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Interspecific interactions influence bird population responses to global changes

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1 Title page

Interspecific interactions influence bird population responses to global changes

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27 Abstract page

28 Abstract

29 Empirical studies often attribute population dynamics to direct effects of environmental changes on species

30 demography. However, environmental changes can also indirectly influence population dynamics through

31 interspecific interactions, referred to as Environment-Species Interaction (ESI). While ESI is likely crucial for

32 predicting species and communities in a changing world, it remains largely overlooked in large-scale studies.

33 To overcome this challenge, we explicitly quantified both the direct influence of climate and land-cover

34 changes on bird population growth over a 20-year period in France, and their indirect influence through

35 competition via ESI. We demonstrated that accounting for interspecific competition improved the

36 predictability of population variations, and that ESI significantly influenced the responses of common bird

37 species to global changes, with varying effects along environmental gradients. This study highlights the

38 importance of incorporating species interactions into dynamic response models to disentangle environmental

39 and biotic effects on species dynamics, and to better understand community responses to global changes.

40

41

42 Main text

43 Introduction

44　　Predictive ecology aims to understand and predict the dynamics of ecological communities, including 45 the identification and attribution of population declines and prediction of future biodiversity loss (Mouquet *et* 46 *al.* 2015). Yet, current efforts to understand the causes of biodiversity change rarely quantify the direct effects 47 of environmental change and the indirect effects of species interactions from dynamic data. Hence, the 48 influence of interspecific competition on the population's response to environmental change remains an 49 unresolved puzzle for many ecological systems. In this study, we overcome this challenge using multi-species 50 dynamic modeling that accounts for both the direct effects of the environment and the effects of intra and 51 interspecific competition on bird species dynamics.

52　　The fate of bird populations facing global changes has been the topic of many published studies (Inger *et* 53 *al.* 2015; Stephens *et al.* 2016; Rosenberg *et al.* 2019; Rigal *et al.* 2023). In the temperate zone, where extensive 54 data is available (Europe and North America), several patterns have emerged. The combined effect of climate 55 and land-use changes tend to favor 'generalist' species with broad ecological niches, leading to decline in more 56 specialized species, particularly those adapted to farmlands and cold climates (Julliard *et al.* 2003; Donald *et al.* 57 2006; Gaüzère *et al.* 2015). Moreover, common species may also be experiencing rapid declines, while certain 58 rare species are showing an increase (Inger *et al.* 2015). The dynamics of common species are particularly 59 noteworthy, as they significantly impact ecosystems processes (Lohbeck *et al.* 2015) and hold significant 60 cultural values for human societies (Schuetz & Johnston 2019).

61　　Our understanding of bird responses to global change generally comes from modeling approaches that 62 assume direct environmental effects on species distributions (Hitch & Leberg 2007) and demography (Julliard 63 *et al.* 2003). However, birds -like other taxonomic groups- are not passive responders to their environment. 64 Instead, they live within communities of interacting species. This coexistence involves complex interactions, 65 such as (regarding birds) competition for resources, mating opportunities, nesting sites, cooperative resource 66 sharing, and predation, which likely shape species distributions and community dynamics (Wisz *et al.* 2013; 67 Tang *et al.* 2023). The influence of these interactions on species dynamics may vary depending on the 68 environmental context. For example, two species may intensely compete for resources where the

69 environment is the most suitable, but they may not compete or even facilitate each other when environmental

70 conditions are stressful and resources limited (Bimler *et al.* 2018).

71   While the direct influence of environmental conditions on species population densities is

72 well-recognized, the indirect effect of environmental conditions on population dynamics through species

73 interactions, known as Environment-Species Interactions (ESI), are less explored (Clark *et al.* 2020; Roberts *et*

74 *al.* 2022). Understanding ESI is crucial as it can impact species responses to environmental variations under

75 diverse contexts (Figure 1). However, if not explicitly considered in analyses, ESI may be confounded with the

76 direct effects of the environment on species. Thus, understanding the influence of the environment on

77 population dynamics through interspecific interactions is essential to reach a better mechanistic

78 understanding and more reliable predictions of species population and community responses to global

79 changes.

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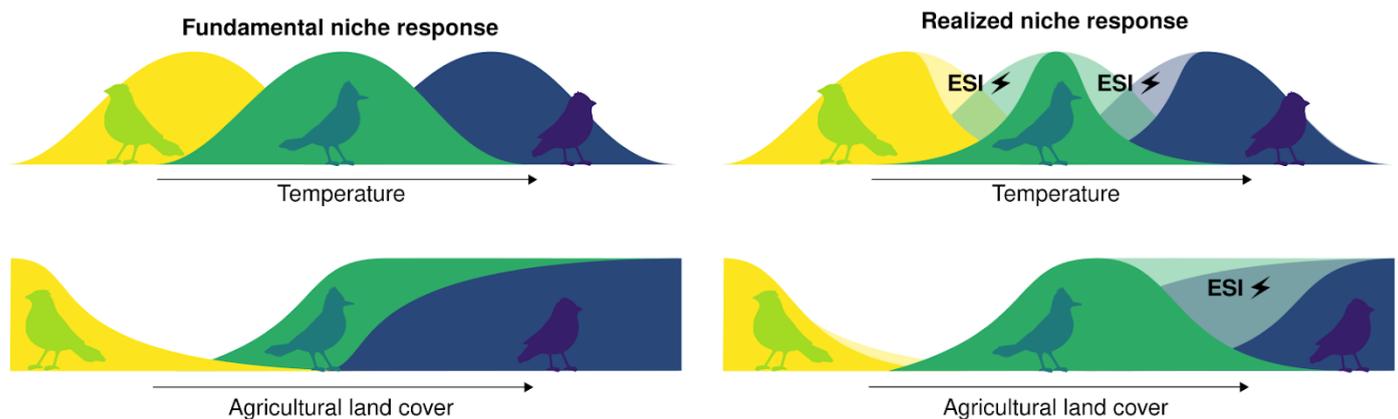
Figure 1. Environment - Species Interaction (ESI) influences on population responses to global changes. Colored density distributions

represent species responses to environmental gradients. On the left side, we consider the fundamental niche as a result of density

independent processes, i.e., the direct effect of the abiotic environment on species abundance. On the right side, density dependent

processes (here, species interactions) affect the response of species to environmental gradients. The apparent difference in observed

species responses is the result of Species-Environment-Interactions (ESI).

87

88   Quantifying the effects of interaction on community responses to global change via ESI is challenging.

89 First, biotic interactions are structured into complex networks of many species potentially interacting directly

90 and indirectly with each other (Soliveres *et al.* 2015). This makes the identification and the validation of

91 community-wide interaction networks difficult. Second, we often lack the time-series data needed to quantify

92 effects of species densities on the growth rates of others (Ives *et al.* 2003). Third, analytical tools used to study

93 biodiversity responses to global changes often lack explicit modeling of ESI using observational data.

94 Theoretical approaches are often based on process-based models with differential equations resolved

95 through analytical analyses or numerical simulations. They are useful to understand the effect of well-defined

96 processes on species dynamics in communities, for example when relying on Generalized Lotka Volterra

97 models (GLV, (Barabás *et al.* 2016). However, fitting these models to large scale empirical observations is often

98 unfeasible. Empirical approaches rely mostly on statistical models like Species Distribution Models (SDMs)

99 and their multi-species extensions (MSDMs and JSDMs) which are fitted to observational data (Guisan &

100 Thuiller 2005; Thuiller *et al.* 2013; Ovaskainen *et al.* 2017). Although SDMs and JSDMs incorporate real-world

101 observations with broad spatial and taxonomic coverage, they cannot explicitly infer ESI due to their

102 incapacity to separate the direct effect of the environment and its effect through interaction with other

103 species (Clark *et al.* 2014; Poggiato *et al.* 2021). Consequently, the influence of ESI on the dynamics of species

104 and communities under global change remains poorly documented. A third approach to address this gap is to

105 combine process-based and statistical approaches by fitting equation parameters to observational data. Such

106 hybrid models (e.g., with GLV-based approaches, (Chalmandrier *et al.* 2022) offer a way to explicitly integrate

107 abiotic and biotic processes as they can model the direct effects of environment and the effect of species

108 interactions from observational data, thereby modeling ESI (Clark *et al.* 2020; Thuiller *et al.* 2023).

109

110   In this study, we used such a hybrid model, a multi-species Bayesian GLV dynamic model called

111 GjamTime (Clark *et al.* 2020), parameterized on time-series abundance data from the French Breeding Bird

112 Survey for 23 common bird species. Leveraging this recent bayesian modeling framework and this

113 high-resolution, standardized bird monitoring scheme in France (Jiguet *et al.* 2012), we explored the impact of

114 explicitly modeling ESI on long-term estimates of bird population and community responses to climate and

115 land-use changes. We estimated a multi-species dynamic model accounting for the direct effects of the

116 environment and the effects of intra and interspecific competition on species dynamics. To assess the

117 influence of ESI on bird species and community responses to global changes, we compared long-term

118 community dynamics scenarios when only considering environmental effects on population growth to those

119 that incorporated both direct and indirect effects through ESI. More specifically, we sought to answer the

120 three following question :

- Q1: *Does explicitly considering interspecific interactions in community dynamic models improve their*
122 *predictability ?*

- Q2: *Which species dynamics are most influenced by interspecific competition, and how is the competitive*
124 *network of common bird species structured ?*

- Q3: *How much and under which abiotic conditions interspecific competition influences species responses to*
126 *global changes ?*

127

Material and methods

Data

130 **Bird population trends** were extracted from the French Breeding Bird Survey (FBBS) over the 2001–2019

131 period. The French breeding bird survey was designed to monitor population dynamics of common passerine

132 bird species in France. In this survey, skilled volunteer ornithologists count birds at a given site, following a

133 standardized protocol, at the same site, year after year (Jiguet *et al.* 2012). Species abundances are recorded

134 across 2792 sites, each covering a 4km² area. Volunteers provide their home locality to the national

135 coordinator, and a 2×2 km site is randomly selected from within a 10 km radius (out of 80 possible sites) by the

136 coordinator. Each spring, volunteers carry out 10 point counts separated by at least 300 m within the selected

137 site, for a fixed period of five minutes. Two sampling sessions are carried out from 1 April to 8 May, and then

138 from 9 May to the end of June, to detect both early and late breeders, with a gap of 4–6 weeks between

139 sessions. Counts are repeated annually on approximately the same date (±7 days) and at dawn (1–4 h after

140 sunrise) by the same observer, in the same order. The highest count from these two sessions is used as the

141 measure of point-level species abundance. We sub-selected sites that were followed by at least five years of

142 monitoring between 2001 and 2019. We only kept species that were the most common in space and time (i.e.,

143 present in more than 50% of site/years pairs, i.e., 6751 site/years pairs), and the most abundant (i.e.,

144 representing more than 10% of the total number of occurrence in the dataset, 28282 individuals). This set of

6

We finally winsorized abundance data to the 99th percentile (abundance values > 32 were capped to 32) to limit the influence of very large flocks of birds appearing during a point count.

Climatic data were extracted from CHELSA (https://chelsa-climate.org/, v.2.1) for each site and each sampling year. We computed the average daily temperature and precipitation during the bird breeding season (April - August).

Land cover data were extracted from CORINE Land Cover (European Environment Agency 2010). Percentage land covers within FBBS site were computed by taking the habitat class area (in square meters) and dividing it by the total area of the site. Because CLC data were available only for 2000, 2006, 2012 and 2018, some FBBS site-year combinations were not covered by the dataset. In this case, we attributed site land cover for the uncovered year to the last year for which we had CLC data available (for example, sites monitored in 2001 were attributed land cover from CLC 2000). More specifically, we focused on three aggregated CLC classes: artificial surfaces, agricultural areas, and forests for three reasons. First, these classes have large coverage across the study sites. Second, they are highly relevant for explaining the population dynamics of our 23 bird species (Guetté *et al.* 2017; Rigal *et al.* 2023). Third, by removing "wetlands", "water body", and "little or no vegetation" classes (which are marginal in most sites), we reduced the number of parameters in the model and avoided the variable to be compositional (i.e., all land cover classes summing to 100%). See supporting information - Environmental data description.

Modeling dynamic community responses

GjamTime is a generalized joint attribute model for dynamics data that allows us to quantify density independent and dependent effects of climate and land cover change on species population growth rate. The model is based on the Generalized Lotka-Volterra equation for S species, here expanded to include interaction with the environment,

$$\frac{dw_s}{dt} = (w_s \times X')\rho_s + (w_s \times W')\alpha_s + \epsilon_s \tag{1}$$

175 This equation expresses the rate of change in the abundance of species w_s in terms of the density-independent

176 rate ρ_s, a vector of coefficients describing the response to environment variables X', and the

177 density-dependent rate α_s, a vector of coefficients describing the response to the density of other S species W'

178 . There is one equation for each of S species, so coefficient vectors become matrices ρ, and α, each with S rows.

179 This equation is then discretized and reorganized in order to be combined with data as in the GJAM model

180 (Clark et al. 2017). **In the model**, the S equations are additionally linked by an $S \times S$ covariance matrix Σ for the

181 error ϵ . In addition to time t and species S there will usually be a location i subscript that is omitted here to

182 reduce clutter. The Model is fitted in a state-space hierarchical Bayesian framework. All details about the

183 model construction and use can be found in (Clark et al. 2020), at https://rpubs.com/jimclark/551105, and at

184 https://rpubs.com/jimclark/631209. Parameters were fitted from empirical data by Markov chain Monte

185 Carlo for 20000 iterations with a burn-in period of 5000 using the function 'gjam' from the R package gjam

186 (Clark *et al.* 2017). We bounded ρ_s by setting priors values between -0.2 and 0.2 based on minimum and

187 long-term maximum population trends previously observed for french breeding birds (Jiguet & Moussus

188 2009). For model incorporating intra- and interspecific interaction, α_s priors were all set between -1 and 0 to

189 allow the model to estimate interaction coefficients for all species pairs. By doing so, we considered that all

190 pairs of species can potentially interact within a 2x2km site. For model incorporating intraspecific interaction,

191 only α_s priors in the diagonal matrix were set to between -1 and 0, to allow the model to estimate intraspecific

192 interaction coefficient for all species. Models convergence were confirmed by visual assessment of the mixing

193 of chains as well as model-fit diagnostic. We checked each chain run separately via trace plots and posterior

194 density, and used running means plot and potential scale reduction factor to assess model convergence.

195 Almost all parameters showed good convergence. Parameters showing the influence of land cover on ρ_s were

196 correlated due to some degree of multicollinearity across the three land cover classes. To see all diagnostic

197 plots in detail, see supporting information - Model Validation.

198

Measuring model predictability (Q1)

199

200 In order to answer Q1, we compared the model incorporating both environmental change (climate + land

201 cover) and interactions (intra and interspecific competition) with the model incorporating environmental

202 change only using the difference in deviance information criterion (DIC). DIC is a hierarchical modeling

203 generalization of the Akaike information criterion particularly relevant in Bayesian model selection. For each

204 model, we also computed the r² as the coefficient of determination as the squared Pearson correlation

205 coefficient between the observed values (abundance for each species at each site/year) and the predicted

206 values. We also reported the Root Mean Square Percentage Error (RMSPE) and the proportion of total

207 variance explained by interactions and environment effects calculated in the *gjam* R package (Clark *et al.*

208 2017).

209

Building the emergent competition network (Q2)

211 We used the density-dependent rates estimates to construct the resulting competition network, represented

212 as an adjacency matrix, and visualized this network using the *igraph* and *ggraph* R packages. To maintain a

213 conservative approach in representing interactions, we focused our interpretation on the 0.975 confidence

214 interval value of the posterior distribution rather than the mean value. For each species, we calculated the

215 "total competition applied" as the row wise sum of α and the "total competition received" as the column wise

216 sum of α and used these values to position each species in the y and x axes of the network shown in Figure 4b.

217

Estimating species abundance index (Q3)

219   To transform observations of the dynamic process into a reference state for the system under specific

220 environmental conditions, we predicted the probabilistic index of species abundance by numerical integration

221 of modeled parameter estimates ρ_s and α_s along climate and land cover gradients (Clark *et al.* 2020). While

222 these abundance indices are often referred to as equilibrium abundance or steady-state abundance (Collins *et*

223 *al.* 2022), it is crucial to acknowledge that they may not necessarily represent a stable coexistence or exist in

224 reality (Clark *et al.* 2020). Instead, the abundance index should be interpreted as a reference point for

225 assessing the relative abundance of a given species in a community under varying environmental conditions.

226   The abundance index was derived by solving the model equation for all species with their growth rates

227 set to zero (equation 1), and different combinations of predictor values. To manage computation time, we

228 estimated the species' abundance index for all combinations of average daily temperature, percent of artificial

229 surfaces, and percent of agricultural areas, each at 10 values, resulting in 10^3 discrete combinations. For each

230 of the 10^3 discrete predictor combinations, we ran 100 simulations and calculated both the mean and the

231 standard deviation of the abundance index. To predict the abundance index in the absence of interspecific

232 competition, we set all interspecific pairwise interaction parameters to 0 by replacing all chain values of

233 interspecific interactions in the model output object by 0, as detailed in the code and data. In order to quantify

234 the effect of interspecific interactions on the abundance index for each predictor combination, we computed

235 the difference between the abundance index obtained with the model fit including interspecific competition

236 and the model omitting interspecific competition.

237

Results

Q1 - Interspecific interactions contribute to species dynamics.

240 Accounting for intra- and interspecific interactions into the modeling of species responses to climate and

241 land-cover changes improved the overall model fit (ΔDIC = 1168452). The R^2 of the model considering the

242 direct effects of climate and land cover change alone was high (R^2 = 0.77), and this value increased further

243 when integrating both the direct effects of climate and land cover change and species interactions into the

244 model (R^2 = 0.85). The degree of improvement in model fit varied across different species (Figure 2). This

245 improvement was attributed to the fact that predicted abundances were generally less dispersed from the

246 observed values when accounting for species interactions (Figure 2). In other words, explicitly including

247 interspecific interactions tended to reduce outlier predictions (when compared to the model with intraspecific

248 interactions only), especially for highly abundant species like *Sturnus vulgaris* and *Columba palumbus* (Figure 3).

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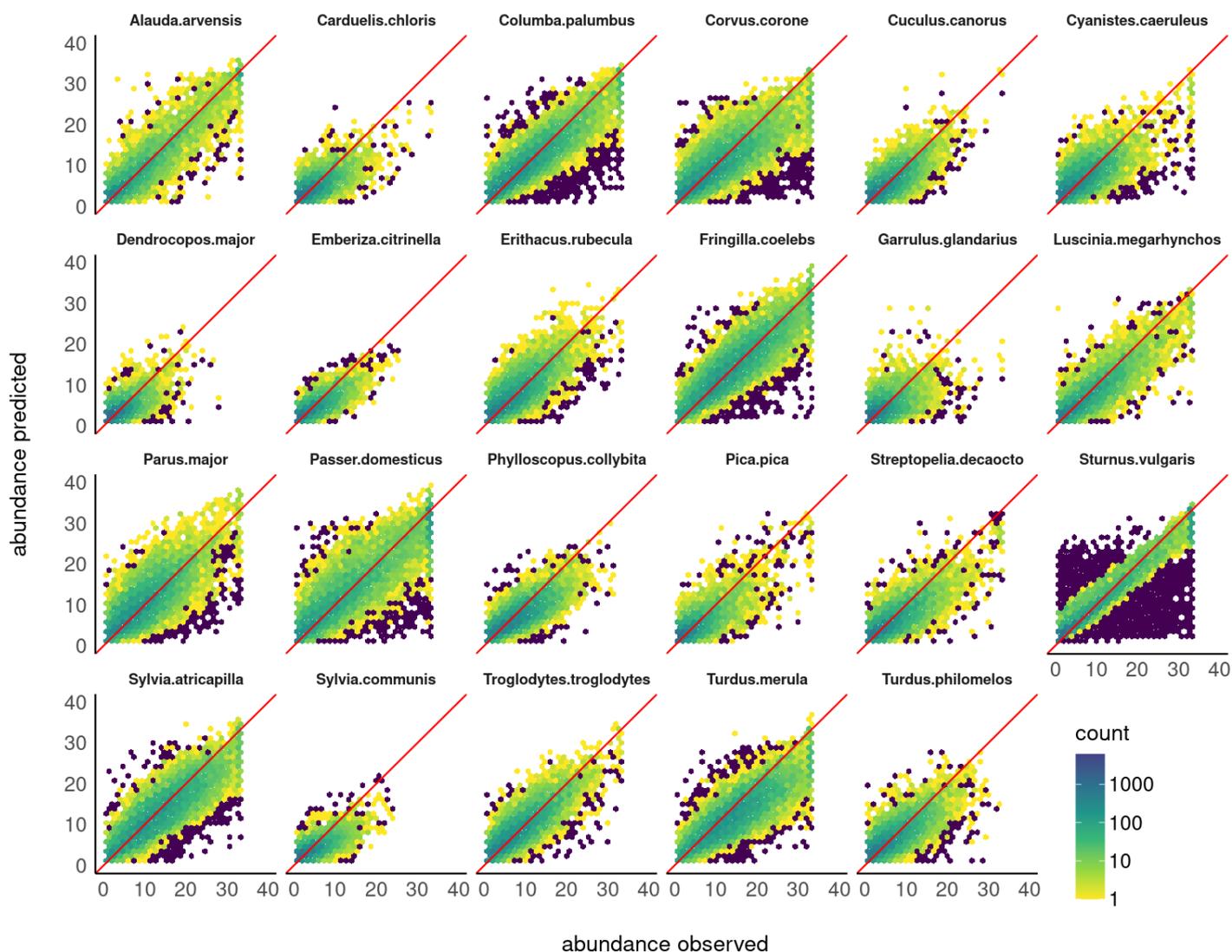
Figure 2. Predicted abundances against observed abundance for each species. Red line shows 1:1 line, colored cells (yellow to blue) show abundance values from models incorporating interactions, purple cells in the background show abundance values from models without interactions.

Climate and land cover change (density independent processes) in combination with intra and interspecific competition (density dependent processes) collectively accounted for up to 30% of population dynamics. The influence of competition was notably significant, explaining more than 10% of the total variation, particularly for several species such as *Passer domesticus* and *Corvus corone*, among others (Figure 3). In contrast, *Parus major* dynamics were only driven by density independent processes. For other species like *Alauda arvensis* and *Sturnus vulgaris*, their dynamics were primarily, though not entirely, explained by independent processes, with a limited contribution from density dependent processes.
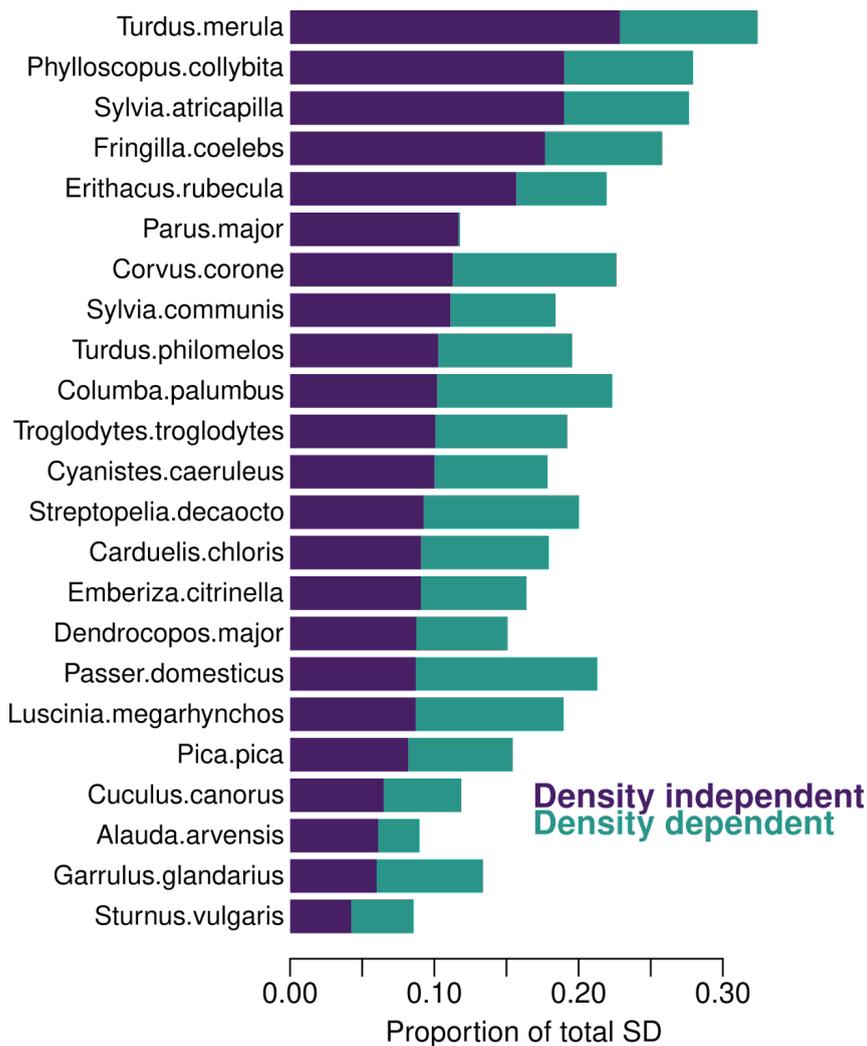
Figure 3. Contributions of interspecific interaction to species population dynamics. Density Independent effects (purple) corresponds to the effect of Climate and land cover change on species population growth. Density Dependent effects (green) relates to the influence of interaction on species population growth. Total model Root Mean Square Error is 2.66. Unexplained variation comes from the species by species covariance matrix for ε in equation 1.

281 ## Q2 - Strong competitors structure the competition network of common French breeding birds

282 Out of the 529 species pairs, 77% of them, showed 95% of the posterior distribution of interaction

283 coefficients that did not include zero (Figure 4). In line with results from figure 2, populations of *Columba*

284 *palumbus, Sylvia communis, Turdus merula* and *Corvus corone* appeared to be particularly impacted by negative

285 interactions from other species (indicated by the dark cells in the columns). Conversely, species like *Alauda*

286 *arvensis, Sylvia communis, Pica pica,* and *Chloris chloris* emerged as strong competitors (evident by dark cells in

287 the rows), playing a notable role in shaping the interaction network of France's most common breeding birds.

288 In particular, *Alauda arvensis* showed a moderate (~ -0.1) but consistent negative effect on most species.

Figure 4. The interaction network of common breeding birds shows directional negative interaction between pairs of species. A: interaction matrix alpha where α_{ij} is plotted against α_{ji}. Cell colors and transparency show the parameter value estimated by the gjamTime model. In order to stay conservative, we here showed 0.975 confidence interval value of the posterior distribution. B: competition network reconstructed from matrix A, the position of species in y shows the total competition applied by the species (as the sum of row in A), the position of the species in x shows the total competition received by the species (as the sum of column in A).
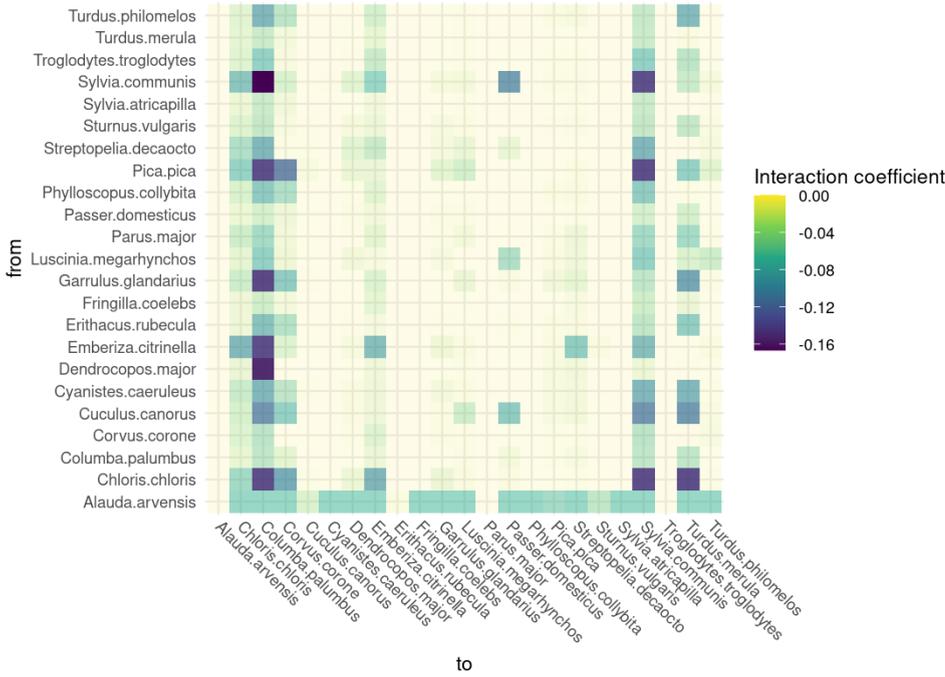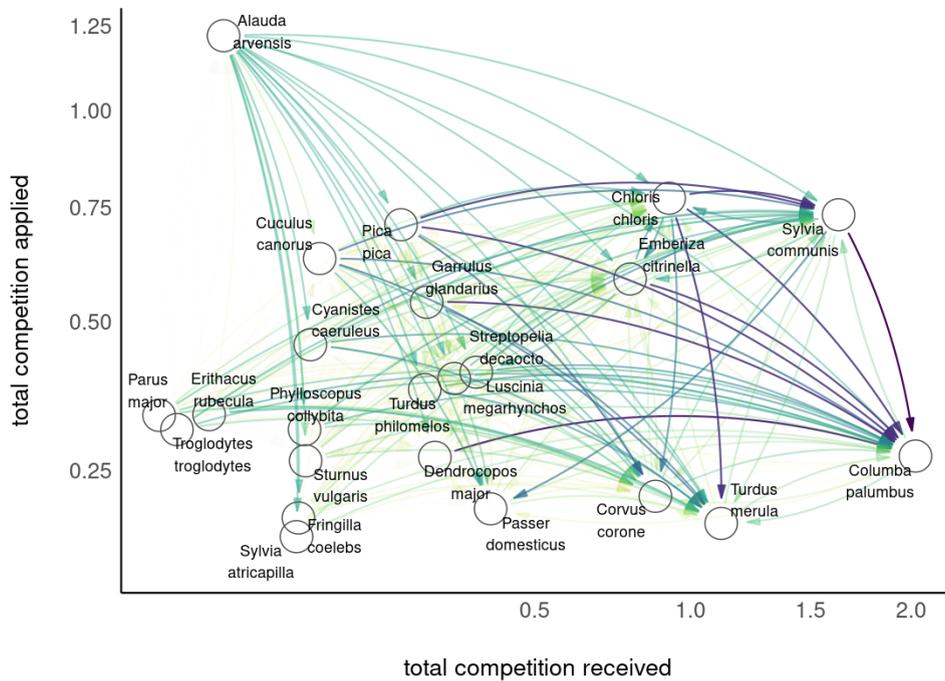
298 Q3 - Environment - Species Interactions influence response of birds to global change

299 The interaction network shown in Figure 4 summarizes the interaction and their strengths among species 300 pairs. However, our study aims to reveal whether these interspecific interactions truly impact species 301 responses to climate and land cover changes via ESI. To evaluate the effect of ESI on species' responses, we 302 thus computed differences in the abundance index when predicted with only intraspecific interactions (from 303 the diagonal of the interaction matrix), or with both intra and interspecific interactions (Figure 5a) along 304 different combinations of spring temperature and agricultural, artificial and forest land cover. Irrespective of 305 temperature or agricultural cover, the majority of species exhibited negative differences in abundance index, 306 indicating that interspecific competition negatively affects local species abundances. However, for some 307 species in specific contexts, the net effect of interspecific competition led to an increase in abundance index 308 (positive difference in abundance index, in blue Figure 5). Examining these differences across various climate 309 and land cover values reveals how ESI might affect species coexistence along interacting environmental 310 gradients. These differences in the abundance index displayed distinct patterns within the environmental 311 space (Figure 5b). For instance, *Fringilla coelebs* exhibited substantial variation in the influence of ESI along the 312 agricultural cover gradient, with differences ranging from negative under high agricultural cover to positive 313 under low agricultural cover and high temperatures (Figure 5b).

314 In some cases, the reduction in abundance due to interspecific competition might be solely responsible for the 315 absence of the species. To exemplify this possibility, we identified cases where the abundance index fell below 316 0.05 due to interspecific interaction (indicated by the red circle and squares in figure 5). For example, this 317 occurred for *Phylloscopus collybita* under specific combinations of agricultural cover and temperature, under 318 low spring temperatures for *Turdus merula*, and under low agricultural cover for *Sylvia atricapilla and Erithacus* 319 *rubecula*, among others (in red, Figure 5b). Note that we used the arbitrary threshold of 0.05 to illustrate the 320 potential for absence due to interspecific competition, but this finding does not provide definite evidence for 321 the absence of a given species under a given climate and land cover condition.
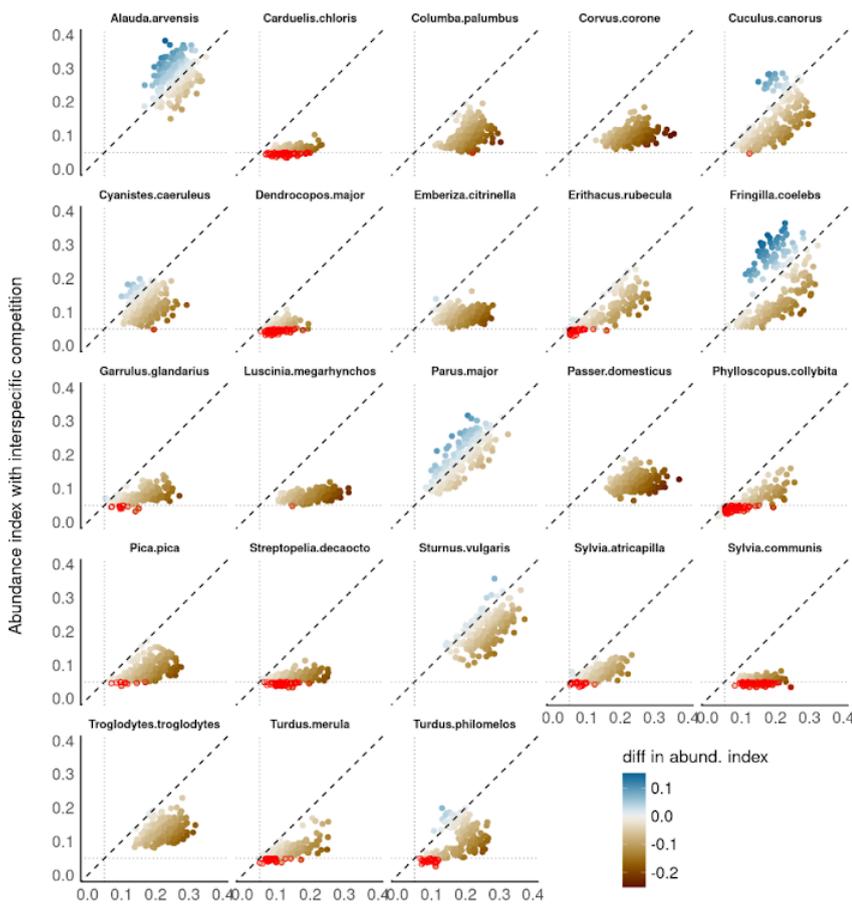
Figure 5. ESI influences abundance index differently across the environmental space. (a) abundance index from models run with full matrix plotted against the abundance index of model with intraspecific interaction only. Point colors show abundance differences. Red circles indicate that the species abundance index drops below 0.05 because of interspecific interactions. (b) Abundance index differences are displayed within a 2 dimensional environmental space (Agricultural cover in y-axis and Spring temperature in x-axis) for each species. The values are shown for low artificial cover.

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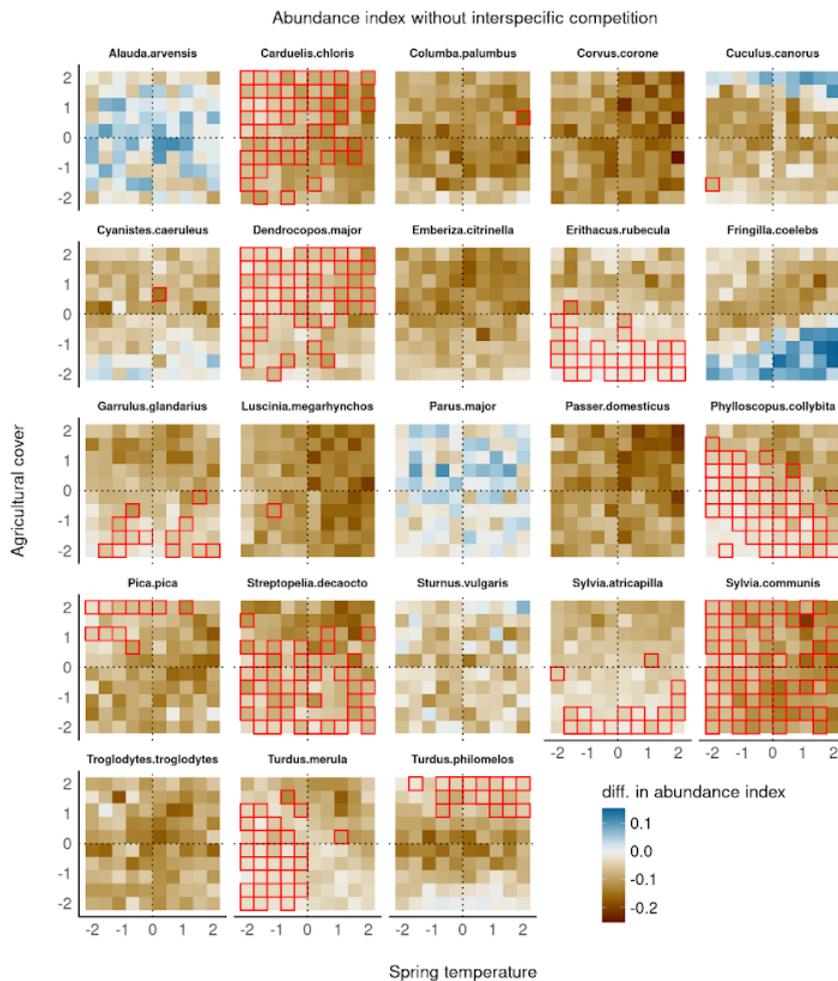
Discussion

343   Species responses to global changes have typically been examined and reported as a direct result of

344 environmental influences on population dynamics, often overlooking the potential indirect effects stemming

345 from the the responses of other species via interspecific interactions. With a limited number of explicit

346 methods for considering species interactions in the analysis of observational data, the field of ecology has

347 encountered challenges in uncovering the indirect impact of ESI on species responses to global changes. In

348 this study, we employed a dynamic framework and used data collected by the French Breeding Bird Survey

349 since 2001 to elucidate both the direct effect of environment (climate and land-cover change) on species

350 dynamics and its indirect effect through interactions with competitors. Our research reveals that

351 interspecific interactions play a significant role in shaping bird population responses to climate and land cover

352 changes in France through ESI. This underscores the importance of adequately quantifying how ESI governs

353 population dynamics and species distribution. Without such quantification, predicting the future of

354 biodiversity status under changing environmental conditions would miss key processes and remain biased.

355

356 *(Q1)*   First, we showed that incorporating interspecific competition via dynamic community modeling

357 enhanced the explanatory power of the model when examining the temporal responses of common breeding

358 bird populations to climate and land use changes. We also found that interspecific competitive interactions

359 significantly influenced the probabilistic estimates of abundance for most species, with a few species showing

360 only marginal effects from interspecific interactions (e.g *Parus major*).

361 (Q2)   Second, we provided insights into the competitive interaction network that shapes multispecies

362 population dynamics and contributes to the coexistence of the most common birds in France during the

363 breeding season. Our results revealed that negative interspecific interactions were predominantly

364 asymmetric, with approximately half of the species consistently influenced by competition from other species.

365 Interpreting these results on the light of community assembly theory (Kraft *et al.* 2015), the structure of the

366 competition network suggests that interspecific interactions among common birds are characterized by

367 hierarchical dominance with strong asymmetry, and in some instances, by brood parasitism (e.g *Cuculus*

368 *canorus*). Such biotic processes are commonly described in plant community ecology (Gaudet & Keddy 1988;

17

369 Mayfield & Levine 2010; Kunstler *et al.* 2012), and have only been recently assessed for birds (Miller *et al.*

370 2017; Barrero *et al.* 2023). Here, estimating the competition network that underlies coexistence among

371 common birds based on dynamic data allows us to illuminate interspecific relationships that are typically not

372 readily observable nor quantifiable from empirical data (Blanchet *et al.* 2020; Poggiato *et al.* 2021). However, it

373 is important to note that these interaction coefficients represent model parameters specific to the context of

374 French breeding birds and the set of 23 species that coexist (or not) in 2x2km squares. Estimated interaction

375 coefficients describe potential pairwise interactions between species across the study, but not all species

376 necesarilly co-occur in all sites every year. Within each site, community composition, environmental

377 conditions, and species responses to the environment interact to ultimately shape species dynamics

378 (Q3)   Third, to account for these local interacting processes, we revealed how environmental variations

379 permeate the network of competitors by influencing species abundance. Overall, the abundance index was

380 lower when explicitly considering interspecific competition, as expected, given that competition exerts a

381 negative impact on population growth. However, species like *Alauda arvensis, Cuculus canorus, Fringilla coelebs,*

382 or *Parus major* exhibited an increase of abundance index in certain contexts where the net effect of

383 competition on abundance index was positive. Although counterintuitive at first, the positive influence of

384 interspecific competition might reveal the effect of intransitive interactions where decrease in abundance of

385 species B due to competition from species A can benefit species C if B outcompetes species C (Laird & Schamp

386 2008; Soliveres *et al.* 2015; Gallien *et al.* 2017).

387 Our results showed clear variations on the effect of competition along combinations of climatic and

388 land-cover gradients across France. The varying influence of ESI along environmental gradients emerges from

389 the fact that abundance of interacting species also varies along these gradients (Figure 1). More generally,

390 there is evidence to suggest that the influence of interspecific interactions may vary with environmental

391 conditions. This phenomenon is often approached through an environmentally dependent interaction matrix

392 (Bimler *et al.* 2018). While in the GjamTime framework, the interaction coefficient matrix is fixed, its effects on

393 species dynamics interact with species responses to the environment through Environment - Species

394 Interactions (ESI). A promising avenue for further development lies in a geographical decomposition of the

395 interaction matrix. For example, fitting model parameters based on data subsets corresponding to

396 biogeographical regions or habitats would allow to describe variations in interactions between homogeneous

397 species pools and interaction networks (Dansereau *et al.* 2023). Pushing further the interpretation of

398 differences in abundance index, we highlighted that under specific combinations of climate and land-cover,

399 some species may be outcompeted and excluded from communities. This result underscores the potential

400 impact of ESI on local extinctions and, consequently, the dynamics of species distributions under global

401 changes. It suggests that species distribution modeling could likely enhance accuracy by incorporating

402 knowledge of species interactions and interdependencies (Poggiato *et al.* 2022).

403 Nonetheless, the empirical parametrization of dynamical models remains a daunting task. First, gathering

404 high-quality data, with a standardized sampling in space and time and that encompasses a broad taxonomic

405 coverage, is notoriously difficult. Second, when modeling species-rich communities, the number of parameters

406 escalates significantly (scaling with the square number of species considered). This high dimensionality makes

407 empirical model estimation a complex endeavor (Godoy & Levine 2014), especially given the substantial

408 computational resources and time required. In particular, these limitations have hindered our ability to

409 incorporate less common species, which may be particularly prone to ESI, but modeling interactions with trait

410 relationships might be a way to overcome the problem (Chalmandrier *et al.* 2022; Blonder *et al.* 2023). Third,

411 these parameters are not straightforward to interpret. In our model, alpha parameters define per capita

412 demographic effects of one species on another, with the interaction effect contingent on the density of the

413 species, which in turn, depends on its response to the environment. This is why estimating the abundance

414 index of species across environmental gradients with and without interactions proves valuable, as it aids in

415 summarizing and interpreting the impact of density dependent processes on community responses to global

416 changes (Clark *et al.* 2020).

417

418 Harnessing empirically parameterized dynamical models offers a complementary and mechanistic approach

419 to understanding and predicting the influence of interspecific interactions on biodiversity dynamics

420 (Chalmandrier *et al.* 2021, 2022). In the context where ESI are pervasive and impactful, the response of a given

421 species to climate change will inevitably hinge on the response of species it interacts with. Consequently,

422 predicting a species' response to future climate will be contingent upon the responses of other species to

423 climate change. Yet, while our study advances our understanding of biodiversity responses to global changes,

424 it underscores the intricacy of deciphering species coexistence through empirical patterns (Münkemüller *et al.*

425 2020; Thuiller *et al.* 2023). Frameworks that facilitate the modeling of species responses to the environment

426 while accounting for their interdependencies are only beginning to emerge (Staniczenko *et al.* 2017; Ohlmann

427 *et al.* 2023). These models propose the integration of a known (directed) interaction network into a niche

428 distribution model to encompass both environmental and species influences, thereby addressing environment

429 - species interactions (Poggiato *et al.* 2022).

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431 To conclude, our findings support the notion that environment - species interaction relationships play a pivotal

432 role in the context of birds' responses to climate and land cover changes during the period 2001-2019. Given

433 the increasing significance of climate change in the years to come (Calvin *et al.* 2023), there is an urgent need

434 to predict and mitigate its adverse consequences on biodiversity. We argue that deepening our understanding

435 and improving predictions of these consequences requires a more explicit integration of community assembly

436 processes into modeling tools. Moreover, the availability of dynamic data for estimating interspecific

437 interactions across various contexts is essential. The enhanced predictions and the deeper understanding of

438 the roles different community assembly processes play within a scrutinized system will serve as a foundation

439 for effective management strategies aimed at safeguarding species and communities affected by climate and

440 land use changes.

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569   distribution modelling. *Biol. Rev. Camb. Philos. Soc.*, 88, 15–30.

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571 # Supporting information

572 Bird data description

573 Spatial distribution of species abundances across the study period

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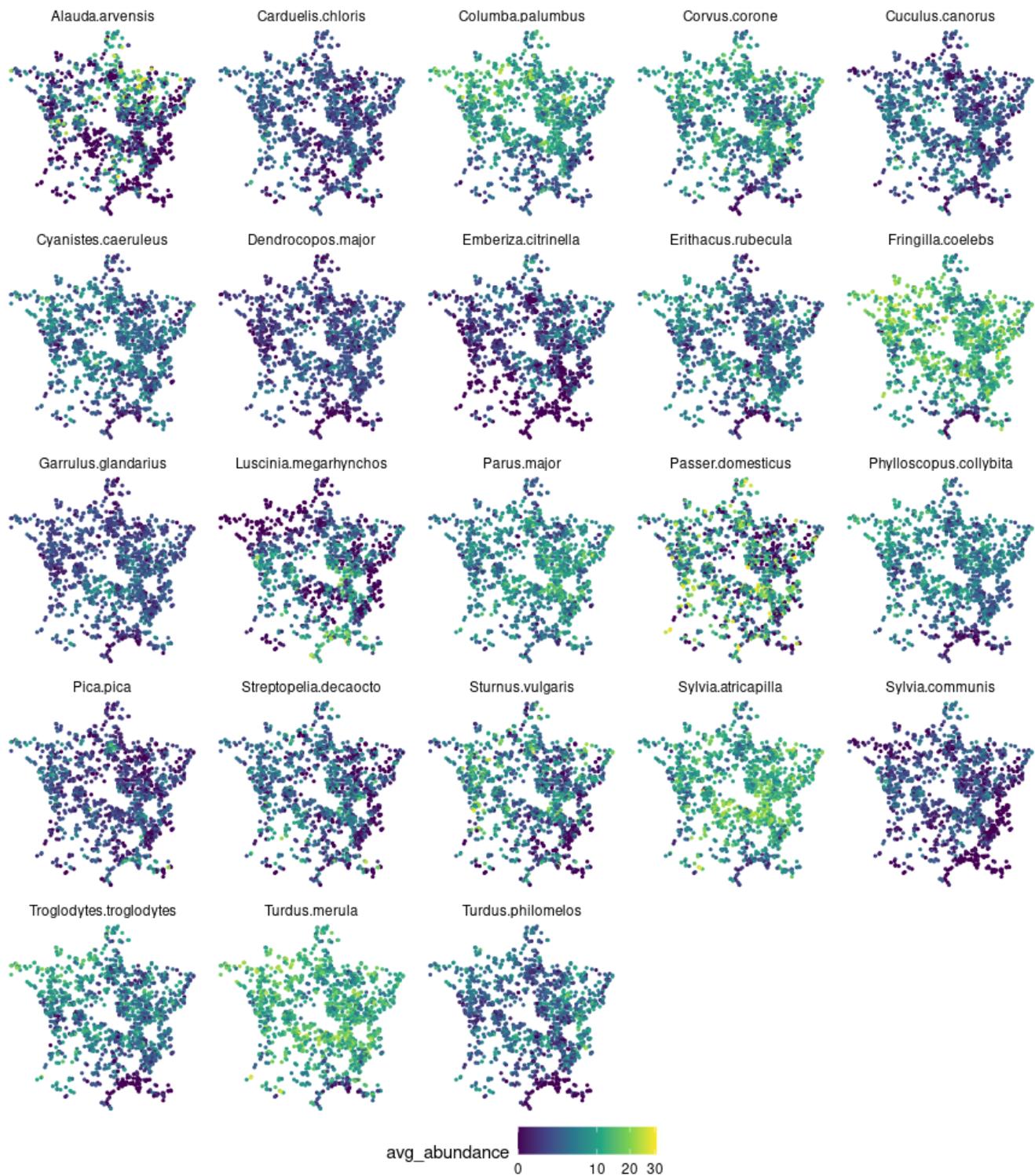
576 Species mean abundances at each FBBS site across the study period (2001-2019).

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2 577   Temporal changes in species abundances at national scale
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32 579 Species yearly mean ± SD abundance of the species across the FBBS sites.
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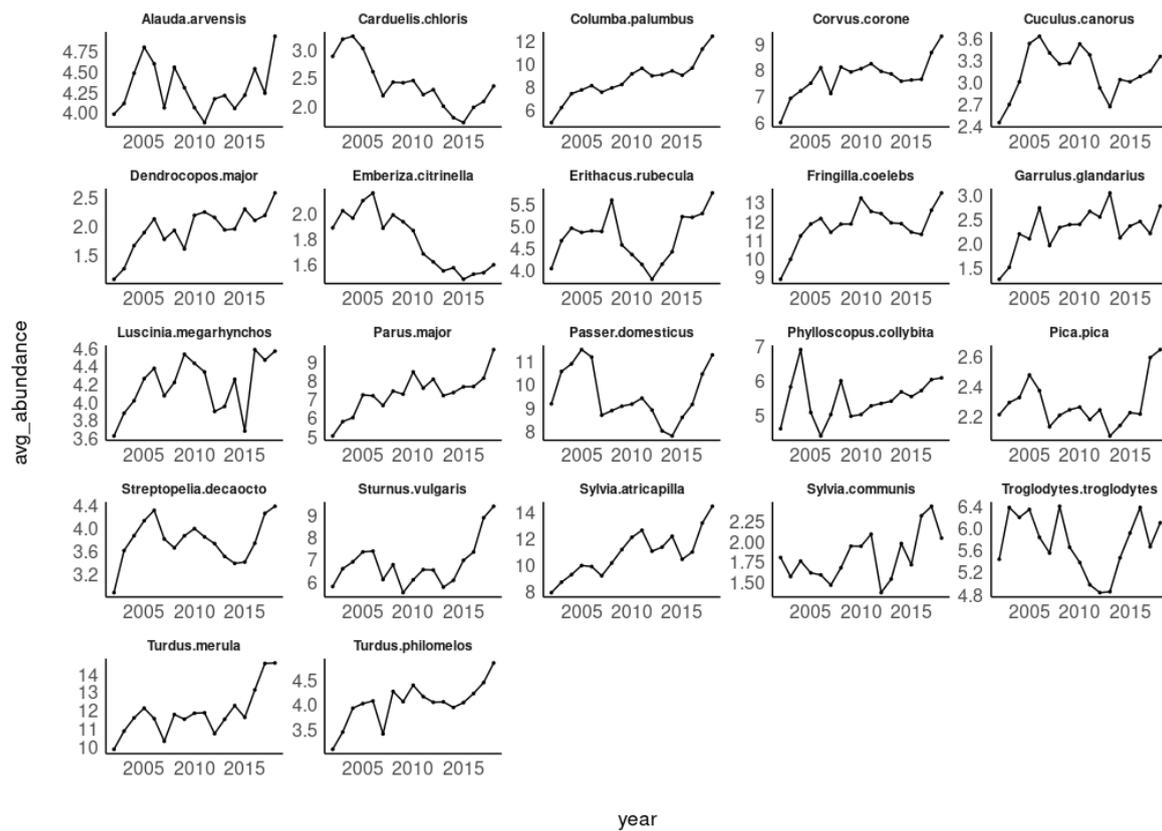
583 Environmental data descriptions

584   Spatial distribution of climate across the study period

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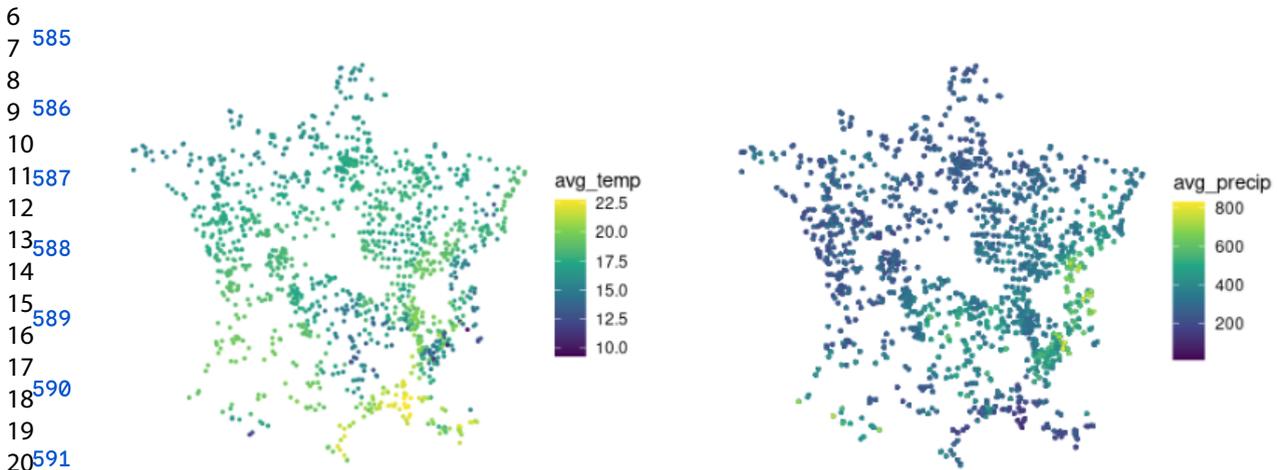
595 *Mean average daily Temperature and Precipitation averaged at each FBBS site across the study period (2001-2019).*

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Spatial distribution of land cover over the study period

Mean percent cover of habitat type at each FBBS site across the study period (2001-2019).

624 Temporal changes in land cover at national scale

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*Yearly mean percent cover of habitat types across the FBBS sites.*
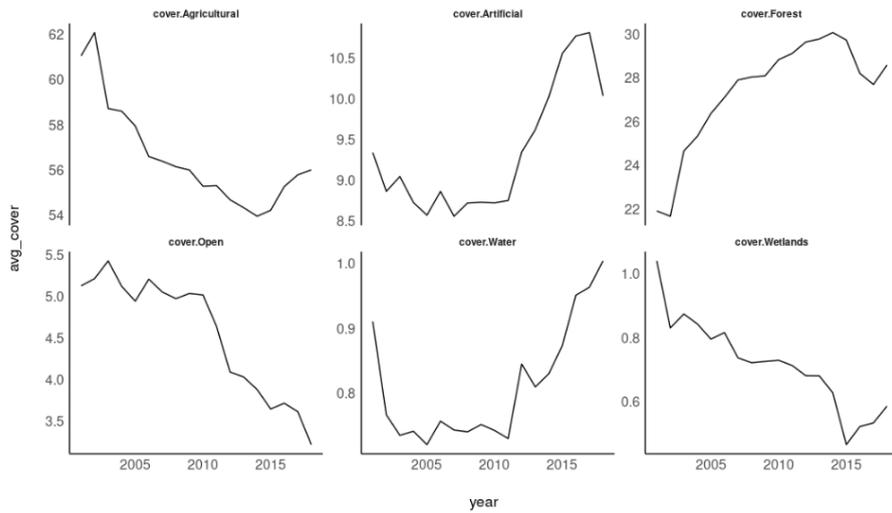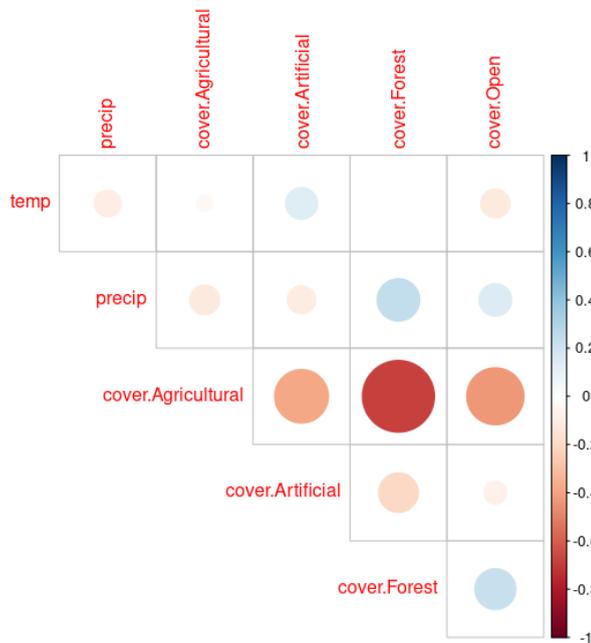
637 *Correlation plot between environmental variables. The overall low correlation between environmental variables does*

638 *not support the use of PCA axis to describe environmental gradients.*

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Environment-Species Relationships based on raw data
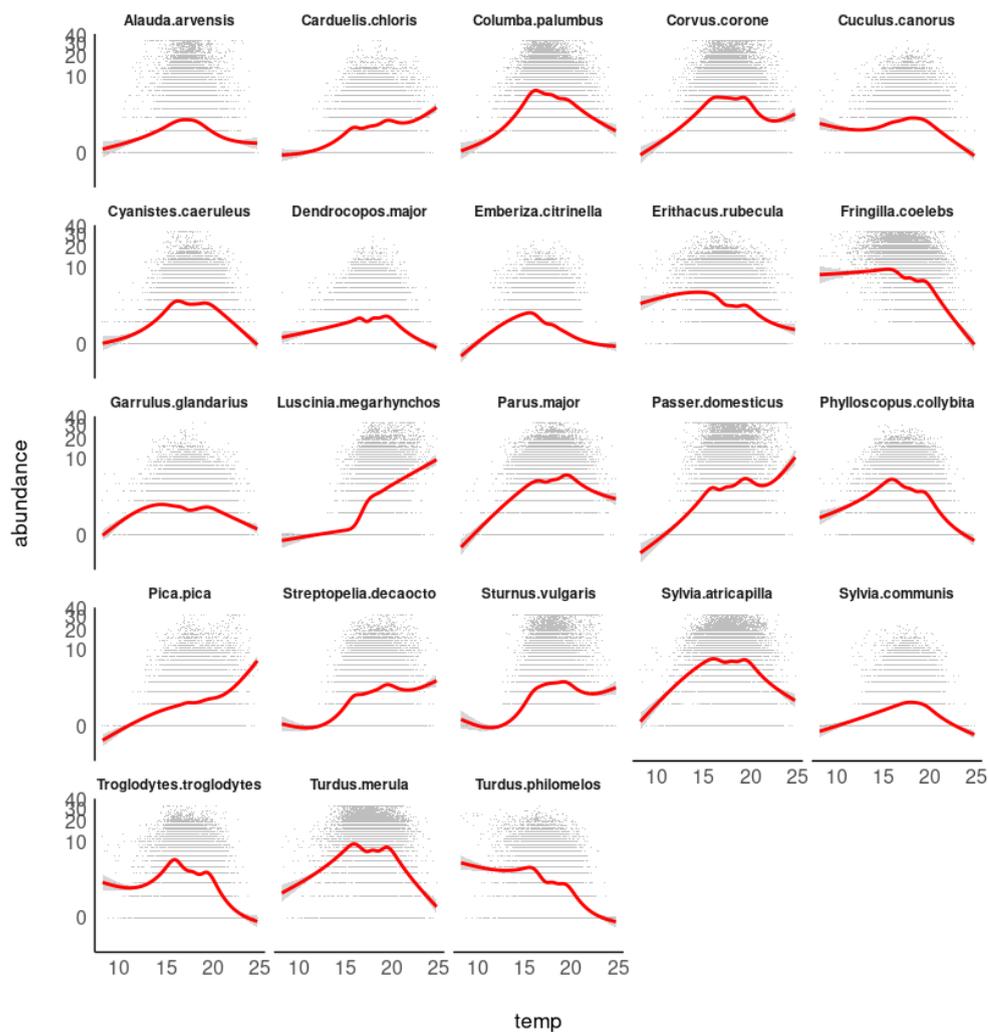
Variation of (log-transformed) abundance values (observed across site and years) with temperature (red lines are smooth fitting curves fitted via generalized additive models).
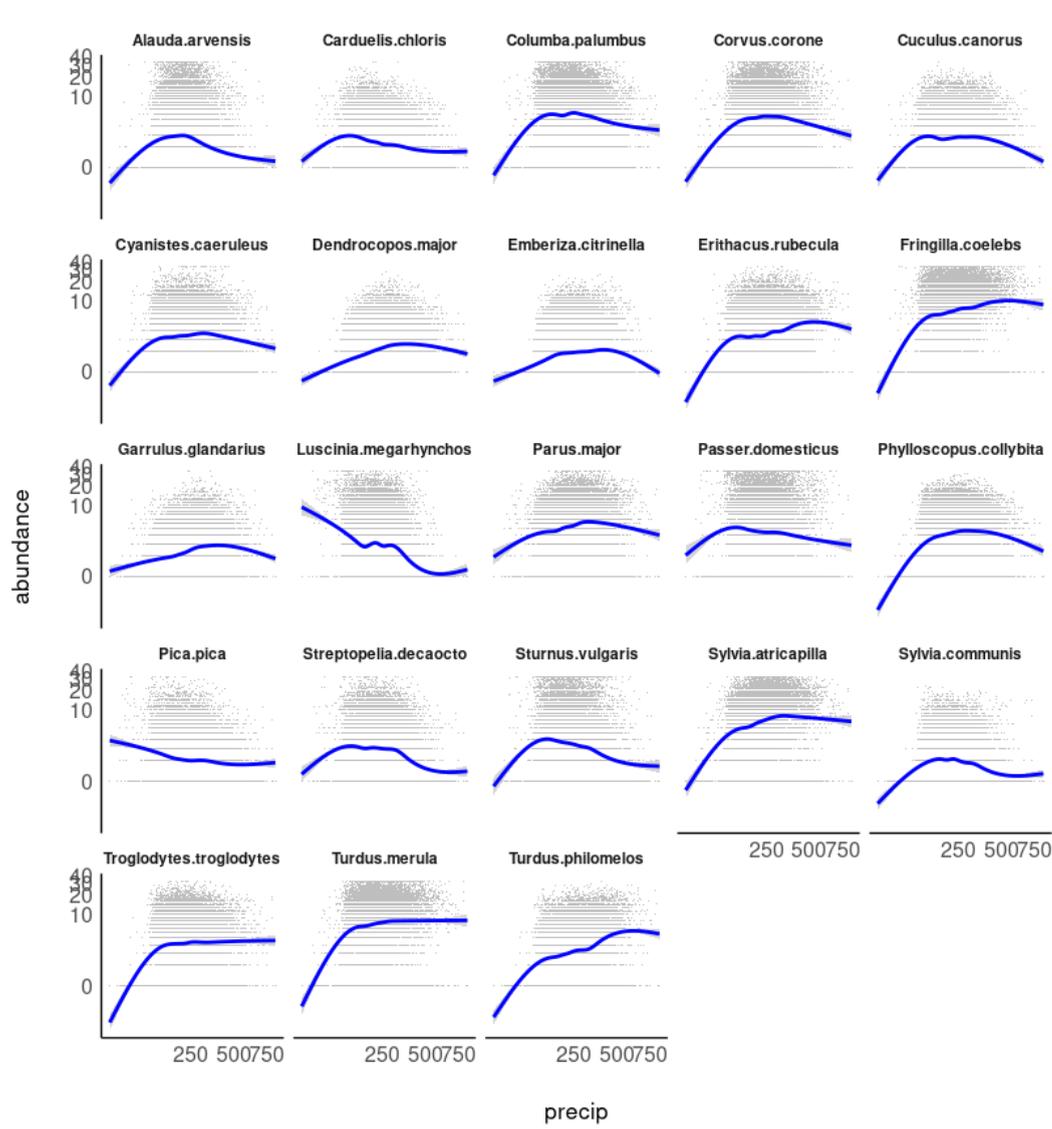
Variation of (log-transformed) abundance values (observed across site and years) with precipitation.
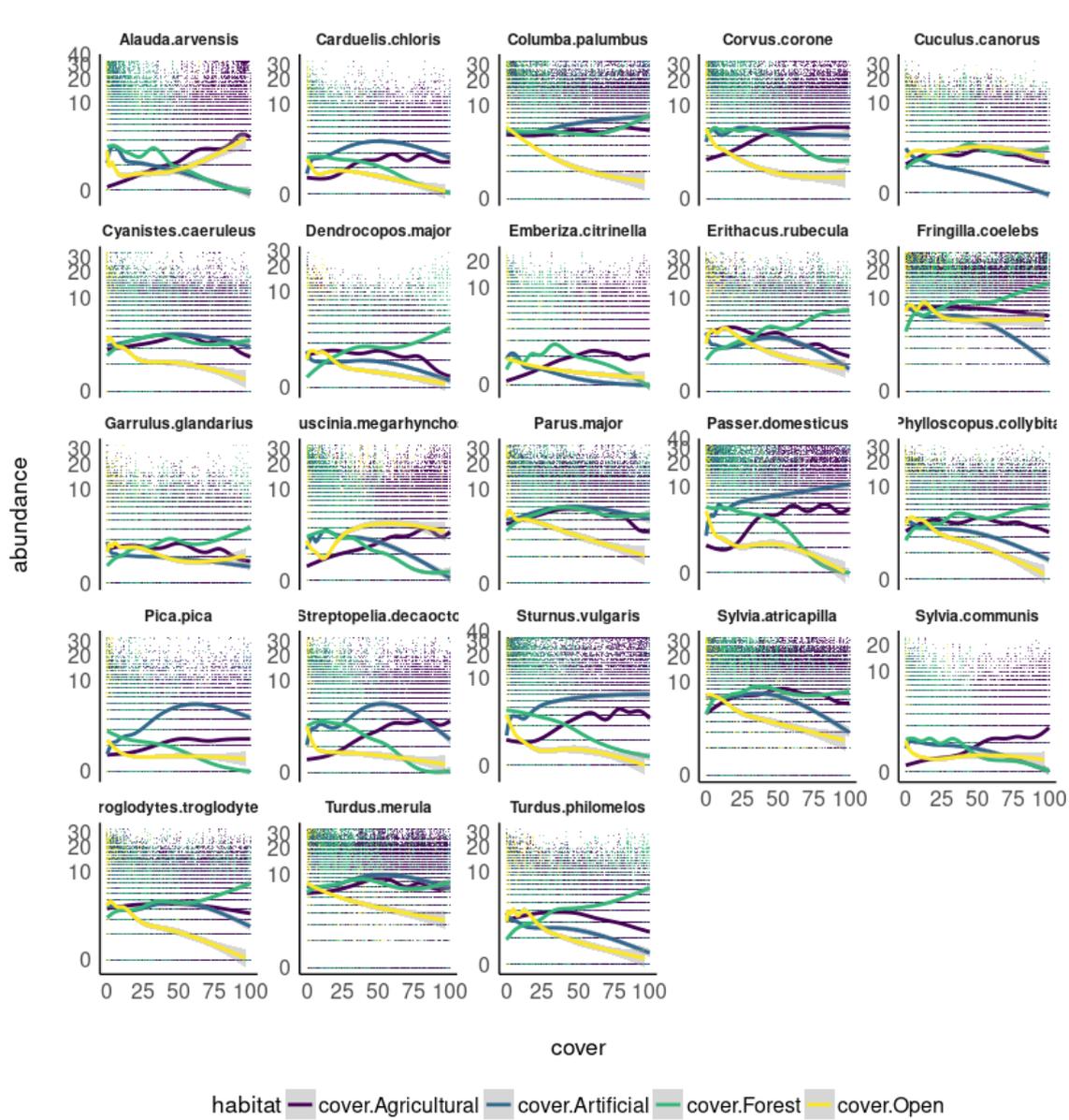
647 *Variation of (log-transformed) abundance values (observed across site and years) with land-cover, measured as percent of 2x2km cell area*

648 *covered by Agricultural, Artificial, Forest or Open land*

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Model validation

To check chain converge and the reliability of model parameter estimation, we plotted, for each parameter :

Posterior density plot

- density of rho parameters : https://cloud.univ-grenoble-alpes.fr/s/zJnMcq29r4dHcbN

- density of alpha parameters : https://cloud.univ-grenoble-alpes.fr/s/tEB76nK5BAp2Xyk

Trace plot

- trace plot rho parameters : https://cloud.univ-grenoble-alpes.fr/s/JN49TNDX83CpzQ6

- trace plot alpha parameters : https://cloud.univ-grenoble-alpes.fr/s/KJcWP5dJZSHFLsS

Running mean plot

Running mean shows whether the chain slowly or quickly approached its target distribution by plotting the running means of each parameter. Using the same scale in the vertical axis allows us to compare convergence between different parameters. Decent convergence is identified when the chain quickly approaches the overall mean, and remains stable along the iterations.

- running means of rho parameters : https://cloud.univ-grenoble-alpes.fr/s/BSiq2nm37JDA6Ls

- running means of alpha parameters : https://cloud.univ-grenoble-alpes.fr/s/cGbn9YtpXnfwf7B

Potential Scale Reduction Factor (Rhat).

The potential scale reduction factor measures convergence of the chains by measuring the degree to which variance (of the means) between chains exceeds what one would expect if the chains were identically distributed. Good convergence is identified when Rhat approches 1, decent convergence when Rhat < 1.2.

- Rhat for rho parameters https://cloud.univ-grenoble-alpes.fr/s/z2n3A5jgJaaz4DD

- Rhat for alpha parameters https://cloud.univ-grenoble-alpes.fr/s/CQWzfg3DDN3sy5z

Cross correlation

- correlation for rho parameters: https://cloud.univ-grenoble-alpes.fr/s/9PHjzM7ZxHLq4t2

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679   -   correlation for alpha parameters: https://cloud.univ-grenoble-alpes.fr/s/d7AopcefHMFFaYa