Decomposing drivers in avian insectivory: large-scale effects of climate, habitat and bird diversity

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103

Abstract

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.

Location

112   Europe.

Taxon

114   Insectivorous birds and pedunculate oaks.

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.

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 predation. 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.

Introduction
169

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).

216

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.
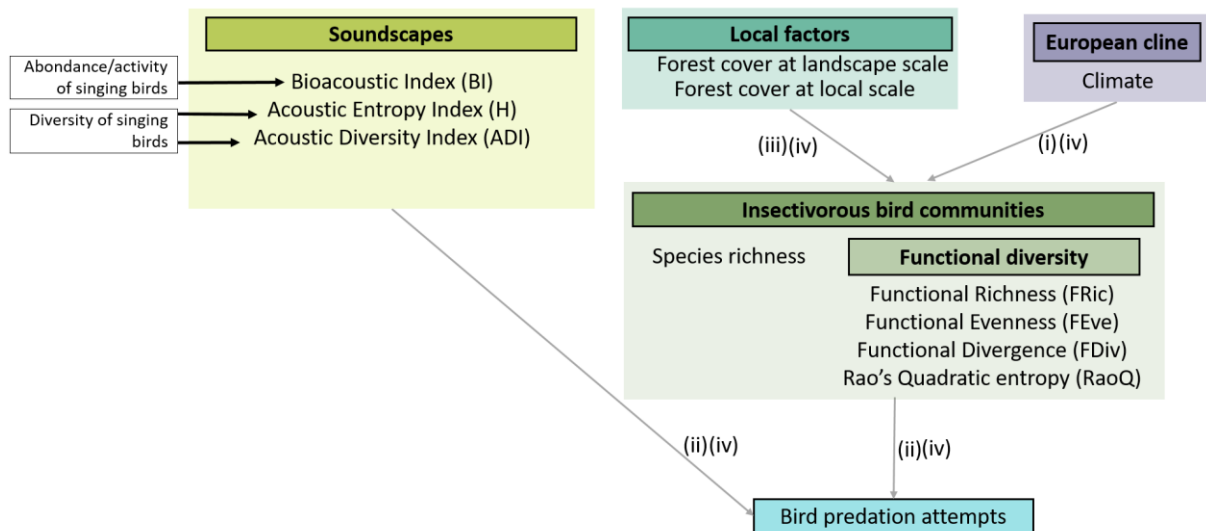
243

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.

Materials and methods

252

Study area

253

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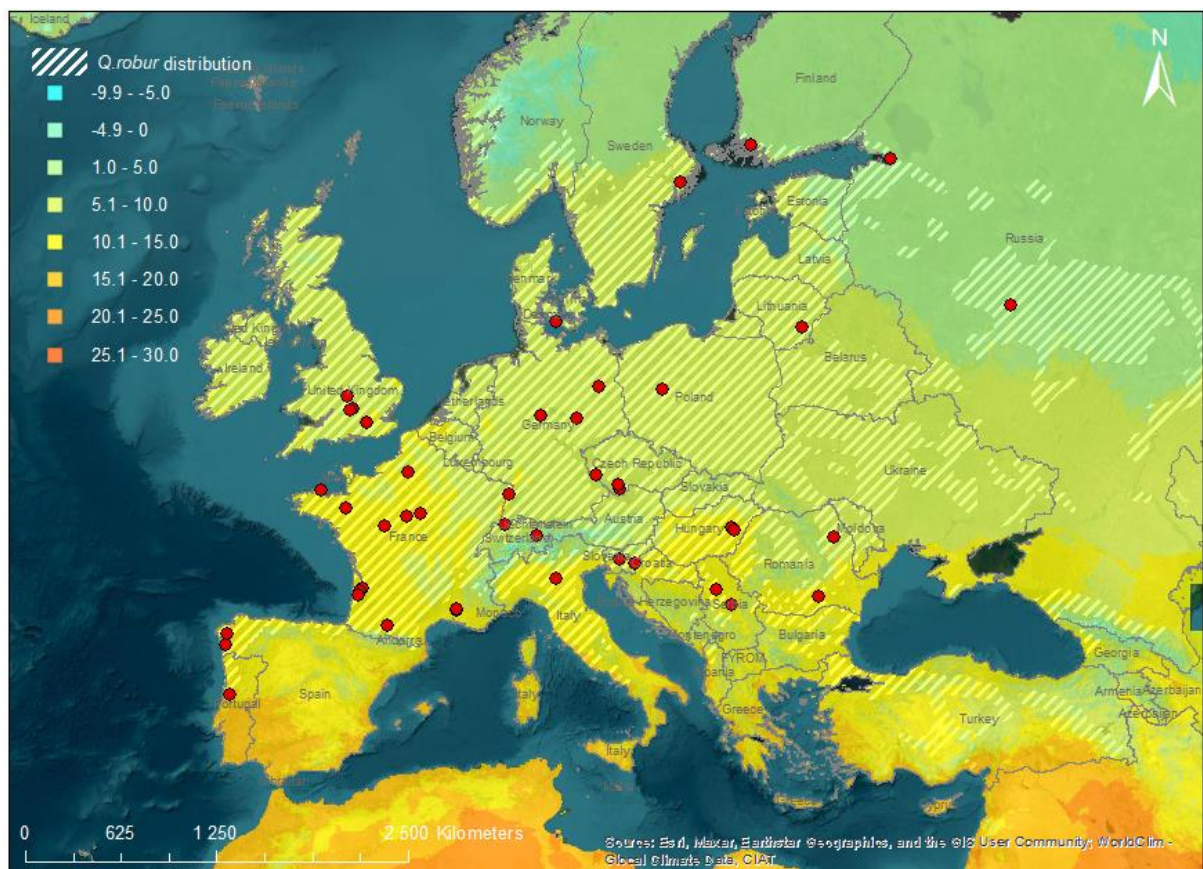
266
267   [double column] *Figure 2: Locations of the 47 sites sampled in spring 2021. Average annual temperature (color scale)*
268   *according to WorldClim (Hijmans, Cameron, Parra, Jones & Jarvis, 2005) and Quercus robur distribution range are indicated.*
269

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 ± SD: 14.5 ± 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.

Acoustic monitoring and related variables

300

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 (± 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).

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
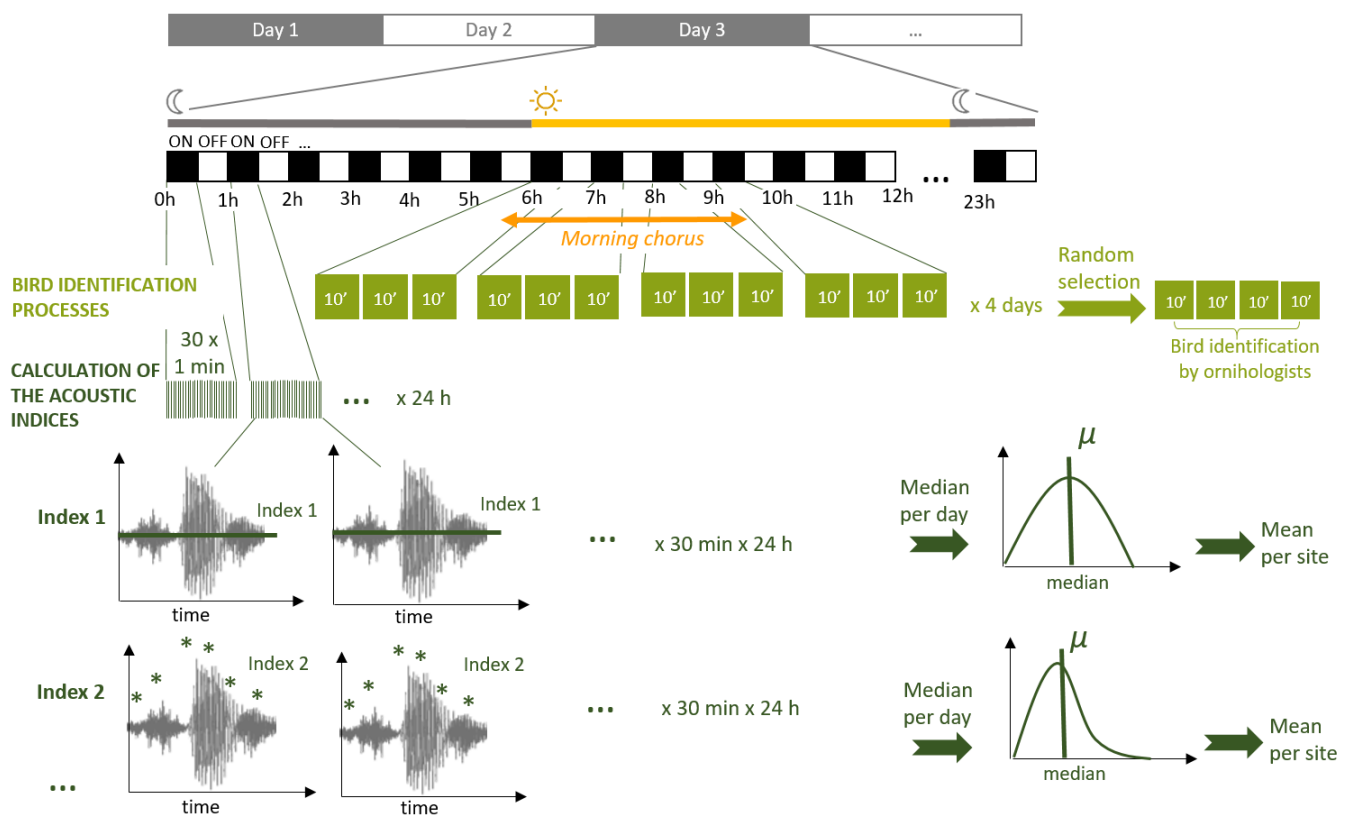
357

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 centroïd) (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 ~86 km^2, Hijmans et al., 2005).

Statistical analyses

423

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

437      $Y_i = \beta_0 + \beta_1 \times Forest_{20,i} + \beta_2 \times Forest_{200,i} + \beta_3 \times Climate_i +$

438          $\beta_4 \times Bird\ diversity_i + \beta_5 \times Acoustic\ diversity_i + \varepsilon_i$ (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 (ΔAICc). Models within 2 ΔAICc 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 ΔAICc < 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 ΔAICc < 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 ± SD: 15.2 ±

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 ΔAICc < 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 ΔAICc < 2 had little importance (RVI < 0.5) and

500   were not significant (Fig. 5c; Table S2.2 in Appendix S2).

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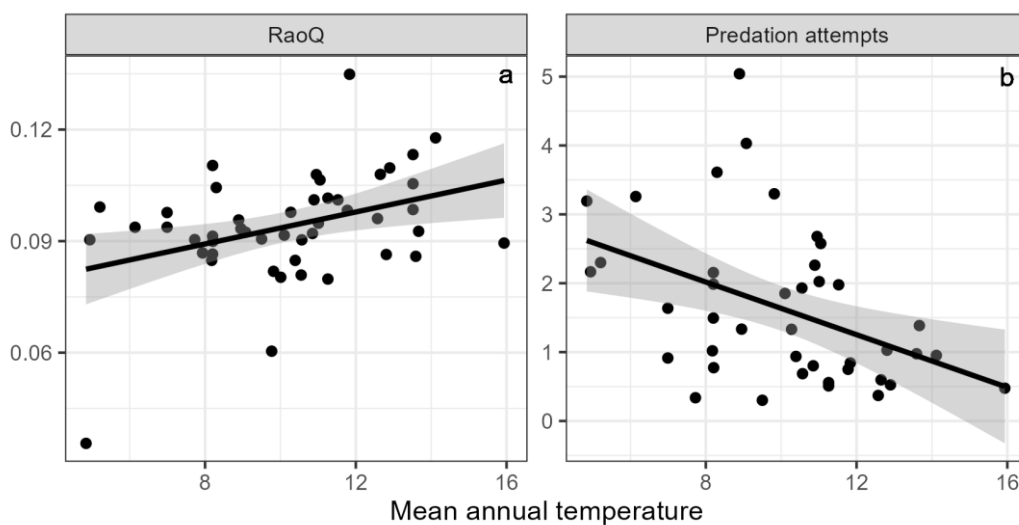
502

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

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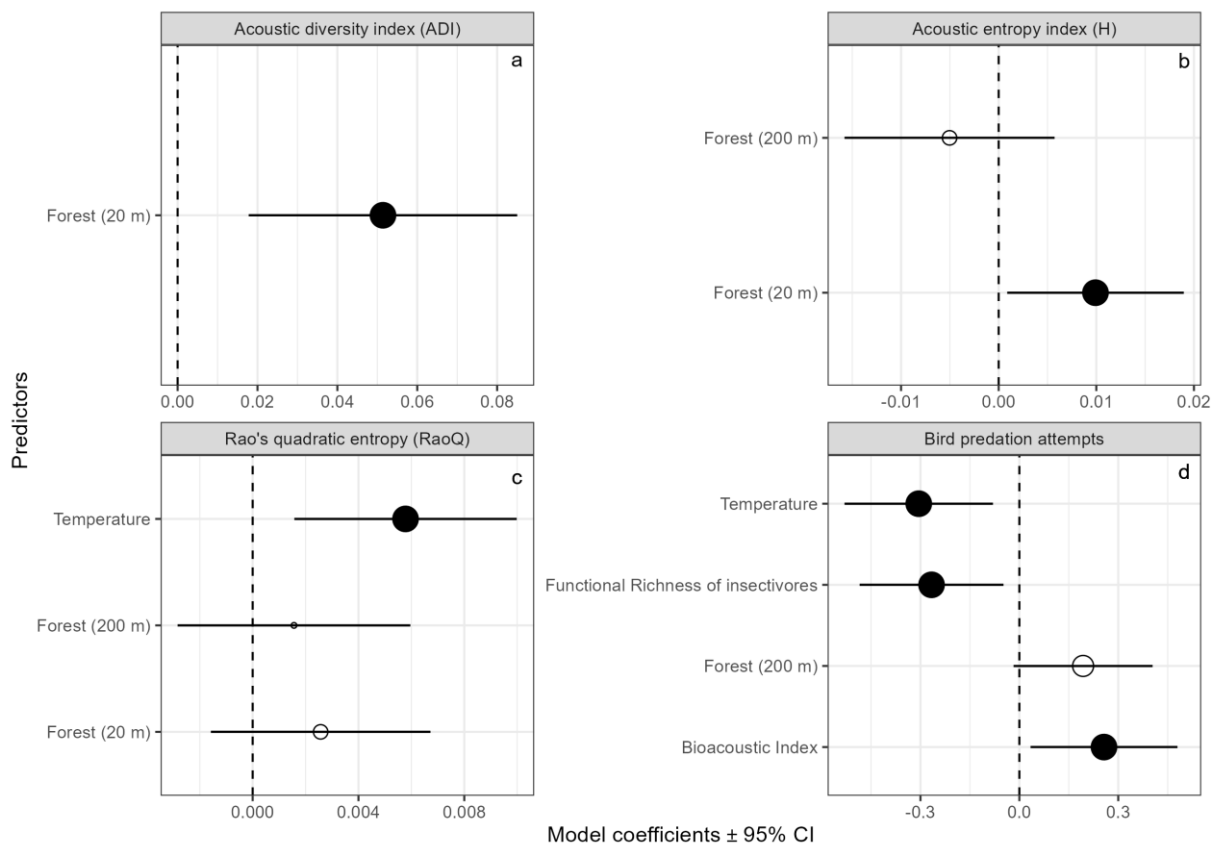
511

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.

Bird predation attempts

518

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 ΔAICc < 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).

Discussion

533

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

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

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

Data availability statement

674

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.

Copyright statement

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Biosketch

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

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

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