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Biotic predictors complement models of bat and bird responses to climate and tree diversity in European forests

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Manuscripts

1   **Research**

2   **Biotic predictors complement models of bat and bird responses to climate and tree**

3   **diversity in European forests**

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23   **Running head:** Biotic drivers of bat and bird diversity

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26

27　**(Abstract)**

28　Bats and birds are key providers of ecosystem services in forests. How climate and habitat

29　jointly shape their communities is well studied, but whether biotic predictors from other

30　trophic levels may improve bird and bat diversity models is less known, especially across

31　large bioclimatic gradients. Here, we achieved multi-taxa surveys in 209 mature forests

32　replicated in six European countries from Spain to Finland, to investigate the importance of

33　biotic predictors (i.e., the abundance or activity of defoliating insects, spiders, earthworms

34　and wild ungulates) for bat and bird taxonomic and functional diversity. We found that 9 out

35　of 12 bird and bat diversity metrics were best explained when biotic factors were added to

36　models including climate and habitat variables, with a mean gain in explained variance of

37　38% for birds and 15% for bats. Tree functional diversity was the most important habitat

38　predictor for birds, while bats responded more to understorey structure. The best biotic

39　predictors for birds were spider abundance and defoliating insect activity, while only bat

40　functional evenness responded positively to insect herbivory. Accounting for potential biotic

41　interactions between bats, birds and other taxa of lower trophic levels will help to understand

42　how environmental changes along large biogeographical gradients affect higher-level predator

43　diversity in forest ecosystems.

2

44 **1. Introduction**

45 Biodiversity is a key driver of many ecosystem functions and services [1,2], particularly

46 through the maintenance of functional trait diversity [3]. Despite the long history of studies

47 examining the local, regional and global drivers of biodiversity, it remains challenging to

48 disentangle the relative importance of climate, habitat and biotic factors [4-6]. An increasing

49 number of studies is questioning the role of multiple biotic interactions across various trophic

50 levels in shaping ecological communities. However, they usually focus only on local scales,

51 while the influence of these interactions on biodiversity across larger geographical extents has

52 rarely been explored [7-9]. Thus, incorporating multispecies interactions in biodiversity

53 response models is still challenging, although it would improve our understanding of large-

54 scale biodiversity patterns as compared to classical studies focusing on single taxa [7-11]. The

55 benefits of considering multi-taxa interactions may be particularly useful for species at higher

56 trophic levels such as birds and bats, which are affected by both direct effects of climate and

57 habitat changes, and their cascading effects across trophic levels [9,12,13].

58 Importantly, the consequences of changes in bird and bat communities for ecosystem

59 functioning cannot be fully understood by focusing only on changes in taxonomic diversity

60 [14-16]. The use of functional traits not only allows monitoring changes in biodiversity

61 response to land use changes [14], but also to clarify the respective importance of multiple

62 assembly processes in shaping species communities along large environmental gradients, e.g.,

63 abiotic filtering, competition or facilitation [15,17,18]. For example, functional diversity can

64 increase at opposite ends of resource availability gradients, depending on whether the traits

65 involved are more related to abiotic filtering or to competitive interactions [17]. Similarly,

66 higher functional dispersion at low productivity levels suggests increased competitive

67 exclusion with the loss of functionally redundant species [15].

68   Taxonomic and functional diversity also tend to show distinct responses to global change

69   [19]. Functional trait diversity and composition, rather than species richness, are often the

70   most important biodiversity-related drivers of ecosystem functioning [12,16]. The number and

71   diversity of species with any particular functional traits in a given community has direct

72   effects on ecosystem-level processes. Functional diversity is therefore an indicator of resource

73   use complementarity and community responses to disturbance [20,21]. A more efficient

74   resource use by species in a given ecosystem can be inferred from higher functional evenness,

75   while strong niche differentiation and low resource competition within species assemblages

76   lead to higher functional dispersion [21-24]. Functional traits related to habitat and resource

77   use are particularly efficient at accounting for changes in ecosystem-level processes such as

78   productivity or trophic interactions. While body mass is a relevant surrogate for bird

79   responses to environmental changes [25], the trophic niche of bird and bat species allows

80   predicting their responses to local habitat changes as well as energy input and food

81   availability along large biogeographical gradients [4,5,26,27].

82   Here, we hypothesize that biotic drivers (i.e., abundance and activity of taxa from lower

83   trophic levels) can complement response models of bird and bat diversity, along a continental-

84   scale gradient (figure 1 and table 1). We first tested if (i) including a set of biotic predictors

85   contribute to explain patterns of bird and bat taxonomic and functional diversity, once

86   accounted for climate (temperature, heat load index and precipitations) and habitat variables

87   (forest composition and structure). We further hypothesized (see table 1) that (ii) insect and

88   spider abundance would positively affect bird and bat abundance and diversity, as key food

89   resources; (iii) earthworm abundance would increase bird and bat diversity either directly or

90   by improving forest soil structure and favouring high soil arthropod abundance; (iv) ungulate

91   browsing would negatively affect bird and bat diversity, by reducing food resources and

92   foraging niches provided by understorey cover; and (v) bird and bat abundance would be

93   positively correlated in mature forest habitats across Europe, as they partly respond to the

94   same biotic drivers (i.e., food resources) at such a large scale.

95   For each biotic predictor, we tested specific hypotheses for the positive, negative or null

96   response of each bird and bat diversity metrics, according to the literature (table 1). We

97   expected an increase in all bird and bat community metrics, including mean body mass, with

98   higher insect herbivore activity due to increased food availability [24-33]; an increase in bird

99   taxonomic and functional diversity with spider abundance, but not in body mass [34-36]; an

100   increase in bat abundance and functional diversity with spider abundance (increased

101   specialized food resources), but neither in species diversity nor body mass [37]; an increase in

102   bird abundance, functional richness and body mass with earthworm abundance as increased

103   resources for large bird specialists [38,39]; no effect of earthworm abundance on bats except

104   on overall bat activity [29]; a decrease on both bat and bird functional diversity and body

105   mass with ungulate browsing due to reduction in understorey cover and changes in shrub

106   composition, but no effect on abundance nor species diversity [40-42].

107

108   **2. Material and methods**

109   **(a) Study sites**

110   A network of 209 mature forest plots was established in 2011 across a latitudinal gradient in

111   Europe ranging from 40°N to 63°N [28], in the framework of the FP7-FunDiv EUROPE

112   project (www.fundiveurope.eu). The network covered six regions within Mediterranean,

113   temperate and boreal forest biomes (Spain, Italy, Germany, Romania, Poland and Finland; see

114   figure 2). The aim of this exploratory platform was to quantify the effects of tree species

115   richness on multiple forest ecosystem functions. Within each region, plots were selected along

116   a gradient of tree species richness ranging from one to five tree species per plot. Each region

117   had a pool of three to five target tree species (for a total of 16 target species across Europe)

118   that are regionally common and economically important. Each sampled forest plot covered an

119   area of 900 m² and was surrounded by a 20 m buffer to avoid edge effects. To maximize their

120   comparability, all plots within a country had similar ages, management and abiotic conditions

121   [43].

122

123   **(b) Bird and bat sampling**

124   We surveyed breeding bird communities using standardized point counts performed by

125   trained observers within a limited distance of 80 m around the observer in April-June 2012

126   (Italy, Germany and Finland) and April-June 2013 (Spain, Romania and Poland). We

127   recorded all birds, except flyovers, which were heard or seen in 15 minutes, during the first

128   four hours after sunrise on days without strong wind, snow or rain. We carefully mapped the

129   location of every recorded individual bird on circular plot fieldsheets to avoid double

130   counting the same individuals. The total number of bird individuals recorded per species in

131   each plot was used as an estimate of bird species abundance. Species detectability was

132   considered to be comparable across the six regions because of similar age and structure in all

133   sampled forest habitat types [43].

134   Bat communities were sampled by passive acoustic monitoring in April-June 2012 (Italy,

135   Germany and Finland) and May-July 2013 (Spain, Romania and Poland) with an automatic

136   ultrasound recorder (Sound Meter SM2BAT, Wildlife Acoustics) located at the center of each

137   plot. Recorders were calibrated to record all bat calls from one hour before sunset to one hour

138   after sunrise, during one night per plot. Recordings were performed only when the ambient

139   temperature was > 10°C, when there was no rain and wind speed was < 30 km.h^{-1}. Bat

140   echolocation calls were identified to species level by a trained operator using dedicated

141   softwares [44]. Several groups of closely-related species difficult to separate based on their

142   calls were merged for data analyses when co-occurring in some countries: *Myotis mystacinus*

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143   */ alcathoe / brandtii*; *Myotis myotis / blythii; Plecotus auritus / austriacus;* and *Pipistrellus*

144   *kuhlii / nathusii*. Bat activity was calculated as the total number of five second sequences with

145   two or more calls per species, as a proxy for species abundance [45].

146

147   **(c) Bird and bat taxonomic and functional diversity**

148   We recorded a total of 76 bird species in the six regions after excluding raptors and flyovers,

149   and a total of 27 bat species, i.e., 72% and 79% of the total pool of forest-dwelling bird and

150   bat species in Europe, respectively [44]. We first calculated the Shannon index of taxonomic

151   species diversity per forest plot. Then, we performed rarefaction and extrapolation curves for

152   Shannon species diversity using the Hill number of order 1, to quantify species diversity

153   patterns that were independent from total community abundance across the 6 studied regions

154   (electronic supplementary material S1). Furthermore, we compiled 10 species life traits

155   related to habitat and resource use to compute functional diversity metrics for both birds and

156   bats (electronic supplementary material S2) [24,44]. For birds, these 10 traits were foraging

157   guild, adult diet, nest site location, migration strategy, mean laying date, home range size,

158   clutch size, body mass, species habitat specialization (SSI) and species thermal index (STI, in

159   °C) [19,46]. For bats, the 10 traits were selected to be as similar as possible to those used for

160   birds, i.e., foraging guild, diet specialization, nursery site, migration strategy, mean birth date,

161   home range size, female fecundity, body mass, STI and SSI. The latter four traits were

162   continuous for both taxa, while all others were categorical (electronic supplementary material

163   S2). Bird and bat STIs were calculated from European distribution maps as the average

164   temperature experienced by a species across its geographical range during the breeding season

165   (see electronic supplementary material S3). Bird and bat SSIs were calculated as the

166   coefficient of variation of species abundance across all habitats in the European breeding bird

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167   survey [47], and in an independent data set provided by the French national bat monitoring

168   scheme [45], respectively (see electronic supplementary material S4).

169   Based on the functional traits, we computed abundance-weighted functional diversity metrics,

170   using log-transformed bat species activity as a measure of bat abundance per plot, and the

171   number of bird individuals recorded as a measure of bird abundance per plot. We calculated

172   functional richness (FRic), functional evenness (FEve) and functional entropy (Rao's Q) as

173   three complementary measures of the multivariate functional trait space using the 'FD' R-

174   package [48]. FRic measures the convex hull volume of the functional trait space, while FEve

175   measures the regularity of trait abundance distribution within this functional space, and Rao's

176   Q the dispersion of species in functional trait space [21,48]. We further performed null

177   models to quantify functional diversity metrics corrected for species richness levels in order

178   to disentangle the drivers of trait diversity *per se*, independent from those of taxonomical

179   diversity. To this end, we reshuffled trait sets among species (i.e., by random permutations of

180   the rows of the species-trait table) without replacement. We then recalculated FD metrics for

181   artificial communities that were equally species-rich as the observed communities and with

182   the same species compositions, but with random sets of traits. We repeated this procedure

183   1000 times, and calculated the standardized deviation of FD (FD_{dev}) values as:

184   $$FD_{dev} = \frac{FD_{obs} - \overline{FD_{exp}}}{sd(FD_{exp})} \ ,$$

185   where FD_{obs} is the observed FD value, $\overline{FD_{exp}}$ is the average of the 1000 randomized (i.e.

186   expected) FD values and $sd(FD_{exp})$ is the standard deviation of the 1000 randomized (i.e.

187   expected) FD values. Thus, FD_{dev} is independent from species richness, and if values are

188   greater than 0, observed FD value was higher than expected based on the taxonomical species

189   richness, whereas values below 0 indicate the opposite (see electronic supplementary material

190   S5).

191

(d) Climate,habitat and biotic predictors

192

193 Using the WorldClim database (http://www.worldclim.org/) and the geographical coordinates

194 of plots, we derived climatic variables for each forest plot (i.e., mean annual temperature and

195 precipitations at a 30 s resolution) and calculated a unitless heat load index based on

196 equations correcting for aspect [49]. According to preliminary analyses [44], the variation of

197 forest habitat structure and composition across all sampled plots could be summarized by a

198 limited number of vegetation attributes, including deciduous tree proportion, tree functional

199 diversity (Rao's Q), understorey species richness and vertical stratification index. In addition,

200 we selected other key taxa sampled in the same plots to build the set of biotic predictors (see

201 detailed hypotheses in table 1 and sampling methods in electronic supplementary material

202 S6). We sampled spider abundance and monitored insect herbivory as a proxy for defoliating

203 insect abundance, to assess overall availability of bird and bat preferred prey in tree canopies,

204 i.e., caterpillars, moths and spiders [28-32]. We further sampled earthworm abundance as

205 food resources for some specialist ground-probing birds, as well as ecosystem engineers

206 having potential bottom-up effects on both bat and bird communities [38,39]. Finally,

207 ungulate browsing was also quantified, as it can negatively affect both forest birds and bats,

208 whose foraging habitat and behaviour might be affected by any browsing-induced changes in

209 understorey density [40,41].

210

(e) Data analysis

211

212 The importance of biotic drivers for bird and bat diversity metrics was evaluated using a

213 hierarchical model fitting framework, comparing a set of competing models with an

214 information-theoretic approach (AIC-based model selection). For each of the 12 metrics

215 tested (bat and bird abundance, species diversity, three indices of functional diversity and

216 mean body mass; see table 2), we increased model complexity in three steps (figure 1) by

217   successively including (i) three climate predictors (mean annual temperature, mean annual

218   precipitation and heat load index); (ii) four habitat predictors (deciduous tree proportion,

219   forest stratification index, understorey species richness, tree functional diversity) and (iii) four

220   biotic predictors from multiple trophic levels (defoliating insects, spiders, earthworms and

221   ungulate browsing). At each step, the best set of predictors (those in the model with the lowest

222   AIC value) was selected before the predictors of the next step were added to the model. We

223   checked for the absence of multicollinearity among climate, habitat and biotic variables using

224   VIF correlation diagnostic tests to exclude potentially collinear predictors. We selected

225   significant predictors at each modelling step using the function 'drop1' in 'lme4' R-package,

226   which allows for a comparison of models based on AIC weights [50]. We performed a χ^2 test

227   on ΔAICc to test for significant decrease in AICc when a given set of predictors was included

228   (see table 2). We did not include interaction terms to avoid model inflation and fitted Linear

229   Mixed Models (LMMs) for all 12 bird and bat diversity metrics, except for total bird

230   abundance, which was fitted with a Generalized Linear Mixed Model (GLMM) with a

231   Poisson error distribution and a log-link function. We used a logit transformation for FEve

232   because it is constrained between 0 and 1 [48].

233   To account for pseudoreplication due to spatial autocorrelation and clustering of forest plots

234   per region, region identity was added as a random factor to the models. We further controlled

235   for differences in common target tree species identity across regions with an additional

236   random effect for target species composition, since not all tree combinations occur in all

237   regions [43]. Bat activity was log-transformed before modelling, and all model predictors

238   were scaled and centred to allow a comparison of their relative effects on bird and bat

239   community metrics. We assessed model performance by reporting marginal (for fixed effects)

240   and conditional (for both fixed and random effects) R^2 at each modelling step [51]. We also

241   tested for the direction of individual effects by modelling univariate relationships between

10

242   biotic factors and bird and bat community metrics using a set of LMMs with the same random

243   effect structure as above. We systematically checked all model residuals for normality and

244   homoscedasticity in LMMs and overdispersion in GLMMs.

245

246   **3. Results**

247   Including biotic predictors significantly improved 9 out of 12 final models of bird and bat

248   community metrics compared to those only including climate and/or habitat (table 2). The

249   mean gain in variance explained by fixed effects (R^2m) when biotic factors were added to

250   fixed climate and habitat predictors was 38.0% for birds and 15.4% for bats (range 14.4-

251   71.8% for birds and 7.2-32.7% for bats). Tree functional diversity was more influential for

252   bird abundance and species diversity while bat diversity responded more to understorey

253   structure (table 2).

254   All bird community metrics except functional evenness were positively correlated to either

255   spider abundance or insect herbivory (see results from univariate LMMs in table 3 and figure

256   3*a*). Bird abundance also significantly increased with earthworm abundance (table 3). In

257   contrast, only bat functional evenness increased with insect herbivory (figure 3*b*). However,

258   bat mean body mass significantly increased with ungulate browsing, while earthworm

259   abundance had a positive effect on bat species diversity and a negative effect on bat body

260   mass (table 3). Moreover, bird functional richness and mean body mass, but not bird

261   abundance, were positively correlated with bat activity (LMMs with t = 1.96, *P* < 0.05; t =

262   2.30, *P* < 0.02 respectively).

263   The results of the null model analysis for functional metrics (FRic, FEve, Rao's Q and CWM

264   body mass) are presented in electronic supplementary material S5. We found consistencies in

265   model predictor selection for bird Rao's Q, bat FEve, and bird and bat mean body mass (see

266   table S5). In contrast, bird and bat simulated FRic differed in model selection from the

267   observed values, as well as bird FEve and bat Rao's Q (table S5).

268

269   **4. Discussion**

270   In the present study, we confirm the importance of different trophic groups, especially

271   arthropod prey such as spiders and defoliating insects, as important determinants for forest

272   bird and bat communities along crossed bioclimatic and habitat gradients. Our results are thus

273   in accordance with several recent studies pointing out that local abundance of bird and bat

274   foraging guilds were best predicted when accounting for interactions between vegetation

275   structure and actual prey abundance [9,26,27,52]. We also found a positive relationship

276   between bat activity and bird functional richness, rather than taxonomic diversity, across

277   European forests. This suggests that a large range of bird functional types are able to coexist

278   in forests with high levels of bat foraging activity, likely linked to higher food availability

279   [42,53].

280   While several metrics of bird and, to a lesser extent, of bat functional diversity were related to

281   high abundances of lower trophic levels, some of these relationships were driven by

282   taxonomic diversity patterns, rather than by trait composition or diversity *per se*. This was

283   supported by the use of null models, in which we calculated the deviation of observed

284   functional diversity patterns from simulated communities that differed in their trait

285   composition, but not in their taxonomic composition, from observed communities. In

286   particular, the significant predictors in the response models based on simulated values for bird

287   and bat functional richness differed from the ones based on observed values, since functional

288   richness is generally correlated to taxonomic richness [21]. On the other hand, we found

289   consistencies in the selection of biotic predictors in observed and simulated models for 4

290   functional diversity metrics, namely bird functional entropy, bat functional evenness and bird

291   and bat mean body mass.

292   In the present work, spider, defoliating insect and earthworm abundances were positively

293   correlated with either bird abundance or functional diversity, as expected from our initial

294   hypotheses. This is consistent with the recognized importance of defoliating caterpillars,

295   spiders and earthworms as preferred food items for forest birds [28-31,34-38]. Defoliating

296   Lepidoptera larvae are key prey items for forest birds during the breeding season, which

297   usually matches the peak in caterpillar abundance [25,31]. Caterpillars and moths are also

298   major food resources for forest bats in temperate forests [26,29,30,32]. However, contrary to

299   expectations, we found that insect herbivory was not affecting all bird and bat community

300   metrics equally. For bats, only functional evenness responded positively to herbivory, as

301   expected [44], while it was not the case for birds, although we expected the strongest response

302   to insect abundance for this particular metric generally indicating an efficient resource use by

303   the predator community [21,24]. Spider abundance had a widespread positive effect on bird

304   taxonomic and functional diversity, as well as mean body mass, while it had little effects on

305   bats, since only specialist gleaning bats feed on spiders [29,34-37].

306   In contrast with our initial hypotheses, earthworm abundance had no effect on bird functional

307   richness or body mass, but as expected, earthworm abundance correlated positively with bird

308   abundance [38]. Earthworms had also additional effects on bat species diversity and body

309   mass, possibly through cascading effects across trophic levels from forest soils to these

310   higher-level predators. The relationships of bird and bat diversity with taxa from other trophic

311   levels can thus partly be explained by foraging niches and diet specialization of particular

312   species or genera. Large ground foraging birds such as thrushes (*Turdus* spp) and waders

313   (woodcock *Scolopax rusticola*, common snipe *Gallinago gallinago* and sandpipers *Tringa*

314   spp) specialize on earthworms during the breeding season [38], while spiders are preferred

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315   prey items for bark-foraging specialists such as treecreepers *Certhia* spp [34]. In contrast,

316   only a few European forest bats, including some *Myotis* spp, can specialize on arachnids but

317   bats do not feed directly on earthworms [29,37]. However, earthworms increase soil

318   biogeochemical heterogeneity and organic matter turnover, so that their activity might lead to

319   higher insect prey abundance ultimately available for both birds and bats [39].

320   Contrarily to our initial hypotheses, we did not detect any negative effects of wild ungulate

321   browsing on birds, but browsing intensity was associated with a decrease in the dominance of

322   small-bodied bat species, as expected. Although these effects were not detectable on birds

323   along the sampled bioclimatic gradient, this suggests that the negative effect of large

324   herbivores previously observed on many taxa also extend to smaller-sized forest insectivorous

325   bats [41]. Such a potentially negative effect of browsing on bats is likely due to indirect

326   changes in resource quality and availability provided by understorey vegetation rather than a

327   direct effect of wild ungulate disturbance [40]. However, how precisely bat species respond to

328   increased ungulate densities in European forests remains to be investigated and should be

329   highly guild-dependent [42]. Smaller foliage-gleaning specialist bats might be particularly

330   sensitive to changes in understorey density and associated food resources following increase

331   in browsing intensity from wild large ungulates, while larger aerial foragers would be

332   favoured by clearer forest understorey created by increased browsing [26]. Most bats actually

333   forage in the forest gaps and only few specialists can use multi-layered forests (e.g., *Myotis*

334   *nattereri* or *M. bechsteinii*) [37], but species such as *M. myotis* also need a low grass layer to

335   forage on carabid beetles. The observed increase in mean bat body mass with ungulate

336   browsing might also be an indication for more free space that can be used by larger bat

337   species in heavily-browsed shrub understoreys.

338   Beyond the direct effects of food resources, these significant biotic factors may thus not

339   always imply a mechanistic interaction, but can also serve as surrogates for mechanisms

340   underlying diversity patterns in bat and bird communities [6,9,13]. In line with our initial

341   hypotheses , the abundance and activity of several lower trophic levels were, across

342   geographical scales, correlated with higher abundances and diversity of birds and bats. On the

343   other hand, some expected relationships were not supported, or were relatively weak

344   compared to similar relationships documented at more local scales. We therefore suggest that,

345   while the effects of abundance and activity of lower trophic levels are often strong enough to

346   improve models explaining bird and bat diversity at continental scale, in some cases

347   relationships were weaker or non-significant, meaning that climate and habitat variables were

348   informative enough to model bat and bird responses at the large spatial extents studied here.

349   Moreover, the use of multi-trait functional diversity metrics can somewhat obscure the

350   relationships between individual traits and environmental gradients, which need further

351   investigation to better infer the exact mechanisms linking the abundance of taxa from distinct

352   trophic levels in diverse forest ecosystems [17,54].

353   The effects of forest structure on bat communities were mediated by understorey richness and

354   stratification and appeared largely negative. Bats use more specialized foraging techniques

355   (i.e., echolocation) than forest birds, which makes them particularly sensitive to understorey

356   vertical structure [26,52]. Overall, we found that forest composition, especially tree functional

357   diversity and the proportion of deciduous trees, was more influential for both bird and bat

358   communities than forest structure. However, the effects of forest composition and structure

359   were not independent, e.g., an increase in the proportion of deciduous trees will also have an

360   effect on structure, e.g., canopy architecture. This is consistent with the hypothesis that

361   increasing forest habitat heterogeneity through higher functional diversity of tree species

362   should increase the abundance of taxa from higher trophic levels such as insectivorous birds

363   and bats [4,27,42]. The mechanism behind this positive effect of tree species diversity on bats

364   and birds is generally related to increased food and roost/nest availability, but defoliating

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365   insect activity could be a key factor underlying the effect of tree diversity, at least partly

366   reflecting overall prey availability for insectivorous vertebrates in mixed forests [30,31,42]. In

367   addition, the buffering effect of deciduous forests on climate-sensitive, cold-dwelling birds is

368   more and more acknowledged at both local and macro-scales [46]. Together with a direct

369   microclimatic buffering during the breeding season, such an effect could also be linked to

370   more abundant and predictable food resources in deciduous forests compared to conifer trees

371   for forest-dwelling bats and birds [32,55].

372

373   **Conclusions**

374   Biodiversity loss is known to cascade across trophic levels in complex ecosystems, with

375   declines in some species affecting the abundance and diversity of other, dependent trophic

376   groups [12,13]. Modelling bat and bird diversity across large biogeographical scales thus

377   requires taking into account not only climate and habitat variables but also direct and indirect

378   multitrophic interactions [7-10]. Our findings confirm that we need to consider biodiversity

379   changes at multiple trophic levels and large spatial scales to predict the future dynamics of

380   biodiversity conservation and ecosystem functioning under global change [56]. In such a

381   context, upper trophic levels are at a higher risk of decline, thus questioning the resilience of

382   ecosystems to global change [13,57]. There is therefore a critical need to better understand

383   and monitor biotic drivers, especially those involving trophic interactions between bats, birds

384   and their prey to predict how climate and land use changes might affect the diversity of these

385   key predators in forest ecosystems.

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387   Data accessibility. Data available from the Dryad Digital Repository at: http://dx.doi.org/10.5061/dryad.t48p8c0

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560   **Table 1.** Main hypotheses tested regarding the role of biotic predictors for bat and bird

561   diversity metrics. Based on available data and previous works compiled from literature, we

562   focused on the following four biotic predictors: (i) defoliating insect activity measured

563   through canopy leaf herbivory rates; (ii) spider abundance sampled by foliage-beating of

564   selected trees and shrubs; (iii) earthworm abundance sampled by standard litter and soil

565   extraction; and (iv) wild ungulate browsing estimated through biomass removal on

566   understorey vegetation (see electronic supplementary material S6 for sampling methods).

567

	Defoliating insect activity	Spider abundance	Earthworm abundance	Ungulate browsing
Birds				
Abundance	Increase	Increase	Increase	No effect
Species div.	Increase	Increase	No effect	No effect
Funct. rich.	Increase	Increase	Increase	Decrease
Funct. div.	Increase	Increase	No effect	Decrease
Body mass	Increase	No effect	Increase	Decrease
Main references	[24,25,28,31]	[34-36]	[38,39]	[40-42]
Bats				
Abundance	Increase	Increase	Increase	No effect
Species div.	Increase	No effect	No effect	No effect
Funct. rich.	Increase	Increase	No effect	Decrease
Funct. div.	Increase	Increase	No effect	Decrease
Body mass	Increase	No effect	No effect	Decrease
Main references	[29,30,32,33]	[29,37]	[29,33]	[40-42]

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577 **Table 2.** Respective performance of climate-only, climate-habitat and climate-habitat-biotic

578 mixed models to predict bird and bat taxonomic and functional community metrics. Best final

579 models are indicated in bold. R²m = marginal Nakagawa's R² for fixed effects; R²c =

580 conditional Nakagawa's R² for both random and fixed effects; FEve and Rao are logit-

581 transformed and log-transformed bat activity was used as a proxy for abundance; ns = not

582 significant. χ² tests indicates significance level of final model according to ΔAICc.

583 Significance levels for tests and individual predictors are as follows: *$P < 0.05$; **$P < 0.01$;

584 ***$P < 0.001$. Codes for response variables and predictors as follows: SDI = Shannon

585 Diversity Index; FRic = Functional richness; FEve = Functional evenness; Rao = Functional

586 entropy; CWM mass = Community Weighted Mean body mass; Temp = Mean annual

587 temperature; Precip = Mean annual precipitation; HLI = Heat Load Index; Decid = deciduous

588 tree proportion; Undric = understorey plant species richness; Stratif = understorey

589 stratification index; Treerao = tree functional entropy; Brows = ungulate browsing; Earth =

590 earthworm abundance; Insect = defoliating insect abundance; Spider = spider abundance.

591

	CLI		CLI-HAB		CLI-HAB-BIO					
	R²m	R²c	R²m	R²c	R²m	R²c	χ²	Significant predictors
Birds								Climate	+ Habitat	+ Biotic
Abundance	ns	ns	0.024	0.294	**0.085**	0.344	**0.004****	-	+ Treerao**	+ Earth*+ Insect**
SDI	0.024	0.389	0.066	0.397	**0.098**	0.453	**0.04***	+ HLI**	+ Treerao**	+ Insect*+ Spider*
FRic	0.090	0.293	ns	ns	**0.121**	0.308	**0.009****	+ Temp*	-	+ Insect*+ Spider*
FEve	**0.083**	0.093	ns	ns	ns	ns	ns	- Prec**	-	-
Rao	0.136	0.270	ns	ns	**0.205**	0.329	**0.01***	- Prec**	-	+ Spider*+ Brows*
CWM mass	0.154	0.264	ns	ns	**0.180**	0.302	**0.04***	+ Temp*- Prec*	-	+ Spider*
Bats								-		
Abundance	ns	ns	0.094	0.283	**0.106**	0.309	**0.04***	-	+ Decid**- Stratif**	+ Spider*
SDI	ns	ns	0.079	0.242	**0.088**	0.219	**0.04***	-	- Stratif***+ Undric*	+ Earth*
FRic	ns	ns	**0.036**	0.248	ns	ns	ns	-	- Stratif*	-
FEve	ns	ns	0.103	0.366	**0.111**	0.286	**0.02***	-	+ Undric*	+ Insect*
Rao	ns	ns	**0.054**	0.262	ns	ns	ns	-	- Stratif**	-
CWM mass	ns	ns	0.035	0.153	**0.052**	0.153	**0.05***	-	- Decid*	+ Brows*

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594　　**Table 3.** Effects of biotic variables on bird and bat community metrics (univariate Linear

595　　Mixed Models). Significant models are indicated in bold; *logit-transformation was used for

596　　response variable; **log-transformed bat activity was used as a proxy for abundance. All

597　　predictors were scaled and centered before modelling. See table 2 for codes of bird and bat

598　　diversity metrics.

599

	Defoliating insects			Spiders			Earthworms			Ungulates		
Birds	estimates	R^2m	*P*	estimates	R^2m	*P*	estimates	R^2m	*P*	estimates	R^2m	*P*
Abundance	**0.045**	**0.025**	**0.01**	0.030	-	ns	**0.046**	**0.025**	**0.05**	-0.0004	-	ns
SDI	0.027	-	ns	**0.047**	**0.022**	**0.02**	0.037	-	ns	0.0004	-	ns
FRic	**0.006**	**0.014**	**0.05**	**0.007**	**0.018**	**0.05**	0.006	-	ns	0.001	-	ns
FEve*	-0.010	-	ns	-0.005	-	ns	-0.030	-	ns	0.019	-	ns
Rao*	-0.009	-	ns	**0.021**	**0.016**	**0.05**	0.009	-	ns	0.017	-	ns
CWM mass	-1.799	-	ns	**5.135**	**0.020**	**0.05**	3.185	-	ns	-0.618	-	ns
Bats												
Abundance**	0.189	-	ns	-	ns	-	0.247	-	ns	-0.168	-	ns
SDI	-0.0005	-	ns	-	ns	-	**0.076**	**0.024**	**0.05**	0.029	-	ns
FRic	-0.001	-	ns	-	ns	-	-0.003	-	ns	0.001	-	ns
FEve*	**0.230**	**0.066**	**0.005**	-	ns	-	0.142	-	ns	-0.005	-	ns
Rao*	0.002	-	ns	-	ns	-	0.0001	-	ns	0.002	-	ns
CWM mass	-0.162	-	ns	-	ns	-	**-0.540**	**0.034**	**0.04**	**0.465**	**0.026**	**0.03**

600   **Figure 1.** Conceptual figure of hypothetical direct and indirect effects of climate (red panel),

601   habitat (green panel) and biotic (yellow panel) predictors on bird and bat diversity metrics.

602   Black and white arrows indicate positive and negative effects, respectively; full and dotted

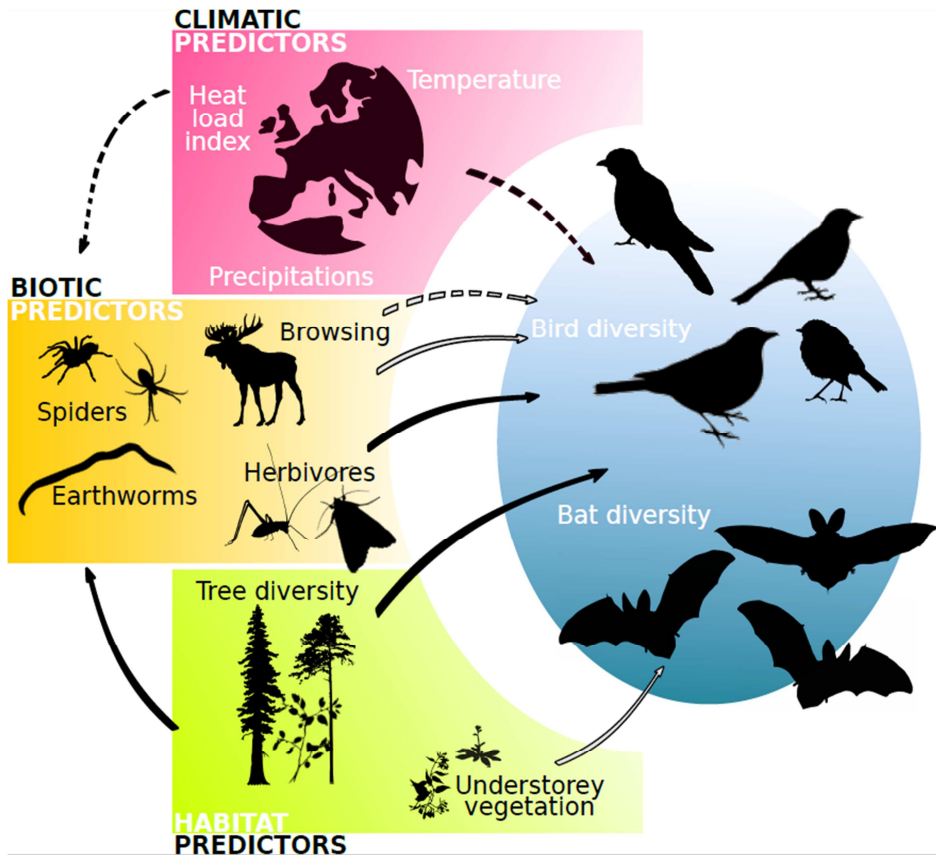603   arrows indicate direct and indirect effects, respectively.
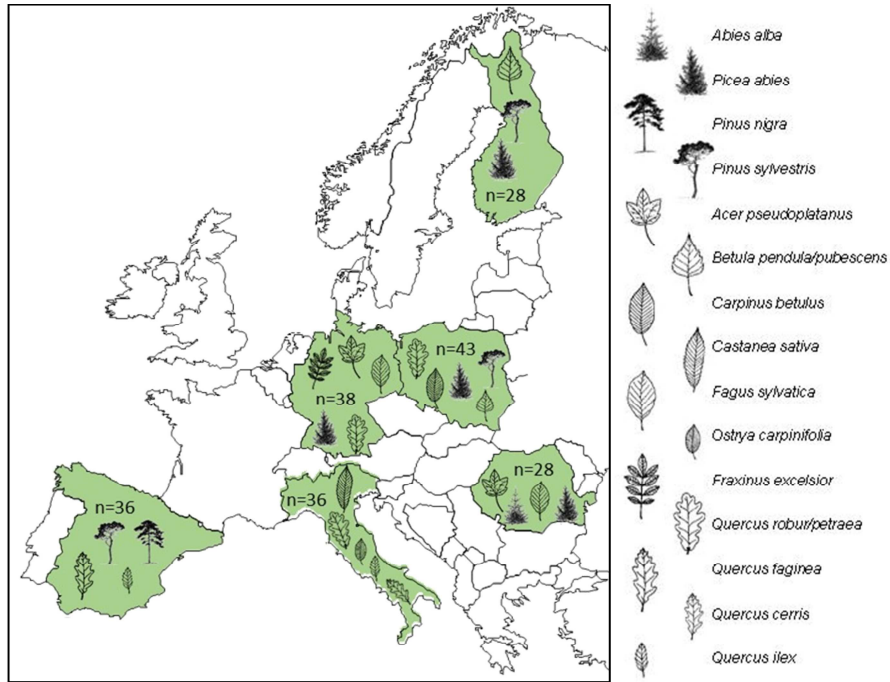
604

605   **Figure 2.** Location map of sampled forest plots of the FunDivEurope exploratory platform in

606   Europe, spread across Spain, Italy, Romania, Germany, Poland and Finland (N = 209). The

607   regional pool of tree species sampled and the number of plots per country are indicated.
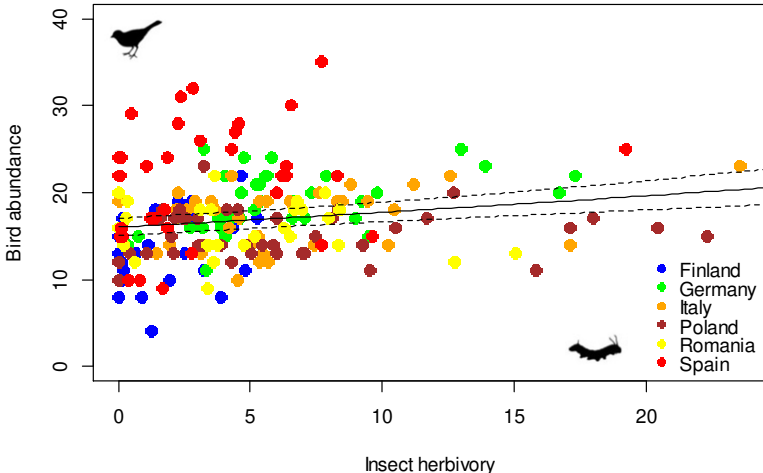
608

609   **Figure 3.** Univariate Linear Mixed Models in response to insect herbivory for a) bird

610   abundance and b) bat functional evenness. See table 3 for model coefficients, R^2m values and

611   *P*-values.

612

a)

b)