring of a given habitat primarily allows the delayed identification of bird species over
223 large gradients with no need for distributed expertise across study sites. The quantification of bird
224 abundance through passive acoustic monitoring remains a technical challenge, but the calculation of
225 certain acoustic indices based on the physical characteristics of the recorded sounds provides relevant
226 proxies to this end (Gasc et al., 2013; Sueur, Farina, Gasc, Pieretti & Pavoine, 2014). Should such indices
227 consistently correlate with macro-scales biotic interactions, ecoacoustics would be a promising
228 complementary approach to existing methods in macroecology and in functional ecology.

229

230 Here, we addressed the hypothesis of continental north-south clines on insectivorous bird community
231 diversity and their predation function, while controlling for local factors throughout the European
232 distribution range of the pedunculate oak (*Quercus robur* L., 1753), a major forest tree species.
233 Specifically, we predict the following (Fig. 1): (i) bird diversity (including bird acoustic diversity,
234 insectivorous bird species richness and functional diversity) and predation attempts increase with
235 warmer climates; (ii) bird predation attempts increase with bird acoustic activity, species richness and
236 greater functional diversity of insectivorous birds; (iii) bird diversity, acoustic activity and bird
237 predation attempts increase with increasing forest cover at both local (neighborhood) and larger
238 spatial scales; (iv) large-scale variability in bird predation attempts is driven by local changes in the
239 diversity and acoustic activity of birds. To test these predictions, we quantified bird predation attempts
240 on plasticine caterpillars and estimated bird species richness, functional diversity and acoustic activity
241 through simultaneous passive acoustic monitoring. We eventually tested the respective responses of
242 these variables and their relationships at the pan-European scale.



243

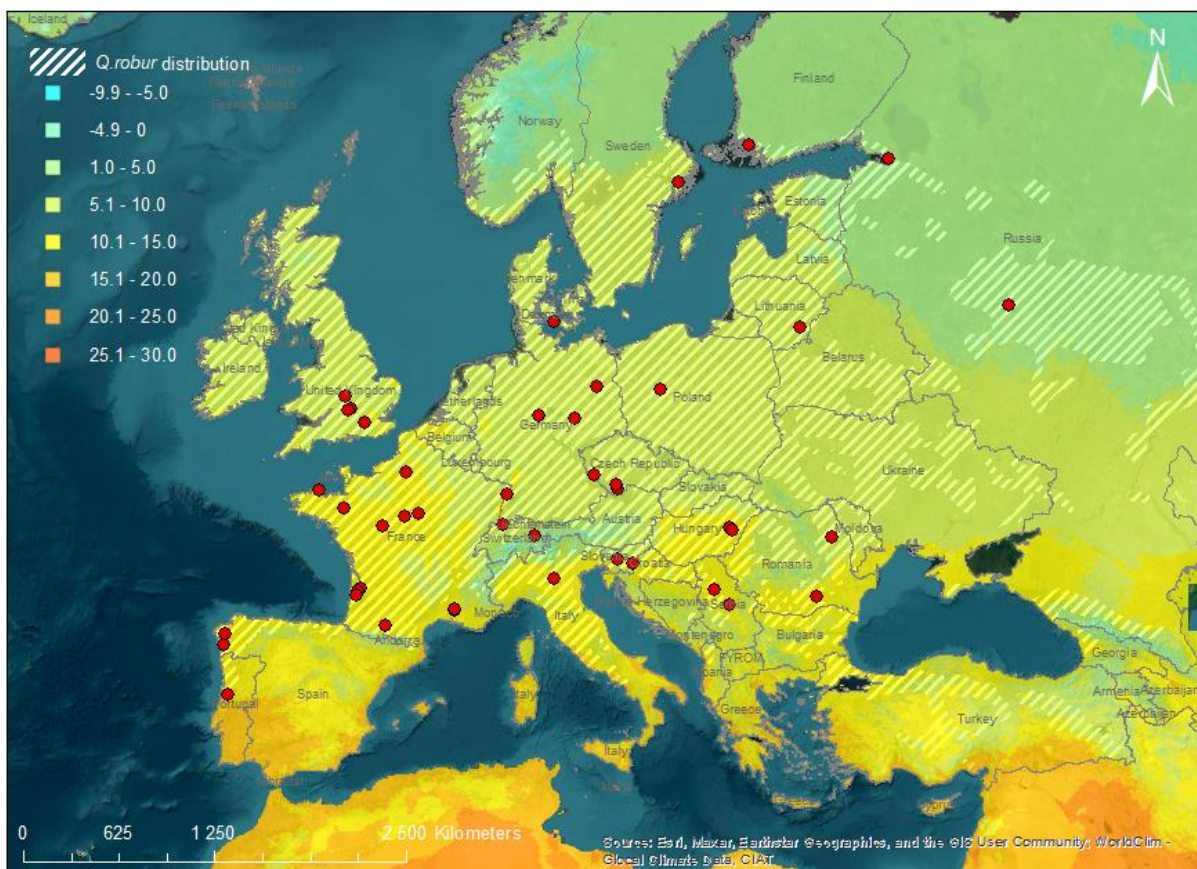
244 [double column] **Figure 1:** Conceptual diagram of the predictions of this study and the relationships already established in the
 245 literature. Boxed elements written in bold correspond to the main categories of variables tested, they are not variables as
 246 such. Variables used in models are shown in regular font. Where several variables described the same category (e.g. BI, ADI,
 247 H, all describing acoustic indices), we used multi-model comparisons to identify the best variable. Items framed in black on a
 248 white background represent untested variables. Black arrows indicate relationships well supported by the literature (see Gasc
 249 et al., 2018; and Fig.2 Sánchez-Giraldo, Correa Ayram & Daza, 2021). Our specific predictions are represented with grey
 250 arrows, solid and dashed lines representing positive and negative (predicted) relationships. Numbers refer to predictions as
 251 stated in the main text.

252 Materials and methods

253 Study area

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

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



266 [double column] **Figure 2:** Locations of the 47 sites sampled in spring 2021. Average annual temperature (color scale)
267 according to WorldClim (Hijmans, Cameron, Parra, Jones & Jarvis, 2005) and *Quercus robur* distribution range are indicated.
268
269

270 Bird predation attempts

271 We measured bird predation attempts in the field by exposing a total of 40 plasticine caterpillars (20
272 plasticine caterpillars twice) on each individual oak. We made plasticine caterpillars of green plasticine,
273 mimicking common lepidopteran larvae (3 cm long, 0.5 cm diameter, see Low, Sam, McArthur, Posa &
274 Hochuli, 2014). We secured them on twigs with a 0.3 mm metallic wire. We attached five plasticine

275 caterpillars to each of four branches facing opposite directions (i.e., 20 caterpillars per tree) at about
276 2 m from the ground.

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

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

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

295 To assess the effect of temperature independently of other variables that could vary with latitude, we
296 also calculated a second bird predation attempts index by standardizing the predation attempts by
297 daylight duration in every site. We ran the same statistical models as for the non-standardized bird
298 predation attempts. The outcomes remained qualitatively the same and the results of this analysis are
299 presented in Table S2.2 in Appendix S2.

300 Acoustic monitoring and related variables

301 We used passive acoustic monitoring to characterize the species and functional diversity of bird
302 communities associated with oaks, as well as to serve as a proxy of the abundance and diversity of
303 vocalizing birds (Fig. 2). In each site, we randomly chose one oak among those used to measure bird
304 predation rates in which we installed an AudioMoth device (Hill et al., 2018) to record audible sounds
305 for 30 min every hour. Automated recording started the day we installed the first set of 20 plasticine
306 caterpillars in trees and lasted until batteries stopped providing enough energy. The recording settings
307 were the following: Recording period: *00.00-24.00 (UTC)*; *Sample rate: 48 kHz*; *Gain: Medium*; *Sleep*
308 *duration: 1800 s*, *Recording duration: 1800 s*.

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

313 Acoustic diversity indices as proxies of bird diversity and activity

314 We processed acoustic samples with functions in the “soundecology” v.1.3.3 (Villanueva-Rivera &
315 Pijanowski, 2018) and “seewave” v. 2.1.8 (Sueur, Aubin & Simonis, 2008) libraries in the R environment
316 version 4.1.2 (R Core Team, 2020), and a wrap-up function made available by A. Gasc in GitHub
317 (<https://github.com/agasc/Soundscape-analysis-with-R>). We first divided every acoustic sample
318 (regardless of its length) into non-overlapping 1 min samples.

319 Acoustic indices capture various dimensions of the soundscape but are not expected to fully reflect
320 any bird biodiversity-related variable. However, several studies have shown that some of them are
321 positively related to the abundance or diversity of vocalizing species (for more details, see Sánchez-
322 Giraldo, Correa Ayram & Daza, 2021, Fig.2 and Gasc et al., 2018), although the strength of this
323 relationships is still poorly understood. We have therefore chosen to consider only those specific

324 indices and we used multi-model statistical inferences to identify those that were the most strongly
325 linked with the response variables of interest (see below).

326 We calculated the following three acoustic diversity indices for each 1 min sample: the Acoustic
327 Diversity Index (ADI) and the Total Acoustic Entropy (H) which are both based on Shannon diversity
328 index and are therefore close to a proxy for bird diversity (Sueur, Pavoine, et al., 2008; Villanueva-
329 Rivera, Pijanowski, Doucette & Pekin, 2011), and the Bioacoustic Index (BI) which is positively related
330 to bird vocal activity and the occupancy of acoustic signal frequency bands (Boelman, Asner, Hart &
331 Martin, 2007; Gasc et al., 2018). We calculated the median of each acoustic index per day and then
332 averaged median values across days for each site separately. We proceeded like this because 24 h
333 cycles summarize the acoustic activity and account for all possible sounds of a given day. Furthermore,
334 other studies have previously shown that median values of acoustic indices for a given day are more
335 representative than mean values of the acoustic activity because they are less sensitive to extreme
336 values (Barbaro et al., 2022; Dröge et al., 2021). This procedure resulted in one single value of each
337 acoustic diversity index per site.

338

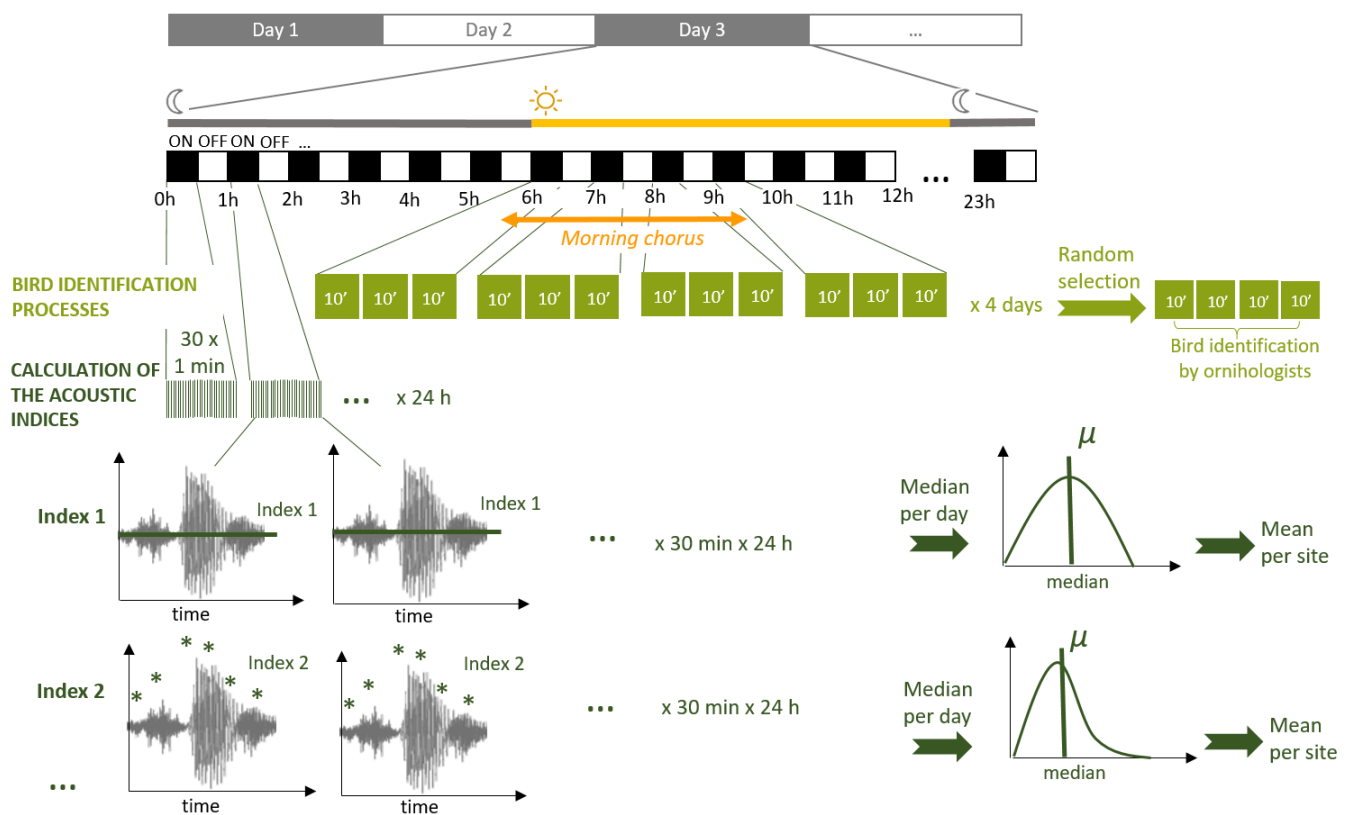
339 Bird species richness and functional diversity

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

342 **Data processing** – For each site, we subsampled the 30 min samples corresponding to the songbird
343 morning chorus (*i.e.*, the period of maximum singing activity), which incidentally also corresponds to
344 the time of the day when anthropic sounds were of the lowest intensity. Specifically, we selected
345 sounds recorded within a period running from 30 min before sunrise to 3 h 30 min after sunrise. We
346 then split each 30 min sample into up to three 10 min sequences, from which we only retained those
347 recorded on Tuesday, Thursday, Saturday, and Sunday. We chose these days on purpose to balance
348 the differences in anthropogenic noises between working days and weekends. For each sound sample,
349 we displayed the corresponding spectrogram with the “seewave” library in the R environment (Sueur,

350 Aubin & Simonis, 2008). We visually sorted sound samples thanks to spectrograms and discarded
 351 samples with noise from anthropogenic sources, rain, or wind, which can be recognized as very low
 352 frequency noise on the spectrogram. We also discarded samples with noise of very high frequency
 353 corresponding to cicada chirps. We then randomly selected one sound sample per site and per day,
 354 with the exception of four sites for which the four samples only covered two to three days. In total, we
 355 selected 188 samples of 10 min (i.e., 4 samples per site).

356



357

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

360 **Bird species identification** – We distributed the samples among 21 expert ornithologists. Each expert
 361 performed aural bird species identifications from 4 (one site) to 52 samples (13 sites), primarily from
 362 her/his region of residence, for auditory acoustic detection of bird species. We established a
 363 presence/absence Site × Species matrix, from which we calculated species richness and functional

364 diversity. It is important to note that, there is no possibility to determine the direction and distance at
365 which birds are singing from audio recordings when using a single device for a given site. As a result,
366 there is no standard method for determining whether or not two vocalizations of the same species at
367 two different times come from one single individual or more, which prevents an accurate estimate of
368 bird abundance. However, experienced ornithologists involved in this study consider that, given the
369 territoriality of birds and the range of the recorders, it is unlikely that they recorded the vocalizations
370 of several individuals of the same species. It therefore seems reasonable to assume that among-site
371 differences in bird species richness were also representative of among-site differences in bird
372 abundance.

373

374 **Functional diversity** – We defined 25 bird species as candidate insectivores for attacking plasticine
375 caterpillars (Table S3.3 in Appendix S3) with those bird species meeting the following criteria: be
376 insectivorous during the breeding season or likely to feed their offspring with insects, forage primarily
377 in forested habitats, and are likely to use substrates such as lower branches or lower leaves of trees
378 where caterpillars were attached to find their prey (Barbaro et al., 2021; Brambilla & Gatti, 2022). We
379 calculated the functional diversity of these candidate insectivores by combining morphological,
380 reproductive, behavioral and acoustic traits.

381 With the exception of acoustic traits, we extracted functional traits from different published sources,
382 listed in Table S3.4 in Appendix S4. Specifically, we used three continuous traits: *body mass*, *mean*
383 *clutch size* and *bill culmen length* (see Fig. 2 in Tobias et al., 2022) combined with four categorical traits:
384 *foraging method* (predominantly understory gleaner, ground gleaner, canopy gleaner), *diet*
385 (insectivores or mixed diet), *nest type* (open in shrub, open on ground, cavity or open in tree) and
386 *migration* (short migration, long migration or resident).

387 We derived acoustic traits calculations from the work of Krishnan & Tamma (2016). We first extracted
388 five pure recordings without sonic background for each of the 25 candidate insectivore species from

389 the online database Xeno-canto.org (Vellinga & Planque, 2015). We then calculated the *number of*
390 *peaks* (i.e., NPIC) in the audio signal (see § Acoustic diversity, above) as well as the *frequency of the*
391 *maximum amplitude peaks* for each vocal element using the “seewave” library (Sueur, Aubin &
392 Simonis, 2008) and averaged these frequencies for each species. Being based on song and call
393 frequency and complexity, these indices inform the adaptation of the vocal repertoire of these species
394 to their environment.

395 We summarized the information conveyed by the 9 traits categories into five indices representing
396 complementary dimensions of the functional diversity (FD) of a community (Mouillot, Graham,
397 Villéger, Mason & Bellwood, 2013): functional richness (FRic, i.e., convex hull volume of the functional
398 trait space summarized by a principal coordinates analysis), functional evenness (FEve, i.e., minimum
399 spanning tree measuring the regularity of trait abundance distribution within the functional space),
400 and functional divergence (FDiv, i.e., trait abundance distribution within the functional trait space
401 volume) (Villéger, Mason & Mouillot, 2008), as well as Rao's quadratic entropy (RaoQ, i.e., species
402 dispersion from the functional centroid) (Botta-Dukát, 2005). These were calculated for each site with
403 the “dbFD” function of the “FD” library v.1.0.12 (Laliberté, Legendre & Shipley, 2014) in the R
404 environment.

405 Environmental data

406 Environmental data refer to local temperature and forest cover. We used the high 10-m resolution GIS
407 layers from the Copernicus open platform (Cover, 2018) to calculate forest cover for all European sites.
408 We manually calculated the percentage of forest cover for the two sites located outside Europe using
409 the “World imagery” layer of Arcgis ver. 10.2.3552. We calculated both the percentage of forest cover
410 in a 20-m (henceforth called *local* forest cover) and 200-m (*landscape* forest cover) buffer around the
411 sampled oaks. We chose two nested buffer sizes to better capture the complexity of habitat structure
412 on the diversity and acoustic activity of birds. Local forest cover is particularly important for estimating
413 bird occurrence probability (Melles, Glenn & Martin, 2003), whereas landscape forest cover is an

414 important predictor of bird community composition in urban areas (Rega-Brodsky & Nilon, 2017).
415 Moreover, both local and landscape habitat factors shape insect prey distribution (Barr, van Dijk,
416 Hylander & Tack, 2021). Preliminary analyses revealed that results were qualitatively the same using
417 10-, 20- or 50-m buffers as predictors of local forest cover and 200- or 500-m buffers as predictors of
418 landscape forest cover (see Table S4.5 in Appendix S4). Because other variables were defined at the
419 site level, we averaged the percentage of forest cover for the sampled trees per site and per buffer
420 size.

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

423 Statistical analyses

424 We analyzed 14 response variables in separate linear models (LMs) (Table S2.2 in Appendix S2): bird
425 predation attempts, species richness of the entire bird community and that of candidate insectivores,
426 functional diversity (each of the four indices) and acoustic diversity (each of the three indices). For
427 each response variable, we first built a full model including variables reflecting two components of the
428 environment: climate and local habitat. The general model equation was (Eq. 1):

$$429 Y_i = \beta_0 + \beta_1 \times Forest_{20,i} + \beta_2 \times Forest_{200,i} + \beta_3 \times Climate_i + \varepsilon_i \quad (1)$$

430 where Y is the response variable, β_0 the model intercept, β_{is} model coefficient parameters, $Forest_{20}$ and
431 $Forest_{200}$ the effects of the local and landscape forest cover respectively, $Climate$ the effect of mean
432 annual temperature and ε the residuals.

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

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

439 It has to be noted that the inclusion of the acoustic component in the second set of models does not
440 imply any direct link between avian predation and acoustic diversity. By comparing models including
441 the acoustic diversity or not, we are asking whether residual variance can be explained by this
442 component while controlling for other sources of variation. If so, then acoustic diversity components
443 with non-null coefficients have to be considered as proxies of predation, i.e., relatively easily
444 measurable variables representative of unmeasured (or unknown) variables with a direct effect on
445 predation.

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

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

458

459 First, we ranked each model according to the difference in AICc between the given model and the
460 model with the lowest AICc ($\Delta AICc$). Models within 2 $\Delta AICc$ units of the best model (i.e., the model
461 with the lowest AICc) are generally considered as likely (Burnham & Anderson, 2002). We computed

462 AICc weights for each model (w_i). w_i is interpreted as the probability of a given model being the best
463 model among the set of candidate models. Eventually, we calculated the relative variable importance
464 (RVI) as the sum of w_i of every model including this variable, which corresponds to the probability a
465 variable is included in the best model.

466

467 When several models competed with the best model (i.e., when multiple models were such that their
468 $\Delta AICc < 2$), we applied a procedure of multimodel inference, building a consensus model including the
469 variables in the set of best models. We then averaged their effect sizes across all the models in the set
470 of best models, using the variable weight as a weighting parameter (i.e., model averaging). We
471 considered that a given predictor had a statistically significant effect on the response variable when its
472 confidence interval excluded zero.

473

474 We run all analyses in the R language environment (R Core Team, 2020) with libraries “MuMIn”
475 v.1.43.17 (Bartoń, 2020), “lme4” v. 1.1.27.1 (Bates, Mächler, Bolker & Walker, 2015). All R codes are
476 provided in Appendix S5 in Supporting Information.

477

478 Results

479 Bird acoustic diversity

480 Of the three acoustic diversity indices (see Fig. S6.6 in Appendix S6 for correlation between indices),
481 only Acoustic Diversity Index (ADI) and acoustic entropy (H) were significantly associated with any of
482 the predictors tested, i.e., temperature, local forest cover and landscape forest cover (Table S2.2 in
483 Appendix S2). ADI and H both increased with local forest cover (i.e., percentage of forest cover in a 20-
484 m buffer around recorders). Landscape-scale forest cover (i.e., percentage of forest cover in a 200-m
485 buffer around recorders) was the only other predictor retained in the set of competing models in a

486 range of $\Delta AICc < 2$ to explain acoustic entropy variation, but this predictor had little importance (RVI <
487 0.5) and its effect was not statistically significant (Fig. 5b; Table S2.2 in Appendix S2).

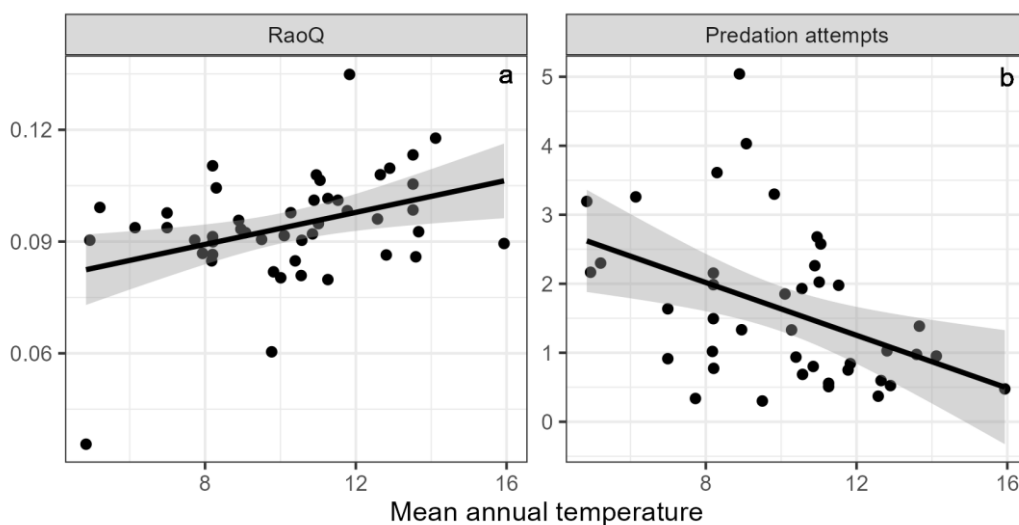
488

489 Bird species richness and functional diversity

490 We identified a total of 87 bird species, among which 25 were classified as candidate functional
491 insectivores. Bird species richness varied from 8 to 23 species per recording site (mean \pm SD: $15.2 \pm$
492 3.7 , $n = 47$ sites) and richness of candidate insectivores from 2 to 9 species (5.7 ± 1.5). The null model
493 was among models competing in a range of $\Delta AICc < 2$ for both total species richness and candidate
494 insectivores (Table S2.2 in Appendix S2).

495 Among the five bird functional diversity and species richness indices, only functional quadratic entropy
496 (Rao's Q) characterizing species dispersion from the functional centroid was significantly influenced by
497 the predictors tested (temperature, local and landscape forest cover, Table S2.2 in Appendix S2).
498 Specifically, Rao's Q increased with increasing temperature (Fig. 4a and Fig. 5c). Other predictors
499 retained in the set of competing models in a range of $\Delta AICc < 2$ had little importance (RVI < 0.5) and
500 were not significant (Fig. 5c; Table S2.2 in Appendix S2).

501



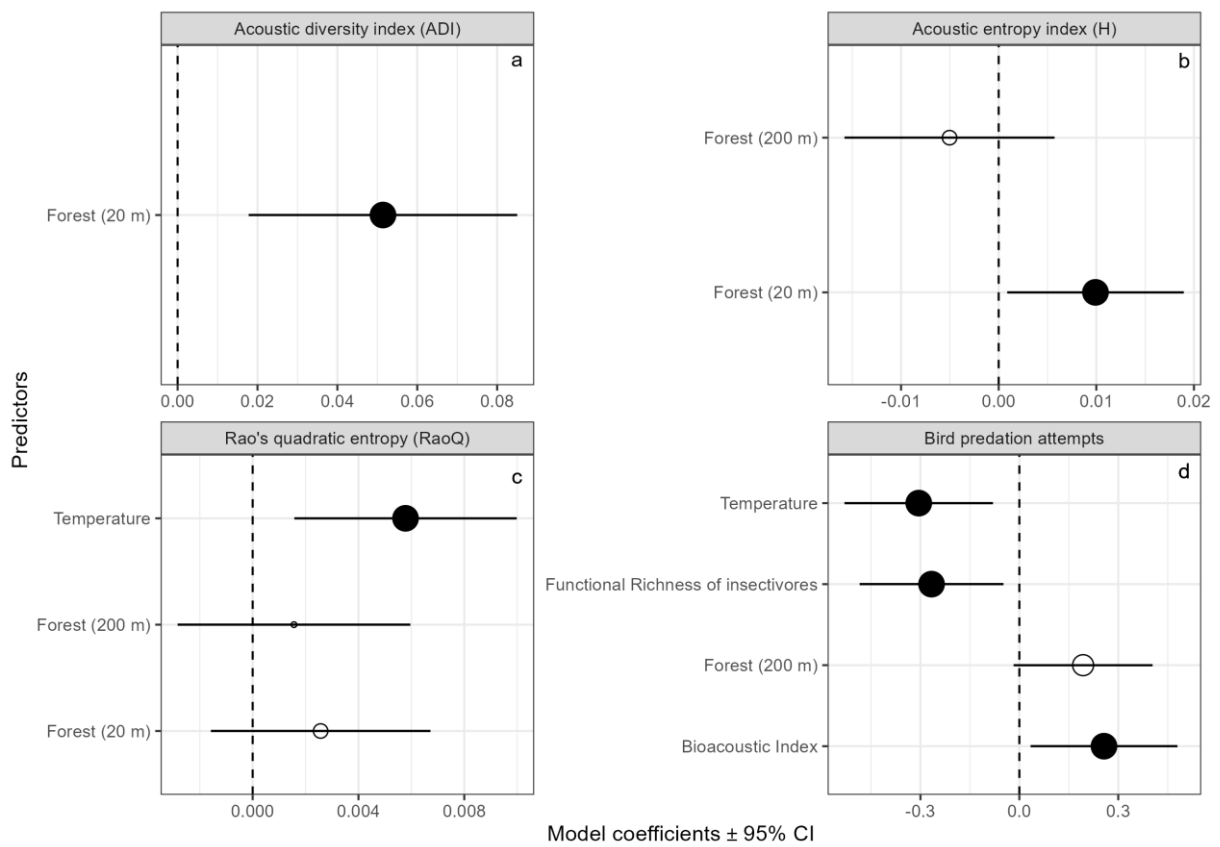
502

503 [double column] **Figure 4:** Scatter diagrams showing changes in (a) Rao's quadratic entropy (Rao's Q) and (b) predation
 504 attempts with mean annual temperature. These relationships were identified as significant in the linear models tested. A dot
 505 represents a site, the prediction line corresponds to a linear regression between the two variables and the gray bands represent
 506 the confidence intervals around this regression.

507
 508

509

510



511

512 [double column] **Figure 5:** Effects of climate (described by the mean annual temperature) and habitat (percentage of forest
 513 cover at 20 or 200 m) on Acoustic Diversity Index (ADI) (a), Acoustic Entropy Index (H) (b), Rao's quadratic entropy (RaoQ) (c),
 514 bird predation attempts (d) and effects of acoustic (Bioacoustic Index), bird diversity (Functional Richness) on bird predation
 515 attempts (d). Circles and error bars represent standardized parameter estimates and corresponding 95% confidence intervals
 516 (CI), respectively. The vertical dashed line centered on zero represents the null hypothesis. Full and empty circles represent
 517 significant and non-significant effect sizes, respectively. Circle size is proportional to RVI.

518 Bird predation attempts

519 Of the 4,860 exposed dummy caterpillars, 22.8% ($n = 1,108$) had bird bill marks. Model selection
520 retained two models in the set of competing models in a range of $\Delta AICc < 2$ (Table S2.2 in Appendix
521 S2). Bird functional richness (FRic) (RVI = 1.00), bioacoustic index (BI) (RVI = 1.00) and temperature
522 (RVI=1.00) were selected in all models. Landscape forest cover (RVI = 0.62) was also selected in one of
523 the two best models.

524 Bird predation attempts decreased with increasing mean annual temperature. Bird predation attempts
525 further increased with bioacoustic index (BI), but decreased with bird functional richness (FRic) (Fig.
526 4b and Fig. 5d). This finding suggests that the acoustic component captures some features of the
527 habitat that influence predation attempts independently of bird functional diversity. Likewise, the fact
528 that temperature was selected a significant predictor of bird predation attempts suggests that climate
529 has an effect on predation that is not only mediated by its effect on bird communities.

530 The results were comparable when we incorporated latitudinal changes in diel phenology in the
531 calculation of predation attempts through the standardization with the daylight duration (see Table
532 S2.2 in Appendix S2).

533 Discussion

534

535 Our study confirms the well documented increase of bird diversity towards warmer regions, a pattern
536 supporting our initial assumption that avian predation would mirror this pattern. Yet, we found the
537 opposite – predation attempts decreased with increasing temperature – which dismissed our
538 prediction that bird diversity and avian predation rate should correlate positively across large
539 geographic gradients. An important result of our study is that even when the functional dimension of
540 bird communities was accounted for, a substantial amount of variability remained to be explained and
541 were only partially accounted for by climate- and habitat-related variables. Altogether, these findings

542 suggest that current theory should be re-assessed, which we discuss below speculating on the main
543 causes of deviation from theoretical expectations.

544

545 **Functional diversity of insectivorous birds and bird predation attempts are both influenced by**
546 **climate, in opposite ways**

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

556

557 Contrary to our predictions (i, Fig. 1), bird predation attempts decreased with increasing temperature
558 and were therefore inconsistently linked with bird functional diversity. More bird predation attempts
559 at lower temperatures could be due to longer daylight duration in spring northwards, leading
560 insectivorous birds to have more time per day to find their prey and thus allowing high coexistence of
561 predators during a period of high resource availability (Speakman et al., 2000). Alternatively, as birds
562 require more energy to thermoregulate in colder temperatures, they may need to feed more in order
563 to maintain their metabolic activity (Caraco et al., 1990; Kendeigh, 1969; Steen, 1958; Wansink &
564 Tinbergen, 1994). Moreover, temperature remained an important, significant predictor of bird
565 predation attempts when we controlled for the duration of daylight (Table S2.2 in Appendix S2), which
566 further supports this explanation. However, we cannot exclude the possibility that the lower predation
567 rates at higher temperatures was due to lower prey detectability.

568

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

570 We predicted that bird predation attempts would increase with bird abundance and functional
571 diversity (ii, Fig. 1). The results only partially match these predictions. The relationship between bird
572 functional diversity and predation attempts conflicted with our predictions. Specifically, we found
573 neutral or negative relationship between these variables, depending on the functional index
574 considered. Only functional insectivore richness was negatively correlated to predation attempts.
575 Negative relationships between predation and predator functional diversity can arise from a
576 combination of both intraguild predation --- predators preying upon predators (Mooney et al., 2010) -
577 -- and intraguild competition (Houska Tahadlova et al., 2022), although we could not tease them apart
578 in the present study. An important step forward would consist in testing whether predation patterns
579 revealed using artificial prey are representative of predation intensity as a whole (Zvereva & Kozlov,
580 2021). For example, functional richness may be a proxy for dietary specialization in such a way that
581 more functionally diverse predator communities would seek more prey of which they are specialized
582 on and thus predate less on artificial caterpillars. It is also possible that a higher diversity of
583 insectivorous birds in warmer regions was linked to higher diversity and abundance of arthropod prey
584 and foraging niches (Kissling et al., 2012) and therefore to greater prey availability (Charbonnier et al.,
585 2016). If so, then the pattern we observed may merely be representative of the 'dilution' of bird attacks
586 on artificial prey among more abundant and diverse real prey (Zeuss, Brunzel & Brandl, 2017; Zvereva
587 et al., 2019). However, the dynamics between herbivore prey abundance and predation activity are
588 complex. A higher abundance of real herbivore prey could also lead to increased predation activity as
589 demonstrated in studies such as Singer, Farkas, Skorik & Mooney (2011), where the presence of
590 abundant herbivorous prey was found to drive higher predation rates by bird predators. This aligns
591 with the notion that predator populations respond to fluctuations in prey density (Salamolard, Butet,
592 Leroux & Bretagnolle, 2000), adjusting their foraging behavior to capitalize on available food resources.
593 A follow-up of the present study should therefore pay special attention to the real prey density pre-

594 existing in each sampling site where artificial prey are to be deployed as a standardized measure of
595 predation rates across sites.

596

597 Although passive acoustic monitoring, as most other relative bird sampling methods, does not allow
598 inferring directly bird absolute abundance, our study further brings methodological insights into the
599 usefulness of eco-acoustics into community and functional ecology. We found that among acoustic
600 indices that have been shown to correlate with bird abundance, activity and diversity, the Bioacoustic
601 index was positively correlated with bird predation attempts. Yet, this index was found to be
602 representative of the abundance and activity of singing birds (Boelman et al., 2007; Gasc et al., 2018).

603 It is thus reasonable to infer substantial causality between vocalizing bird abundance, their acoustic
604 activity, and the top-down control they exert upon insect prey. Such an interpretation is in line with
605 previous studies having reported positive relationships between bird abundance and predation
606 attempts on artificial prey (Roels, Porter & Lindell, 2018; Sam, Koane & Novotny, 2015). It is further
607 substantiated by the fact that if a species is recorded in a given site during the breeding season, it
608 indicates that it is probably feeding on that territory and can potentially affect predation rates. Our
609 study indicates that despite knowledgeable limitations inherent to the current development of
610 analytical tools, passive acoustic monitoring has the potential to provide acceptable proxies for the
611 characterization of bird biodiversity, the habitat they live in, and, to some extent, the ecosystem
612 services they provide. The present study therefore opens pathways for new research on the link
613 between functional and acoustic ecology.

614

615 **Local forest cover predicts bird acoustic diversity, whereas landscape forest cover increases bird**
616 **predation**

617 Acoustic diversity increased with closeness of canopy cover in the immediate neighborhood (20m
618 radius) of sampled trees (iii, Fig. 1). The most responsive indices were the Acoustic Diversity Index (ADI)
619 and the acoustic entropy (H), both designed to predict bird acoustic diversity across different habitats

620 under various ambient sound conditions (Fuller, Axel, Tucker & Gage, 2015; Machado, Aguiar & Jones,
621 2017). The former is related to a greater regularity of the soundscape and the latter is related to the
622 amplitude between frequency bands and time. They therefore correspond to soundscapes containing
623 multiple vocalizing species (Sueur, Pavoine, et al., 2008; Villanueva-Rivera, Pijanowski, Doucette &
624 Pekin, 2011). Acoustic entropy is also known to respond significantly to local forest habitat (Barbaro et
625 al., 2022), which is generally a good predictor of bird occupancy probability (Morante-Filho, Benchimol
626 & Faria, 2021).

627

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

636

637 **Large-scale variability in avian predation is not mediated by large-scale changes in bird communities**

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

641

642 At the European scale, climate may directly drive both bird activity and abundance according to
643 available resources (Pennings & Silliman, 2005). Even changes in the abundance of a single, particularly
644 active, predator species along the European climatic gradient could explain the observed pattern
645 (Maas, Tschardtke, Saleh, Dwi Putra, Clough & Siriwardena, 2015; Philpott et al., 2009). For example,

646 the blue tit *Cyanistes caeruleus* and the great tit *Parus major* are typical and widespread canopy
647 insectivores of European oak forests and are particularly prone to predate herbivorous caterpillars
648 while showing considerable adaptive behavior to prey availability (Mols & Visser, 2002; Naef-Daenzer
649 & Keller, 1999). If the predation attempts on the plasticine caterpillars were to be predominantly due
650 to these species, then it would be their abundance and foraging activity that would play a role in
651 predation attempts rather than the overall diversity of insectivores (Maas et al., 2015). Here, we based
652 our assessment of functional bird composition on candidate insectivore occurrences obtained from
653 standardized acoustic surveys, which on one hand insures that we have no observer, site, or
654 phenological biases on species occurrences, but on the other hand also makes it difficult to precisely
655 account for each species' abundance. Other complementary methods to assess the relative roles of
656 each individual bird species on predation rates should be deployed further to better account for actual
657 predatory bird abundance and activity, including DNA sampling (Garfinkel, Minor & Whelan, 2022),
658 camera traps (Martínez-Núñez et al., 2021) or species-specific bird surveys involving tape calls or
659 capture methods.

660

661 **Conclusion**

662 We found a positive association between temperature and bird functional diversity, and at the same
663 time, a negative relationship between temperature and avian predation. Our study therefore provides
664 partial support for the climatic clines in biodiversity hypothesis, but demonstrates that predation does
665 not follow the same pattern. As cross-continental studies exploring the large-scale relationship
666 between climate and the strength of biotic interactions generally ignore local factors, we argue that
667 characterizing the contrasting habitats of the study sites is a good way to circumvent some
668 inconsistencies in the results. We identify pre-existing real prey density and single key bird species
669 abundances as two particularly important variables deserving further attention. Furthermore,
670 predicting ecosystem services — here, potential pest regulation service — on a large scale by
671 standardized proxies such as acoustic ecology for predator diversity and plasticine caterpillars for

672 predation function seem to be good ways to reduce methodological biases and strengthen our
673 understanding of the macro-ecology of biotic interactions.

674 Data availability statement

675

676 For the moment, there is an embargo on data and codes which will be lifted after open acceptance.
677 Schille et al., 2024, « Data and codes for the article "Decomposing drivers in avian insectivory: large-
678 scale effects of climate, habitat and bird diversity" », <https://doi.org/10.57745/0E0JEA>, Recherche
679 Data Gouv.

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686

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970 **Biosketch**

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

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

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

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979 R.B. processed audio recordings for bird species identification. L.S. processed and analyzed the data

980 with guidance from B.C. and L.B. L.S., B.C., L.B. led the writing and all authors contributed critically to

981 the revisions.