

Unveiling the food webs of tetrapods across Europe through the prism of the Eltonian niche

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Key Words:	food webs, functional traits, metaweb, stochastic block model, trophic diversity, trophic groups

1 Unveiling the food webs of tetrapods across 2 Europe through the prism of the Eltonian niche

3 **Running title: Food webs of tetrapods across Europe**

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20

21 **Abstract**

22 **Aim.** Despite recent calls on integrating interaction networks into the study of large-scale
23 biodiversity patterns, we still lack a basic understanding of the functional characteristics of large
24 interaction networks and how they are structured across environments. Here, building on recent
25 advances in network science around the Eltonian niche concept, we aim to characterize trophic
26 groups in a large food web, and understand how these trophic groups vary across space.

27 **Location.** Europe and Anatolia.

28 **Taxon.** Tetrapods (1,136 species).

29 **Methods.** We combined an expert-based metaweb of all European tetrapods with their spatial
30 distributions and biological traits. To understand the functional structure of the metaweb, we first
31 used a stochastic block model to group species with similar Eltonian niches, and then analysed
32 these groups with species' functional traits and network metrics. We then combined these groups
33 with species distributions to understand how trophic diversity varies across space, in function of
34 the environment, and between the European ecoregions.

35 **Results.** We summarised the 1,136 interacting species within the metaweb into 46 meaningful
36 trophic groups of species with a similar role in the metaweb. Specific aspects of the ecology of
37 species, such as their activity time, nesting habitat and diet explained these trophic groups. Across
38 space, trophic diversity was driven by both biotic and abiotic factors (species richness, climate
39 and primary productivity), and the representation of trophic groups differed among European
40 ecoregions.

41 **Main conclusions.** We have characterized the Eltonian niche of species in a large food web,
42 both in terms of species interactions and functional traits, and then using this to understand the
43 spatial variation of food webs at a functional level, thus bringing together network science,
44 functional ecology and biogeography. Our results highlight the need to integrate multiple aspects
45 of species ecology in global change research. Further, our approach is strongly relevant for
46 conservation biology as it could help predict the impact of species translocations on trophic
47 diversity.

48 **Key words**

49 Food webs, functional traits, metaweb, stochastic block model, trophic diversity, trophic groups

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52 Introduction

53 Understanding spatial biodiversity patterns and underlying ecological processes is a central
54 research axis of biogeography (Humboldt & Bonpland, 1805). Owing to the historic importance of
55 this issue, its current relevance for conservation, and its revived momentum in the era of big data,
56 recent work has allowed new comprehensive syntheses on the ecological and evolutionary drivers
57 of large-scale diversity patterns (Ficetola, Mazel, & Thuiller, 2017; Jetz, Thomas, Joy, Hartmann, &
58 Mooers, 2012; Mazel et al., 2017). The majority of these studies have used functional or
59 phylogenetic information to group species or quantify diversity (Davies & Buckley, 2011; Safi et
60 al., 2011). While functional and phylogenetic data have offered many insights into ecological
61 processes (e.g. Sundstrom, Allen, & Barichievy, 2012), they are only indirect proxies for how
62 species interact in communities. Biotic interactions, such as trophic interactions, can shape
63 macroecological patterns of diversity (Gotelli, Graves, & Rahbek, 2010), in addition to the better-
64 known effects of the abiotic environment. Especially in the context of global change, where species
65 interactions are altered (Valiente-Banuet et al., 2015), with cascading effects on the response of
66 multiple species to global change (Bascompte, García, Ortega, Rezende, & Pironon, 2019;
67 Tylianakis, Didham, Bascompte, & Wardle, 2008; Van der Putten, Macel, & Visser, 2010; Wisz et
68 al., 2013), it is of prime importance to integrate interaction networks into the study of biodiversity
69 patterns (Baiser et al., 2019; Pellissier et al., 2017; Tylianakis & Morris, 2017).

70 Food webs are particular interaction networks that represent both the species composition of a
71 community together with the fluxes of biomass associated with their interactions, thus providing
72 the potential to reconcile the structure and function of biodiversity (Thompson et al., 2012). So
73 far, food webs have been analysed and compared across space through either network-level
74 metrics or species-level metrics (Baiser et al., 2019; Kortsch et al., 2019), but we still lack the
75 capacity to unveil how large food webs are structured in terms of the roles of the species that
76 compose them, and consequently to understand how the structure and function of food webs
77 varies across environmental gradients (Pellissier et al., 2017). Both the complexity of interaction
78 networks, and the scarcity of empirical interaction network datasets across large spatial scales,
79 have hindered this progress.

80 One approach to reduce the complexity of large food webs while preserving their structure is to
81 group species together based on their role in the food web, or their Eltonian niche, defined as the
82 “place of an animal in a community, its relation to food and enemies” (i.e. to prey and predators)
83 (Elton, 1927). There have been two lines of research that seek to understand the role of species in
84 food webs. The first approach focuses on the position of a species within a food web, using
85 methods from network science to aggregate species into a number of trophic groups that contain
86 species with similar sets of prey and predator species (Cirtwill et al., 2018). The stochastic block
87 model (Allesina & Pascual, 2009; Daudin, Picard, & Robin, 2008; Karrer & Newman, 2011), in
88 particular, provides the opportunity to aggregate species that have the same probability of
89 interacting with the rest of the species in the network, i.e. similar Eltonian niches (Gauzens,
90 Thébault, Lacroix, & Legendre, 2015). The second approach focuses on the use of functional traits

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3 91 to deduce the role of a species within a food web and infer their interactions (Gravel, Albouy, &
4 92 Thuiller, 2016). For example, a trophic interaction between two species results from a match
5 93 between the vulnerability traits of the prey species and the foraging traits of the predator species
6 94 (Gravel et al., 2016; Rossberg, Brännström, & Dieckmann, 2010). Characterizing a species from its
7 95 position in the network topology on the one hand, and from its functional traits on the other, have
8 96 thus been two contrasting approaches to determine a species' Eltonian niche. However,
9 97 integrating both perspectives to understand how and which biological traits define the role of
10 98 species in a food web has seldom been investigated (Baskerville et al., 2011; Coux, Rader,
11 99 Bartomeus, & Tylianakis, 2016; Kéfi, Miele, Wieters, Navarrete, & Berlow, 2016). Here, we used a
12 100 novel food web dataset of all European tetrapod species to merge these approaches by first
13 101 modelling the trophic role (or Eltonian niche) of species in the food web using recently developed
14 102 methods in network science, and then describing how these trophic roles relate to species'
15 103 functional traits. We expect the food web to be structured into functionally meaningful trophic
16 104 groups that aggregate species with overlapping sets of prey and predator species in the food web,
17 105 due to similarities in their foraging and vulnerability traits (Laigle et al., 2018).

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25 106 Combined with species geographic distributions, the Eltonian niche concept further enables the
26 107 structure of food webs to be portrayed across space, adding a new dimension to spatial
27 108 biodiversity patterns. Trophic diversity, defined as the number of trophic roles played by species
28 109 (Bascompte, 2009), appears as a convenient measure to map food web patterns across
29 110 macroecological scales. Ecogeographical rules observed for species richness, such as the
30 111 latitudinal gradient, have not yet been investigated for species roles in food webs (Baiser et al.,
31 112 2019), and divergences between species richness and trophic diversity patterns have the
32 113 potential to reveal the underlying ecological processes driving patterns of biodiversity at
33 114 macroecological scales. We expect different environments to select species based on their role in
34 115 interaction networks (Tylianakis & Morris, 2017). For instance, in more favourable climatic
35 116 conditions and more productive ecosystems, high competition for resources should lead to high
36 117 trophic specialization and trophic complementarity (Poisot, Mouquet, & Gravel, 2013), translating
37 118 into a more diverse range of trophic roles filled locally, therefore a higher trophic diversity, than
38 119 in harsher environmental conditions with the same number of species (Gaston, 2000).

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45 120 Here, following on recent calls to bridge the gap between contrasting views of the niche (Gravel
46 121 et al., 2018), we built a large food web made up of the 50,408 potential trophic interactions
47 122 between all the tetrapod species across Europe (i.e. the metaweb of 1,136 species of birds, reptiles,
48 123 amphibians and mammals). We first inferred trophic groups in the metaweb using the stochastic
49 124 block model and investigated the functional trait structure of these trophic groups. Second, we
50 125 combined the metaweb with species distribution data, to explore how these trophic groups vary
51 126 across space, in quantity and in quality. We hypothesized that: (1) the metaweb of European
52 127 tetrapods can be simplified into trophic groups which are determined by the functional traits of
53 128 the species that compose them, and (2) divergences between patterns of trophic diversity and
54 129 those of species richness across the European continent should provide insights into the
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3 130 underlying ecological processes that contribute to food web structure and function at macro-
4 131 ecological scales.

8 132 **Material and Methods**

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10 133 An overview of the material and methods is depicted in Fig. S1.

13 134 **Study area, species distributions and biological traits**

15 135 The study area included Europe (including Macaronesia and Iceland) and Anatolia. We extracted
16 136 the distributions for all tetrapods naturally occurring within the study area from Maiorano et al.
17 137 (2013), which were modelled by combining the extent of occurrence for each species with their
18 138 habitat requirements (see Maiorano et al. (2013) for a full description of species distribution
19 139 data). In total, our analyses focused on 508 bird, 288 mammal, 237 reptile and 103 amphibian
20 140 species. Species distributions were mapped in a regular grid of 300 m resolution, where cells had
21 141 values of zero for unsuitable habitat, one for marginal habitat (habitat where the species can be
22 142 present, but does not persist in the absence of primary habitat (Maiorano et al., 2013)) and two
23 143 for primary habitat. Here, we treated primary habitat only as “suitable habitat”, which provides a
24 144 better prediction of the actual species distribution (Ficetola, Rondinini, Bonardi, Baisero, & Padoa-
25 145 Schioppa, 2015). All range maps were up-scaled to a 10x10 km equal-size area grid (ETRS89; total
26 146 of 78,873 cells). We considered species potentially present in a 10x10 km cell when they had least
27 147 one 300 m suitable habitat cell within it.

28 148 For the same set of species, we gathered biological trait data from Thuiller et al. (2015). We used
29 149 traits that are linked to trophic interactions (Luck, Lavorel, McIntyre, & Lumb, 2012) and
30 150 restricted our analyses to comparable traits between the four groups. These consisted of
31 151 information on:

- 32 152 • diet (17 categories: mushrooms, seeds/nuts, fruits/berries, mosses/lichens, vegetative
33 153 plant parts, invertebrates, vertebrates, fish, small mammals, large mammals, herptiles,
34 154 bird eggs, small birds, large birds, bones, carrion, coprophagous)
- 35 155 • nesting habitat (tree hole, ground, rocks, artificial, underground water, cave/burrow,
36 156 lodge, temporary water, brooks/springs/small rivers, puddles/ponds, brackish waters)
- 37 157 • activity time (diurnal, crepuscular, nocturnal, arrhythmic)
- 38 158 • foraging behaviour (grazer, opportunistic, hunter, browser)
- 39 159 • morphology (body mass for birds and mammals, body length for herptiles)

41 160 **The network of potential trophic interactions**

42 161 The network of potential trophic interactions between all European tetrapod species (hereafter,
43 162 the metaweb) was built using a combination of expert knowledge, published information and field
44 163 guides (a list of references is found in Appendix 1). Trophic interactions between a predator and
45 164 its prey were identified from published accounts of their observation, morphological similarities

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3 165 between potential prey and literature-referenced prey and, in the absence of this information, the
4 166 diet of the predator's sister species. The full dataset and methods description will be made publicly
5 167 available in Maiorano et al. (in revision). The metaweb contained 1,136 tetrapod species and a
6 168 total of 50,408 potential trophic interactions. In this metaweb, 883 basal species did not prey on
7 169 European tetrapod species (i.e. basal species here could feed on plants, detritus, invertebrates,
8 170 fish, domestic animals or were coprophagous), 213 intermediate consumer species had both prey
9 171 and predator species amongst European tetrapods, and 40 top predator species had no predator
10 172 species. The metaweb had a connectance of 0.0385.

15 173 **Trophic groups definition**

17 174 To build trophic groups, we used a stochastic block model (SBM) on the metaweb of potential
18 175 trophic interactions (R-package mixeR version 1.8 (Daudin et al., 2008; Miele, 2006)), following
19 176 on previous studies (Baskerville et al., 2011; Gauzens et al., 2015; Kéfi et al., 2016; Mariadassou,
20 177 Robin, & Vacher, 2010). The SBM is a random graph model with several groups of nodes (also
21 178 known as 'group model' in Allesina & Pascual (2009) or 'block model' in Newman & Leicht
22 179 (2007)). A parameter of this model is an aggregated graph with groups of nodes, linked to one
23 180 another through edges that represent the probability of connection between any two nodes in the
24 181 corresponding groups. Consequently, two nodes belonging to the same group have the same
25 182 probability of connection with all other nodes in the graph. Given a network, the statistical
26 183 machinery of the SBM aims to recover the groups defining similar groups of species in terms of
27 184 the interactions they have with each other (Gauzens et al., 2015). The goodness of fit of the model
28 185 is assessed using the Integrated Classification Likelihood (ICL) information criterion. Applied to
29 186 the metaweb, the SBM inferred groups of species such that two species belonged to the same
30 187 group if they had the same probability of interacting with all other species in the metaweb - in
31 188 other words, they potentially preyed on similar sets of species, and were potentially preyed upon
32 189 by similar sets of species. Using the SBM, we partitioned the species in the metaweb along a range
33 190 of 10 to 60 groups, hereafter referred to as trophic groups. We defined the optimal number of
34 191 groups based on the partitioning of the metaweb that maximised the ICL criterion (Fig. S2). We
35 192 then computed the average trophic level of each trophic group (R-package NetIndices (version
36 193 1.4.4) (Soetaert, Kipyegon Kones, & van Oevelen, 2015)). We also computed the in- and out-degree
37 194 of the species (defined as the number of predator and prey links of a species, respectively) in the
38 195 potential metaweb (R-package igraph (version 1.2.4) (Csárdi, 2019)) and expressed the
39 196 distribution of in- and out-degree within each trophic group (Fig. S3).

51 197 **Functional composition of trophic groups**

52 198 To visualize the metaweb, we removed the links between species that never co-occurred in space
53 199 (in terms of range and habitat co-occurrence) and used the software Gephi (version 0.9.2, Bastian,
54 200 Heymann, & Jacomy, 2009) (Fig. 1). We then described the composition of the groups in terms of
55 201 the taxonomy (at the class level) and generalism of the species (Fig. S3).

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3 202 We then performed a multivariate analysis to understand the composition of trophic groups in
4 203 terms of the biological traits of the species they contained. We did so by using a co-inertia
5 204 approach called the Outlying Mean Index (Dolédec, Chessel, & Gimaret-Carpentier, 2000) that is
6 205 usually meant to identify the ecological niche of species as a function of the environment (function
7 206 *niche* in package *ade4* (version 1.7-13) in R (Dray, Dufour, & Thioulouse, 2018)). Here, we took
8 207 advantage of this approach to characterize the different trophic groups (species x trophic groups
9 208 matrix) as a function of the biological traits (species x traits matrix). In other words, we mapped
10 209 the trophic groups in the space of the functional traits of the species they contained.

15 210 **Quantifying and mapping trophic diversity across Europe**

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18 211 To characterize how trophic diversity varied across space, we first mapped trophic diversity (as
19 212 the number of trophic groups found in each grid cell) alongside species richness (the number of
20 213 species in each grid cell). Then, we tested the response of trophic diversity to species richness,
21 214 environmental variables and the interactions between these drivers using a linear model.
22 215 Bioclimatic data at 10km resolution was downloaded from Worldclim v2
23 216 (<http://www.worldclim.org>), and net primary productivity (NPP) from SEDAC
24 217 (<https://sedac.ciesin.columbia.edu/data/collection/hanpp/sets/browse>). We tested the
25 218 pairwise correlations between all environmental variables and selected those that were not
26 219 correlated (Fig. S4). We then ran linear models accordingly with different combinations of
27 220 explanatory variables and selected the model with the smallest AIC. We mapped the residuals of
28 221 the linear model including species richness alone and compared it with the residuals of the full
29 222 model (that included average annual temperature, net primary productivity and temperature
30 223 seasonality in addition to species richness) (Fig. S5). Finally, to understand how each
31 224 environmental variable influenced the relationship between species richness and trophic
32 225 diversity, we computed the predictions of the linear model for the first, second and third quartile
33 226 of each environmental variable to plot their statistical interaction with species richness.

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36 227 We then investigated how the trophic groups and types of interactions in the tetrapods' food web
37 228 varied across the different European ecoregions, defined by the European Environment Agency
38 229 (EEA 2019) to represent "extents of areas in Europe with relatively homogeneous ecological
39 230 conditions, on the basis of climatic, topographic and geobotanical data, within which comparisons
40 231 and assessments of different expressions of biodiversity are expected to be meaningful". We
41 232 compared ecoregional metawebs across 11 ecoregions: alpine, Anatolian, arctic, boreal,
42 233 continental, Macaronesia, Mediterranean, Pannonian and steppic. We built each ecoregional
43 234 metaweb by sampling the species occurring in the ecoregion and the interactions between co-
44 235 occurring species within the ecoregion from the European metaweb. We then aggregated each
45 236 ecoregional metaweb using the 46 trophic groups defined on the European metaweb. The links
46 237 between two given groups represented the sum of interactions realized in the ecoregion (i.e. the
47 238 number of pairs of species belonging to these groups that co-occurred and interacted in the
48 239 ecoregion). We also computed the geographic specialization of species to each European
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240 ecoregion (computed as the ratio between a species' ecoregional range and its European range),
241 then computed the median value of specialization for each group.

242 All analyses were conducted in R version 3.4.3 (R Core Team, 2017).

243 **Results**

244 **Defining trophic groups in the European metaweb of tetrapods' trophic** 245 **interactions**

246 Based on the ICL criterion, the SBM partitioned the European metaweb into 46 groups (Fig. S2). A
247 qualitative examination of the partitioning suggested that groups were homogenous in terms of
248 taxonomy, trophic level and the degree of generalism of the species within them (Fig. 1 & S2). We
249 organized the 46 trophic groups within four trophic levels to visualize the flow of biomass, from
250 herbivores to intermediate consumers, mesopredators and finally top predators.

251 The Outlying Mean Index revealed that specific traits strongly explained the trophic groups (Fig.
252 2). The first component was primarily driven by the feeding behaviour and diet of species, with
253 secondary consumers and carnivores (e.g. hunters) belonging to different trophic groups than
254 herbivore species (e.g. grazers and browsers), consistent with the organization of the trophic
255 groups into the aforementioned trophic levels. The second component was driven by the activity
256 time and the nesting habitat of species, with diurnal species separated from nocturnal species in
257 these trophic groups, meaning that the time of activity determines the types of prey or predator
258 of a species, and species nesting in aquatic habitat belonging to different trophic groups than
259 species nesting in terrestrial habitat. This second component especially structured the trophic
260 groups within intermediate and basal trophic levels.

261 **Mapping trophic diversity across Europe**

262 Trophic diversity generally decreased with latitude in a similar manner to species richness, i.e.
263 there was a latitudinal gradient for trophic diversity as well for species richness (Fig. 3A & 3B).
264 Species richness and trophic diversity were both at their lowest in northern latitudes. Several
265 trophic groups (e.g. groups composed by herptiles) were completely absent from both the arctic
266 and boreal ecoregions, reducing the complexity of these regional metawebs (Fig. 4), parallel to a
267 regional decrease in trophic diversity. Because of these low diversities, a single type of interaction
268 was strongly represented in the Arctic metaweb, involving a group of mesopredators (e.g.
269 predatory seabird species and the arctic fox) preying on a group of basal species in the Arctic
270 (mainly small birds and rodents). Then, trophic diversity and species richness both peaked at
271 intermediate latitudes (Fig. 3A and 3B): species richness peaked at around 600 species / 100 km²
272 and trophic group diversity peaked at 46 groups / 100 km², frequently reaching these highest
273 values in mountainous areas. To illustrate, the alpine metaweb displayed the highest species
274 richness, trophic diversity, and link density of all ecoregional metawebs (Fig. 4). However, in

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3 275 southern Europe, trophic diversity patterns diverged from species richness patterns (Fig. 3A and
4 276 3B): trophic diversity remained close to its maximum, while species richness was lower in
5 277 southern Europe than in intermediate latitudes. This was exemplified with the Mediterranean and
6 278 Anatolian metawebs in southern Europe (Fig. 4), where all trophic groups of the European
7 279 metaweb were represented by at least one species, but with fewer species representing them
8 280 overall, than in the alpine metaweb for instance.

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12 281 Modelling for latitude and species richness alone showed that trophic diversity declined
13 282 significantly towards northern latitudes and increased significantly with species richness, as
14 283 expected ($R^2 = 0.89$). Further, the latitudinal gradient of trophic diversity was fully accounted for
15 284 when including environmental variables to the linear model (annual mean
16 285 temperature, temperature seasonality and net primary productivity) in addition to species
17 286 richness (Fig. S5). More precisely, trophic diversity increased significantly with annual mean
18 287 temperature and NPP and displayed a quadratic response to temperature seasonality (i.e. mild
19 288 seasonality was linked to higher trophic diversity while extreme seasonality, both high and low,
20 289 was detrimental to trophic diversity) (Table S1). Further, results show that the environmental
21 290 variables significantly affected the linear relationship between trophic diversity and species
22 291 richness (Fig. 3C & S6, Table S1). For instance, trophic diversity was generally higher where
23 292 annual mean temperatures were warmer in Europe, while holding species richness constant (Fig.
24 293 3C). Conversely, in colder environments, trophic diversity was lower than explained by species
25 294 richness alone. Interestingly, in colder environments, trophic diversity was also gained more
26 295 quickly as species were added to the local assemblage.

35 296 **Discussion**

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38 297 In this paper, we investigated the spatial structure of food web from a functional perspective.
39 298 Building on the Eltonian niche concept, we showed that species interacting in a large food web
40 299 can be aggregated into a few dozen trophic groups of species with the same role in the food web
41 300 by using a novel network science approach, the stochastic block model. We then showed that
42 301 trophic groups were coherent with the trophic level, trophic specialization, functional traits and
43 302 taxonomy of species within them. Second, our analysis revealed a latitudinal gradient in trophic
44 303 diversity (richness of trophic groups) that varies with the well-known species richness gradient,
45 304 but is also additionally explained by environmental conditions (e.g. warmer temperatures, mild
46 305 seasonality) and net primary productivity. Taken together, these results show that the Eltonian
47 306 niche provides an unmatched opportunity to unveil the structure and function of large food webs
48 307 at a continental scale.

54 308 **Recovering species' Eltonian niche from large food webs with the stochastic block** 55 309 **model**

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58 310 The stochastic block model goes further in capturing the different dimensions of a species role in
59 311 the food web than the trophic level concept, which overlooks important aspects of species'

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3 312 ecological role such as their taxonomy, trophic specialization and biological traits (Cirtwill et al.,
4 313 2018). In addition, the trophic level is a concept that implies a hierarchy in the food web that is
5 314 not always relevant (Cousins, 1987; Polis & Strong, 1996). This is especially important for other
6 315 types of networks (e.g. multiple interaction types (Pilosof, Porter, Pascual, & Kéfi, 2017) where
7 316 there are many loops and no clear trophic levels. Conceptually, the trophic groups resulting from
8 317 the stochastic block model are linked to trophic guilds since they represent a group of species that
9 318 exploit the same resources, i.e. that have a similar role in a food web (Simberloff & Dayan, 1991).
10 319 However, the two approaches differ in methodology: while guilds are usually based on expert
11 320 opinion, the stochastic block model explicitly uses the interaction network. Such a data-driven
12 321 approach to identify species roles has the potential to bring to light some similarities between
13 322 pairs of species that otherwise might have been ignored. In other words, the stochastic block
14 323 model enables to bridge the gap between network theory and functional ecology (Gravel et al.,
15 324 2016).

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17 325 Further, we showed that trophic groups were driven by species functional traits. The metaweb
18 326 studied here included tetrapods species exclusively, therefore basal trophic groups sometimes
19 327 contained secondary consumers such as piscivorous and insectivorous species, and basal groups
20 328 were not always as homogenous in terms of taxonomy, as trophic groups further up the trophic
21 329 levels. Nonetheless, biological traits associated to species foraging and vulnerability traits
22 330 explained trophic groups across all trophic levels. Unsurprisingly, diet categories and feeding
23 331 behaviour strongly determined species trophic role. Then, activity time and nesting habitat also
24 332 structured the trophic groups, particularly within lower trophic levels. Interestingly, activity
25 333 times of predators did not necessarily coincide with the activity time of their prey: indeed,
26 334 nocturnal predators may preferentially feed on diurnal prey, provided that their foraging habitat
27 335 coincides with their prey's nesting habitat. Overall, these results exemplify that a species' Eltonian
28 336 niche (i.e. the potential occurrence of a trophic interaction), as recovered with the stochastic block
29 337 model, is determined by temporal, spatial and functional aspects of a species' ecology.

30 31 32 33 34 35 36 37 38 39 40 41 338 **From Eltonian niches to food web structure at macroecological scales**

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44 339 In our study, we have not addressed the intraspecific variability in species interactions (Poisot,
45 340 Stouffer, & Gravel, 2014) nor the realized Eltonian niche of species, which can only be deduced
46 341 from empirical food web datasets that are unavailable at macro-ecological scales. Besides,
47 342 comparison of empirical food webs between several locations is impossible to date unless only
48 343 one dimension is considered (e.g. along a linear gradient, or time: Matias & Miele, 2017; Miele &
49 344 Matias, 2017). Instead, we have used the potential interactions that are either known or expected
50 345 to occur between all tetrapod species in Europe (i.e. the metaweb, *sensu* Dunne, 2006), thus
51 346 recovering the potential Eltonian niche of species. Indeed, if the potential niche of a species
52 347 represents the set of abiotic environmental conditions in which it could thrive without accounting
53 348 for its biotic interactions (Hutchinson, 1957), then the potential Eltonian niche of a species should
54 349 represent the set of species that it could interact with if they coexisted.
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3 350 Our results showed that trophic diversity, defined as trophic group richness or the range of
4 351 Eltonian niches in an area, increased linearly with species richness across Europe, but also reveal
5 352 interesting deviations from this linear relationship. We found that generally, trophic diversity was
6 353 higher in southern Europe than would be explained from species richness alone, reflecting a
7 354 higher niche differentiation in more favourable environments, where the climate is milder and
8 355 ecosystems are more productive. Conversely, in northern Europe, in the Arctic or Boreal
9 356 ecoregions for example, where climatic conditions are harsher and ecosystems less productive,
10 357 trophic diversity was lower than would be explained by species richness alone. This could be due
11 358 to the absence of some trophic groups (mostly those represented by herptiles) in northern
12 359 latitudes, due to their physiology (Snyder & Weathers, 1975). In addition, in northern Europe,
13 360 trophic diversity was more sensitive to species richness: as species are added to the community,
14 361 they tend to fill different Eltonian niches, maximising trophic complementarity (Poisot et al.,
15 362 2013) in these simple food webs. Our results further support earlier findings suggesting that niche
16 363 breadth increases with latitude, leading to fewer niches overall in northern latitudes (Baiser et al.,
17 364 2019; Cirtwill, Stouffer, & Romanuk, 2015).

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25 365 The particular case of the alpine metaweb suggests environmental heterogeneity is an additional
26 366 driver of trophic diversity. The alpine metaweb contained the highest diversity in terms of species,
27 367 trophic groups and types of interactions. It is well established that in the Alps, the elevational
28 368 gradient, combined with spatial heterogeneity, naturally provide a diversity of habitats which
29 369 results in a higher diversity of niches available in the Alps (Kadmon & Allouche, 2007; Tylianakis
30 370 & Morris, 2017). Furthermore, the alpine ecoregion is a highly fragmented ecoregion, widespread
31 371 across Europe, with isolated inlets in Scandinavia, the Alps, the Balkans, and the Pyrenees,
32 372 therefore comprising a wide variety of climatic and land cover conditions (Fig. 4), which can
33 373 explain high trophic diversity in the alpine metaweb.

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39 374 In addition to driving regional differences in trophic diversity, different types of environments
40 375 were composed of different trophic groups: some trophic groups and their interactions were
41 376 specialized to certain ecoregions, supporting the well-established principle in biogeography that
42 377 different environments select for different functions (Buffon, 1761), in particular different trophic
43 378 roles (Tylianakis & Morris, 2017). For example, top predator feline species and snakes predating
44 379 upon smaller reptiles and rodents is a type of interaction that is particularly well-represented in
45 380 the Mediterranean metaweb. On the other hand, despite regional differences in environmental
46 381 conditions, some trophic groups were common to all ecoregional metawebs, which could be
47 382 represented by wide-ranging, generalist species (Devictor, Julliard, & Jiguet, 2008). More
48 383 fundamentally, such similarities in the trophic composition between different ecoregions echo
49 384 with Elton's conception of the niche: different communities can display convergence in ecological
50 385 roles and function, even when species composition differ (Simberloff & Dayan, 1991). Overall, our
51 386 results suggest that trophic diversity is driven by the interplay between the functional traits,
52 387 Eltonian niche, and geographic distribution of species and environmental conditions. Our study
53 388 does not disentangle the factors upon which the environment selects species, and in fact, it would
54 389 be vain to attempt to tease apart these drivers. In addition, there is a need to integrate aspects of

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3 390 history together with the current biotic and abiotic conditions across space to understand
4 391 diversity patterns in all of their complexity. The history of land use in particular has been shown
5 392 to be a major driver of diversity patterns (Niedrist, Tasser, Lüth, Dalla Via, & Tappeiner, 2009;
6 393 Pimm & Raven, 2000), especially in Europe where a complex history of local extinctions, species
7 394 reintroductions and translocations has unfolded over the past centuries, particularly for large
8 395 tetrapods such as the wolf or the bear (Chapron et al., 2014). Ultimately, our study has illustrated
9 396 how the environment can filter species assembly, based on the interplay between their trophic
10 397 role, biological traits and taxonomy, and further supports the relevance of using trophic diversity
11 398 as a new dimension of functional diversity in an area.

16 399 **Perspectives**

19 400 In the era of big data, there is an ever-increasing availability of information on potential
20 401 interactions, together with high resolution distribution data and life history traits. Harnessing
21 402 these data with novel developments in network science while relying on fundamental niche
22 403 concepts should lead to a new approach for addressing pressing topics, such as the potential
23 404 effects of environmental changes on biodiversity and ecosystem functioning, or identifying
24 405 conservation priorities to sustain multi-trophic communities. Here, we have shown that the
25 406 trophic groups inferred using the stochastic block model encompass multiple dimensions of the
26 407 role of species in a community. As global change triggers communities to be disrupted and
27 408 interactions to be broken, understanding the Eltonian niche of species has the potential to inform
28 409 conservation planning. For example, trophic groups can help predict the impacts of species
29 410 translocation as populations go locally extinct, or the invasive potential of species as their
30 411 distributions shift. Overall, this study calls for the integration of multiple aspects of species'
31 412 ecology to understand how they assemble across space: ecologists need to account not only for
32 413 species' response to environmental gradients (i.e. their Hutchinsonian niche (Guisan & Thuiller,
33 414 2005)), but also for their biological traits, their biotic interactions and their Eltonian niche, to
34 415 understand biodiversity patterns across space and time.

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418 **Figure captions**

419 **Figure 1 - Trophic groups as a function of trophic level.** The nodes of this network represent
420 the trophic groups, with their size proportional to the number of species in the group. Groups are
421 positioned according to the average trophic level of the species they contain, from the bottom of
422 the metaweb (basal preys) to the top (top predators), and coloured according to in-degree (i.e.
423 predatory generalism). Silhouettes represent the characteristic species found in each trophic
424 group and reflect the taxonomic coherence of these groups. The width and intensity of the links
425 between two given groups represent the number of realized links between them (i.e. the number
426 of species pairs belonging to both groups and that co-occur at least once in Europe.

427 **Figure 2 - Trait niche of trophic groups.** This bi-plot characterizes the mean position of each
428 trophic group along the two-dimensional space represented by the species biological traits. Traits
429 are coloured according to their category (activity time, secondary consumer characteristics,
430 primary consumer characteristics, aquatic or terrestrial nesting habitat type). The length and
431 orientation of each arrow reflects the relative importance of a given trait in explaining the
432 variation between the groups. Groups are positioned in this multivariate space and represented
433 by the same silhouettes used in Fig. 1.

434 **Figure 3 - Species richness and trophic diversity across Europe.** Left panel: Maps
435 representing species richness (top left) and trophic group richness (bottom left) across Europe.
436 Right panel: Interaction plot between annual mean temperature and species richness in driving
437 trophic diversity. The scatterplot of trophic diversity as a function of species richness is overlaid
438 with the interaction plot between the annual average temperature and species richness effects on
439 trophic diversity, based on predictions from the linear model. The three categories of annual
440 average temperature represent the 1st, 2nd (median) and 3rd quartiles. The lines and the data
441 points in the scatterplot are coloured accordingly to these three categories.

442 **Figure 4 - Regional metawebs of European tetrapods.** The size of the nodes represents the
443 number of species representing a given trophic group in the ecoregion; the width and intensity of
444 the links represent the number of interactions that exist between two given groups in this
445 ecoregion. Nodes are coloured according to the median specialization of the species to the
446 ecoregion within each trophic group: the darker the node, the higher the specialization of the
447 trophic group to the ecoregion.

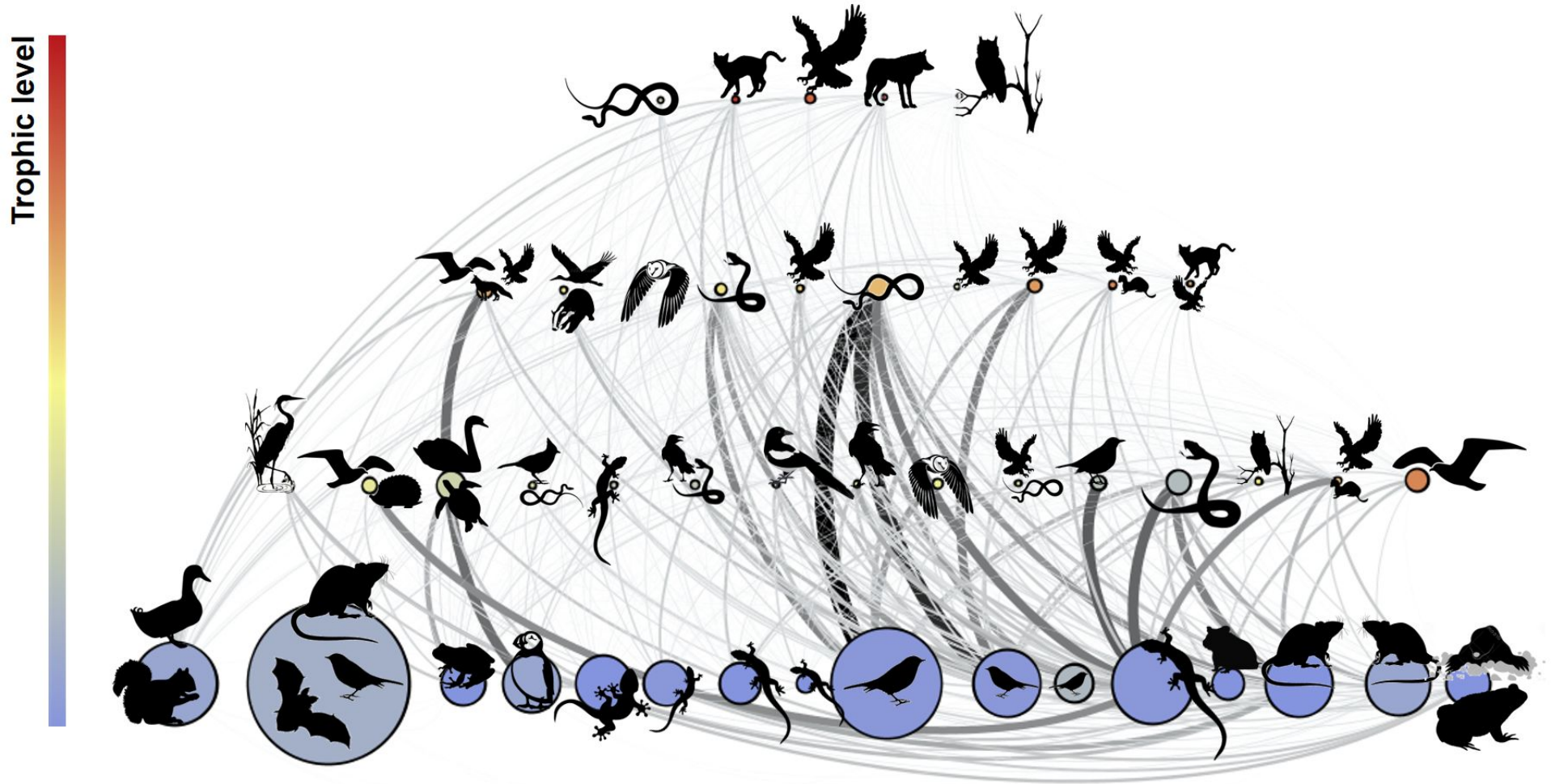


Figure 1

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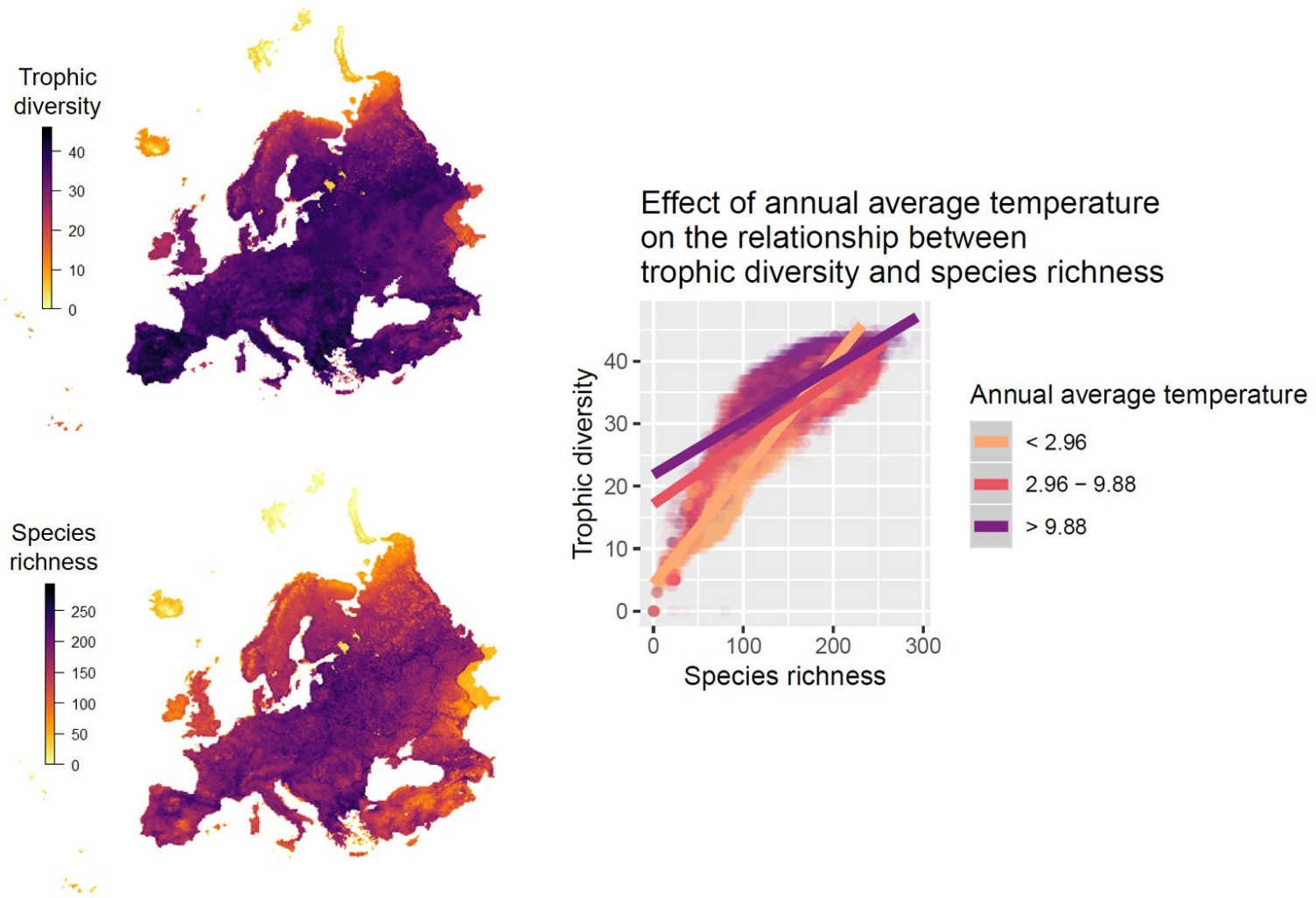


Figure 3

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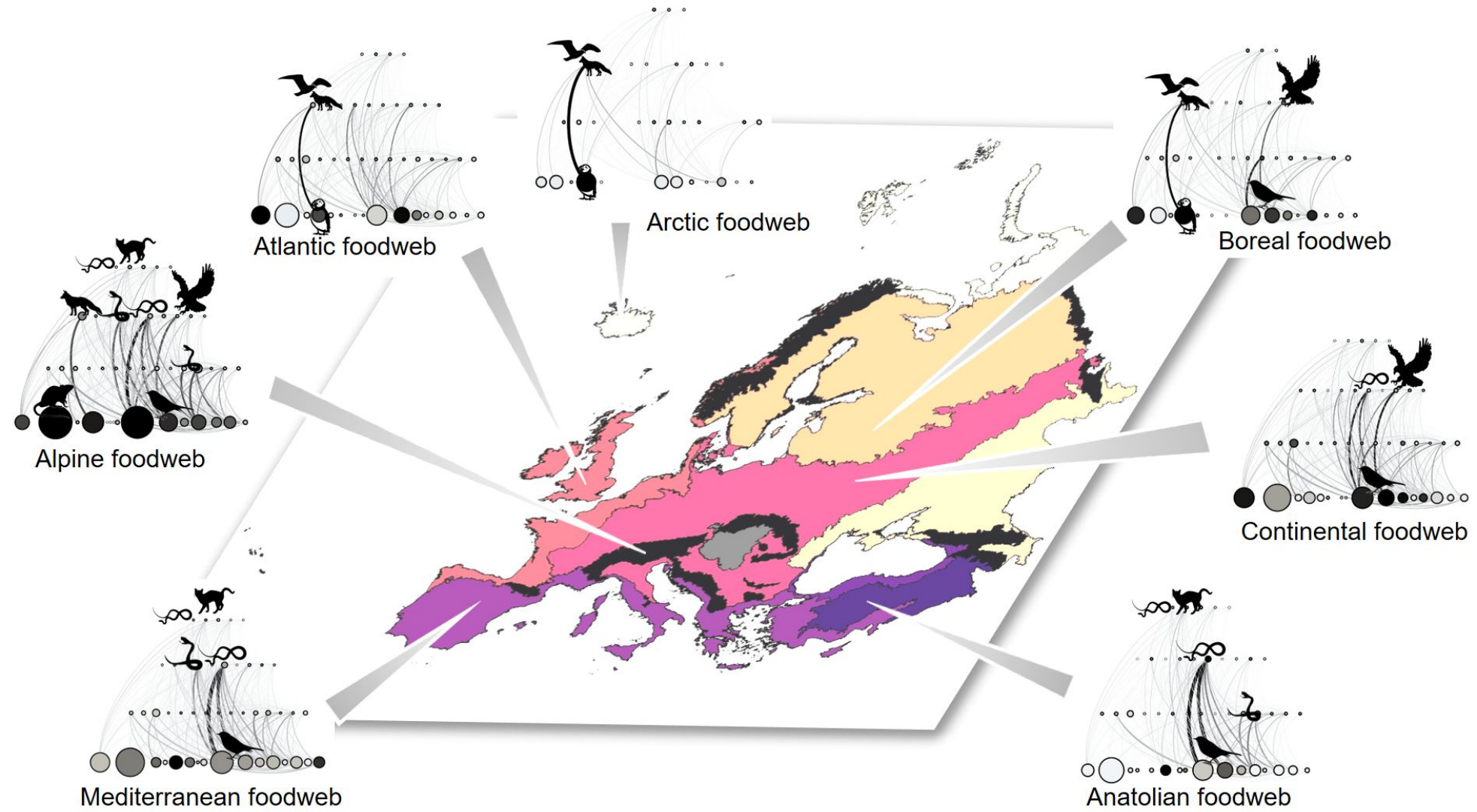


Figure 4

Data availability statement

We used the data on species trophic interactions, species distributions and biological traits built by LM, GFF, WT and AM, who have written a data paper (Maiorano et al., in revision) to make the data publicly available in the coming months. Processed versions of the data (e.g. outputs of the stochastic block model) will be made available as supplementary material after acceptance.

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45 Biosketch

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47 LOC recently started a PhD in Ecology and Evolutionary Biology aiming to understand the
48 influence of interaction networks on predictions of biodiversity patterns in the context of global
49 change, in order to better inform conservation planning. WT, LJP and LOC conceptualized and
50 wrote the paper. LM, GFF, WT and AM built the trophic and trait data. LOC carried out the analyses
51 with the help of JB, LJP, WT and MO. CMA and MO gave additional perspectives to the paper. All
52 authors contributed significantly to the manuscript.
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Appendix 1 – List of references used to build the metaweb of trophic interactions between European tetrapod species.

The trophic links for mammals were compiled from the Handbook of the Mammals of the World composed of nine volumes (Wilson and Mittermeier 2009-2019). Furthermore, we considered multiple books on the mammalian fauna of the single countries and all volumes of Mammalian Species (published by the American Society of Mammalogists) available for species included in the database. The trophic links for breeding birds were compiled from the Handbook of the Birds of Europe, the Middle East and North Africa (9 volumes; Cramp et al. 1977-1994), the Handbook of the Birds of the World (16 volumes; del Hoyo et al 1992-2013), and the Handbook of the Birds of the World Alive website (del Hoyo et al. 2014). The trophic links for amphibians and reptiles were compiled from the Handbuch der Reptilien und Amphibien Europas (Arntzen et al. 1999; Bohme 1984; Fritz 2001; Grossenbacher and Thiesmeier 2003; Thiesmeier et al. 2004) plus multiple books and papers on the herpetofauna of the single countries. Trophic links for each species were compiled by the authors using a standardized data input protocol in MS Excel. For each species, we included in the database all trophic links reported in the publications using the highest possible taxonomic detail. Most of the time the information was available at the level of family or higher; for instance, the food habits of *Falco tinnunculus* (the common kestrel) are described as: “in Europe up to 90% voles, with some mice and shrews; open area passerines normally less important [...]; also lizards and insects [...]”, therefore we included as potential prey species all mammals of the families Arvicolinae, Muridae, and Soricidae, all birds of the family Alaudidae, and all reptiles of the family Lacertidae.

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SUPPLEMENTARY MATERIAL

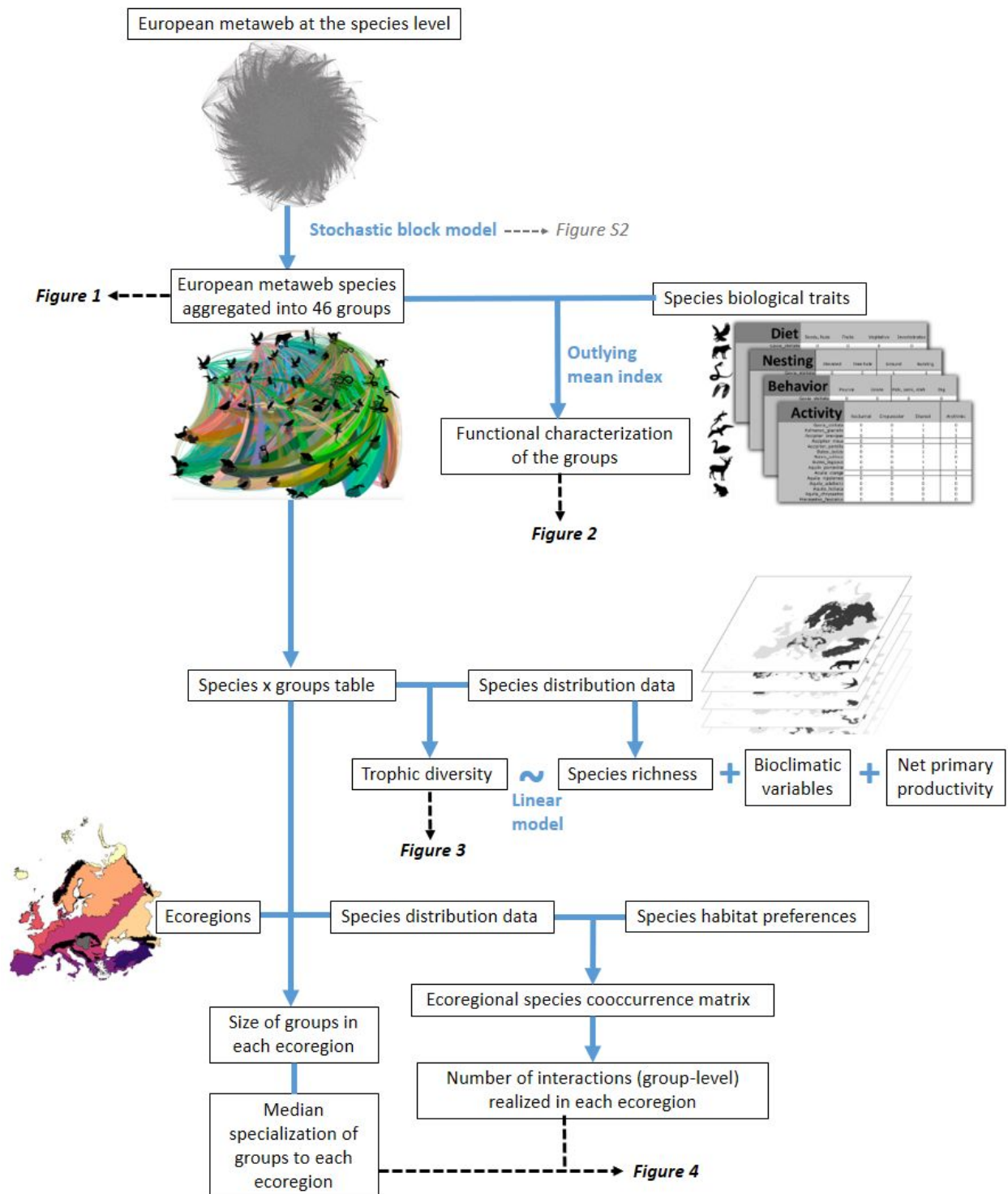
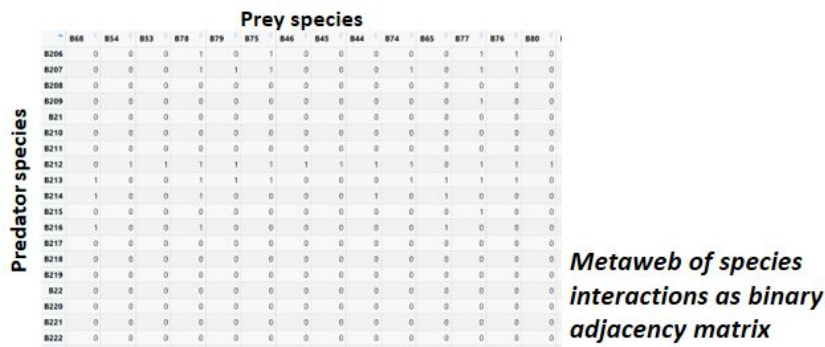


Figure S1 - Overview of the workflow, depicting how the different pieces of data (e.g. metaweb of trophic interactions, species biological traits, species distributions) come together to build and characterize the trophic groups, and then using them to analyse the structure and function of the metaweb across Europe.



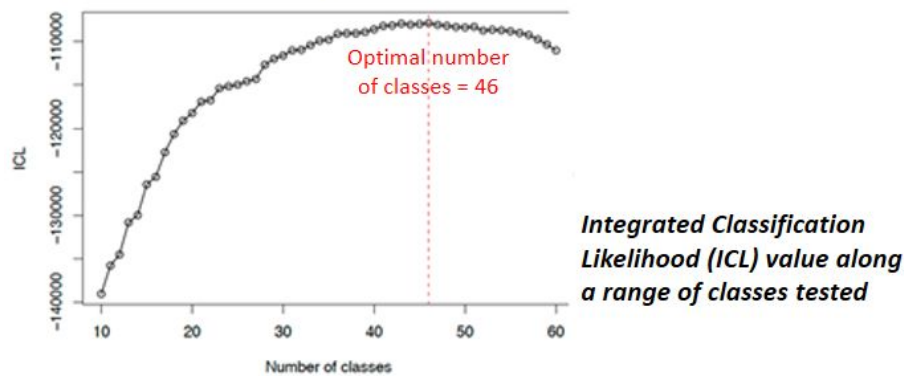
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1. For a given number of classes, the stochastic block model partitions the adjacency matrix into « blocks » of homogenous interaction probability



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2. To select the optimal number of classes, the network is partitioned along a range of number of classes. The optimal number of classes is given by the highest ICL value.



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Figure S2 - Optimal partitioning of the metaweb by the stochastic block model. Given an adjacency matrix representing interactions between predator species (rows) and their prey (columns), the stochastic block model reorganized the adjacency matrix to group species into Q classes, such that each class has a given probability of interacting with all other classes. Upper panel: adjacency matrix of trophic interactions between species. Middle panel: reorganized adjacency matrix of the metaweb, where species (in rows and columns) are grouped within the 46 trophic groups (classes). Lower panel: Integrated classification likelihood information criterion as a function of the number of groups (or classes) that the stochastic block model built from the metaweb of potential trophic interactions between tetrapod species, exploring a range of partitionings of the metaweb along a range of 10 to 60 groups (or classes). The optimum partitioning of the metaweb maximises the Integrated Classification Likelihood and is highlighted with a vertical red line on the graph.

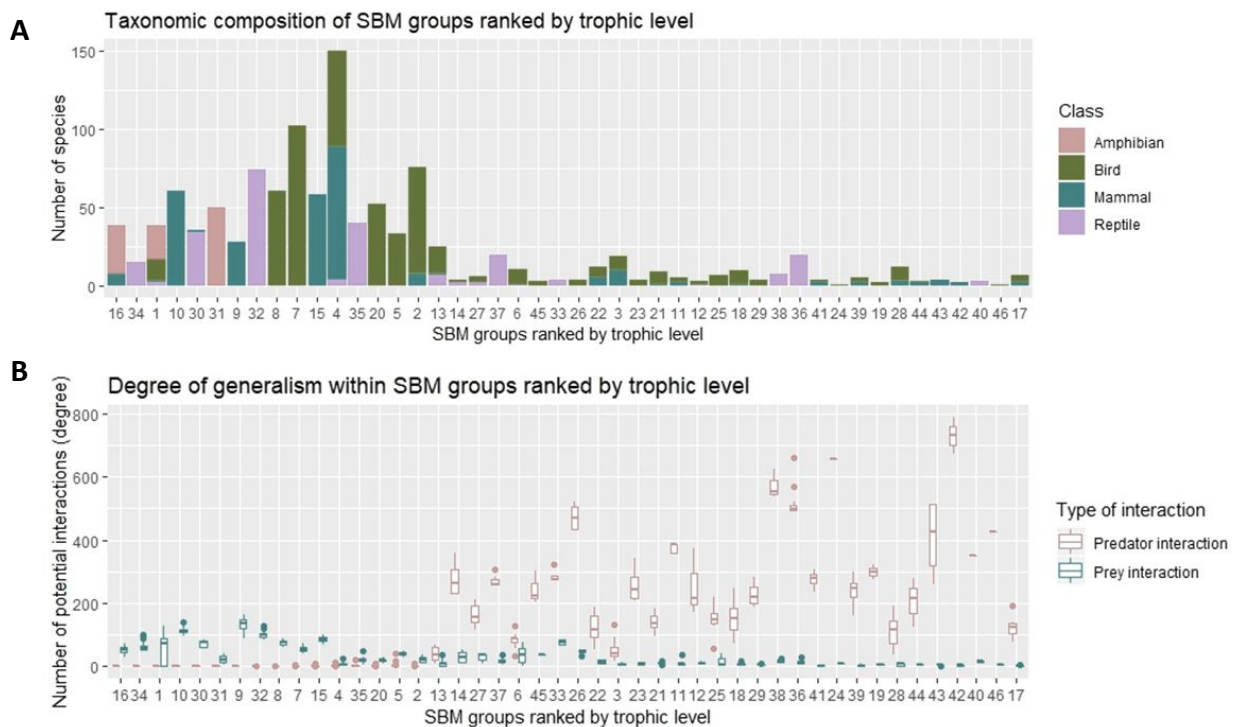


Figure S3 - Taxonomy and generalism of species within the trophic groups.

A. Trophic group composition in terms of species taxonomy. Colours represent the class of species. Trophic groups are on the x-axis, ranked from left (basal prey groups) to right (top predator groups) according to the average trophic level of species in the groups.

B. Boxplots representing the in-degree (i.e. number of predator interactions, in red) and out-degree (i.e. number of prey interactions, in blue) of species within the groups. Trophic groups are on the x axis, ranked from left (basal prey groups) to right (top predator groups) according to the average trophic level of species in the groups.

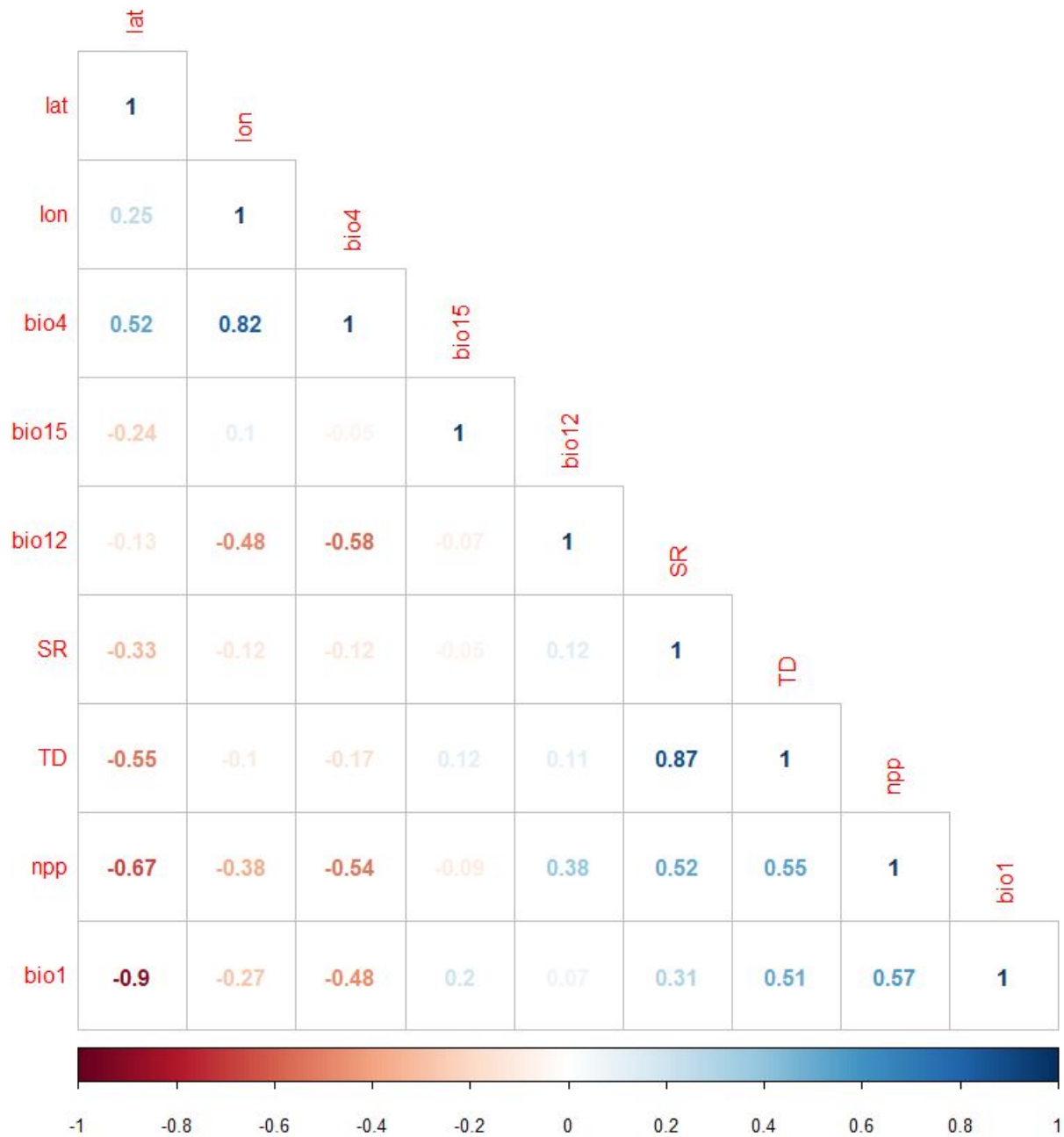
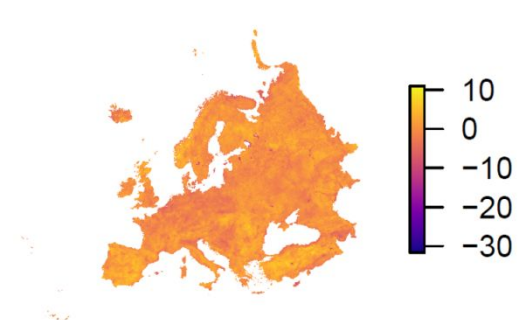
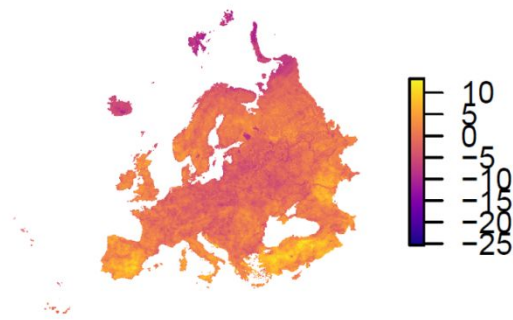


Figure S4 - Pairwise correlations between environmental variables. Lat: latitude, Lon: longitude, Bio1: annual mean temperature, Bio4: temperature seasonality (standard deviation *100), Bio12: annual precipitation, Bio15: Precipitation Seasonality (Coefficient of Variation), npp: net primary productivity, TD: trophic diversity, SR: species richness.

Residuals of model including species richness only

Residuals of full model



$\text{lm}(\text{TD} \sim \text{SR01}, \text{data} = \text{scaled_EU_all})$

$\text{lm}(\text{TD} \sim \text{SR01} * \text{bio1} * \text{bio4} * \text{bio4_2} * \text{npp}, \text{data} = \text{scaled_EU_all})$

Figure S5 - Maps of the residuals of the linear models across the study area. Left panel: residuals of the model including species richness only as explanatory variable (AIC = 583,964.8). Right panel: residuals of the model including species richness and environmental variables (annual mean temperature (bio1), a quadratic relationship with temperature seasonality (bio4), net primary productivity (npp)) (AIC = 491,404).

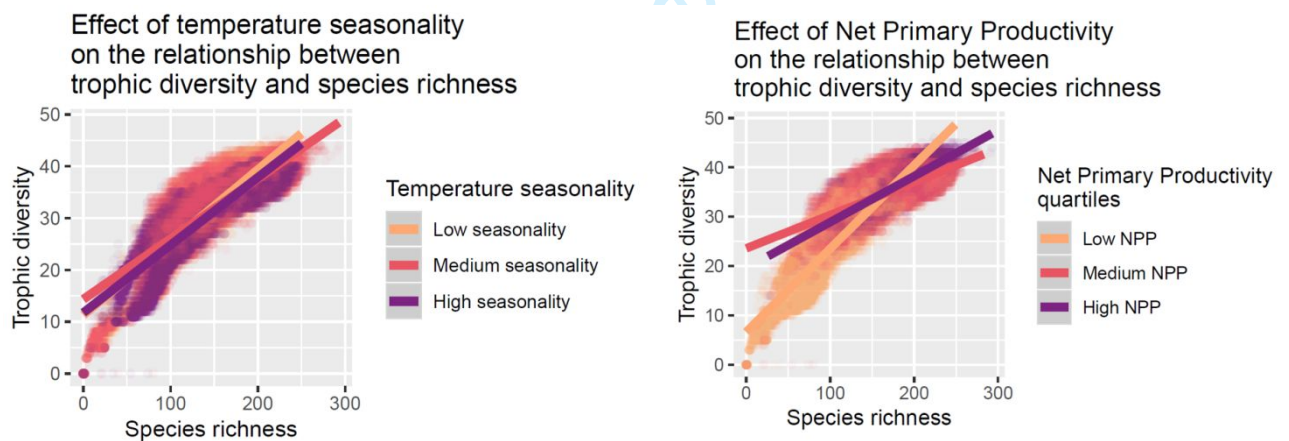


Figure S6 - Interaction plot between environmental variables (left: temperature seasonality; right: net primary productivity) and species richness in driving trophic diversity. These figures show a scatterplot of trophic diversity as a function of species richness, overlaid with the interaction plot between each environmental variable and species richness, using predictions from the linear model. The three categories represent the 1st, 2nd (median) and 3rd quartiles for each environmental variable. The lines representing the predictions and the data points in the scatterplot are coloured accordingly to these three categories.

	Estimate	Std. Error	t-value	Pr(> t)
Intercept	-26.463	1.142	-23.166	<2 e-16
SR01	196.814	4.917	40.024	<2 e-16
bio1	41.819	1.702	24.573	<2 e-16
bio4	151.157	9.2	16.429	<2 e-16
(bio4) ²	-302.267	21.1	14.325	<2 e-16
npp	32.261	8.471	3.808	0.0001
SR:bio1	-212.111	7.412	-28.616	<2 e-16
SR:bio4	-979.823	31.933	-30.684	<2 e-16
SR:npp	-314.654	18.999	-16.562	<2 e-16

Table S1. Output of the linear model testing the effects of (standardized) environmental variables (Bio1, Bio4, NPP), species richness (SR) and their interactions on trophic diversity (the number of trophic groups in any given pixel). Resolution used = 10 x 10 km pixels.