

1 TITLE

2 Spatial analyses of multi-trophic terrestrial vertebrate assemblages in Europe

3

4 RUNNING TITLE

5 Distribution of multi-trophic food webs

6

7 ABSTRACT

8 **Aim** While much has been said on the spatial distribution of taxonomic and phylogenetic
9 diversity of vertebrates, how this diversity interacts in food webs and how these interactions
10 change across space is largely unknown. Here, we analyzed the spatial distribution of tetrapod
11 food webs and asked whether the variation in local food web structure is driven by random
12 processes or by natural and anthropogenic factors.

13 **Location** Europe.

14 **Time period** Present.

15 **Major taxa studied** Tetrapods.

16 **Methods** We combined an expert-based food web (1140 species and 70,601 links) of all
17 European tetrapods with their respective spatial distributions. We mapped seventeen different
18 food web metrics representing complexity, chain length, vertical diversity and diet strategy
19 across Europe and tested whether their distribution reflects the spatial structure of species
20 richness using a null model of food web structure. Then, to avoid multi-collinearity issues, we
21 defined composite descriptors of food web structure that we then related to a set of
22 environmental layers summarizing both natural and anthropogenic influences, and tested their
23 relative importance in explaining the spatial distribution of European terrestrial vertebrate food
24 webs.

25 **Results** From the seventeen metrics, seven showed a non-random spatial distribution across

26 Europe and could be summarized along two major axes of variation in food web structure. The
27 first was related to species richness, mean trophic level and proportion of intermediate species,
28 while the second was related to connectance and proximity of species within the web. Both
29 descriptors varied with latitudinal gradients. Best descriptors of food web structure were mean
30 annual temperature and seasonality (positively correlated with the first axis), and human
31 footprint (positively correlated with the second one).

32 **Main conclusions** We provide the first comprehensive spatial description of vertebrate food
33 web structure across Europe, and demonstrate the importance of climate and anthropogenic
34 pressure in shaping the spatial structure of European tetrapod food webs.

35

36 **KEY WORDS:** biodiversity, environmental gradients, food web comparison, metaweb, network
37 properties, null model, tetrapod communities

38 **INTRODUCTION**

39 Documenting large-scale biodiversity distribution and understanding what drives variation
40 between or within different regions of the world has long fascinated naturalists (Wallace, 1876).
41 The recent and ever-increasing rise of large-scale distribution databases (e.g. IUCN, BirdLife,
42 Map Of Life) has led to new comprehensive analyses of biodiversity distribution. Thanks to
43 available data on species traits and phylogenetic relatedness, global and regional distributions
44 of species, traits and phylogenetic diversity are now well documented for terrestrial vertebrates
45 (Jetz & Fine, 2012; Jetz *et al.*, 2012; Mazel *et al.*, 2014, 2017).

46 Such measurements of biodiversity (taxonomic, functional and phylogenetic diversity) focus
47 on a group of species co-occurring in a certain area or region, which are subsequently compared
48 with measurements of other areas to identify localities with higher or lower biodiversity (e.g.
49 hotspots *vs.* coldspots, Mazel *et al.* 2014). However, species assemblages are not just the mere
50 sum of species co-occurring in an area, they share a myriad of biotic interactions (e.g. predation,
51 competition, facilitation, etc.) that originate a variety of ecological networks through space.
52 While past biogeographic studies have investigated how species or trait diversity vary in space
53 and the underlying role of environment (e.g. Davies *et al.*, 2011; Safi *et al.*, 2011; Mazel *et al.*,
54 2017), we know little about the spatial distribution of ecological networks (Pellissier *et al.*
55 2017).

56 Food webs are representations of communities' trophic interactions, where each node in the
57 network represents a species and each edge is a directional feeding interaction from a prey to a
58 predator. Food web ecology has focused on the trophic relationships between species within
59 discrete communities with the goal of inferring the underlying processes acting upon them, such
60 as the relation between species diversity and food web structure, community assembly
61 processes, and even robustness of those communities to species extinctions (Montoya *et al.*,
62 2006). However, since the pioneering work of Kitching (2000) on latitudinal gradients of

63 aquatic food-web structure, food web ecology has shifted from finding food web structural
64 generalities across isolated communities to searching for large-scale spatial distribution of
65 ecological networks, such as latitudinal gradients, and relations with climate and resource
66 availability (Post, 2002; Kortsch *et al.*, 2015; Wood *et al.*, 2015; Montoya & Galiana, 2017;
67 Pellissier *et al.*, 2017; Poisot *et al.*, 2017; Roslin *et al.*, 2017).

68 Large-scale spatial distribution of food web structure may be driven by multiple factors. First,
69 food web structure follows both species richness and compositional gradients (Riede *et al.*,
70 2010; Baiser *et al.*, 2012) and any process acting upon these features of biodiversity, such
71 environmental sorting of species, will cause food webs to be spatially structured (Pellissier *et*
72 *al.*, 2017). Second, food web topology may reflect community adaptations to environmental
73 stability. The latitude-niche breadth hypothesis for instance postulates that species have more
74 specialized diets in the tropics and become more generalist towards the poles, as higher
75 environmental stability and amount of energy in the tropics allow for greater species packing
76 (MacArthur, 1955; Schleuning *et al.*, 2012). Yet, this hypothesis does not seem to be verified
77 across different systems (Cirtwill *et al.*, 2015) and lacks testing across large spatial scales.
78 Third, resource availability in conjunction with disturbances and environmental variability may
79 also affect food web topology. Low resource availability for primary consumers limits species
80 richness and food chain length, while disturbances and ecosystem size drive food chain length
81 at intermediate levels of resource availability (Kaunzinger & Morin, 1998; Post, 2002). Again,
82 such observations are not ubiquitous (Zanden & Fetzer, 2007), and this last hypothesis has yet
83 to be tested across large environmental gradients and for complex (i.e. speciose) food webs.

84 Here, motivated by these hypotheses we built the first comprehensive food web of European
85 terrestrial vertebrates. For this, we used a combination of expert knowledge and literature, and
86 mapped the food web structure of all vertebrate assemblages naturally occurring in Europe,
87 west Russia and Turkey, using a uniform spatial grid at 10 km resolution. Since the above-

88 mentioned hypotheses focus on different facets of food web topology we analyzed a large set
89 of food web descriptors such as complexity metrics (species richness, connectance, number of
90 trophic interactions), vertical diversity metrics (proportion of basal, intermediate and top
91 predator species), feeding strategy metrics (generality, vulnerability and omnivory), and trophic
92 level metrics. We compare local observations of food web metrics to a null model in order to
93 reveal significant associations with environmental variables.

94 Most network metrics cannot be dissociated from each other because they covary with either
95 the number of species or connectance (Vermaat *et al.*, 2009; Riede *et al.*, 2010; Baiser *et al.*,
96 2012; Poisot & Gravel, 2014). Hence, we decomposed the food web structure into two
97 composite descriptors (Pellissier *et al.*, 2017) and investigated how the environment, landscape,
98 and anthropogenic pressure influenced their spatial distribution.

99 We expected annual temperature and precipitation to be good predictors of food web spatial
100 structure because they are major drivers of species sorting and community assembly over large
101 spatial scales (Currie, 1991; Vázquez & Stevens, 2004; Riede *et al.*, 2010; Ledger *et al.*, 2012).
102 Likewise, ighly productive sites should provide more resources for consumers, therefore
103 supporting higher trophic levels (Wright, 1983; Post, 2002). Thus, we expected higher trophic
104 levels in areas with high productivity. We also anticipated habitat fragmentation and human
105 disturbance to shape European food webs. High levels of fragmentation may reduce the strength
106 of interactions between species or even prevent species from interacting, ultimately leading to
107 networks with lower link density (Hagen *et al.*, 2012).

108

109 **MATERIALS AND METHODS**

110 **Study area and species distributions**

111 The study area included Europe (excluding Macaronesia region and Iceland), and western
112 regions of Turkey and Russia (hereafter referred to as ‘Europe’). We extracted species ranges

113 for terrestrial vertebrates (tetrapods) naturally occurring within the study area from Maiorano
114 *et al.*, (2013). In total, our analyses focused on 510 bird, 288 mammal, 239 reptile and 103
115 amphibian species (see Appendix S1 Table S1.1 in Supporting Information for full species list).
116 Species range data followed a regular grid of 300 m resolution (WGS84), where cells took
117 values of zero for unsuitable habitat, one for secondary habitat and two for primary habitat
118 (Maiorano *et al.*, 2013). We treated secondary and primary habitat equally as “suitable habitat”.
119 All species range maps were up-scaled to a 10x10 km equal-size area grid (ETRS89; total of
120 78,873 cells). We considered species potentially present in a 10x10 km cell (hereafter referred
121 as local assemblage) when they had least one 300 m suitable habitat cell within it. In
122 supplementary material S3 we showed that the proportion of suitable habitat needed for a
123 species to be present in each cell did not affected the spatial distribution of species richness nor
124 connectance, hence not affected the spatial distribution of local food web structure (see below).

125

126 **European tetrapod metaweb and local food web structure**

127 A trophic metaweb compiles all predator-prey interactions between species of a given regional
128 species pool (Pascual & Dunne, 2006). Here, we designed the most complete metaweb of
129 European terrestrial vertebrates from expert knowledge, published information and field guides
130 (see supplementary material for reference list). As in previous studies (e.g. Lurgi *et al.*, 2012),
131 all vertebrates species whose diet did not include another species of the metaweb (such as
132 herbivores, insectivores, piscivores and detritivores) were defined as basal species. Then, we
133 searched for trophic interactions between species that fed upon other vertebrates (and
134 omnivores) from an exhaustive literature review. We defined a trophic interaction as predation
135 on any life stage of a species (e.g. egg and larval when applicable, juvenile or adult). Trophic
136 interactions between a predator and a prey were identified from published accounts of their
137 observation, morphological similarities between potential prey and literature-referenced prey

138 and, in the absence of this information, the diet of the predator's sister species. Twelve general
139 diet categories were added to the metaweb, which included detritus, coprophagous, mushrooms,
140 mosses and lichens, algae, fruits, grains, other plant parts, invertebrates, fish, domestic animals
141 and carrion.

142 The metaweb comprised 70,601 trophic interactions distributed across 1140 terrestrial
143 vertebrate species (60% of basal species, from which X % were herbivores and X % of non-
144 herbivore basal species, 33% of intermediate species and <1% of top predator species) and a
145 connectance of 0.05. On average, species had 62 interactions (including prey and predator
146 interactions) and were 2 interactions away from each other.

147 We defined local food webs by intersecting the metaweb with local community composition
148 (Gravel et al. 2018). In the few cases where a given species was present in a cell, but had no
149 available prey, or did not share a common habitat type with any of its prey, the species was
150 considered absent in that particular location (i.e. assuming a false positive in the distribution
151 data; Gravel *et al.*, 2011). We assumed that basal resources are widely distributed across the
152 landscape and therefore that basal species always have a resource.

153 For each local food web, we calculated seventeen food web properties pertaining to four
154 groups: complexity, strategy, vertical diversity and trophic level. Complexity metrics included
155 species richness, connectance, clustering coefficient, characteristic path length and link density
156 (average distance between species and average number of interactions per species,
157 respectively). Strategy metrics refer to dietary niche properties of species, and included
158 generality (mean number of prey) and vulnerability (mean number of predators), their
159 respective standard deviations, proportion of omnivore species and average trophic similarity
160 between species. Vertical diversity metrics quantify the proportion of species along three major
161 trophic levels, basal, intermediate and top level. Note that we defined basal species as non-
162 autotroph species without terrestrial vertebrate prey. Trophic level metrics refer to vertical

163 trophic position of species within a food web, and included the mean trophic level and the
164 maximum trophic level. See Table 1 for the list of metrics and their definitions. Food web
165 metrics were calculated using the ‘igraph’ and ‘cheddar’ R packages (Csardi & Nepusz, 2006;
166 Hudson *et al.*, 2013) in R v. 3.4.1 (R REF).

167

168 **Climatic, energetic and habitat variables**

169 We extracted four climatic variables from the WorldClim database (Hijmans *et al.*, 2005) at
170 30° resolution: annual mean temperature, temperature seasonality (standard deviation of
171 monthly mean temperature), total annual precipitation and coefficient of variation of
172 precipitation. We chose these variables since they correlate with vertebrates ranges (Boucher-
173 Lalonde *et al.*, 2014). We approximated the amount of resources available to the primary
174 consumers in each cell with estimates of net primary productivity (grams of carbon per year at
175 0.25 decimal degrees spatial resolution; Imhoff *et al.*, 2004). We also represented the
176 anthropogenic influence on natural landscapes using the human footprint index from the Last
177 of the Wild database v2 (1 km spatial resolution; WCS & CIESIN, 2005). We resampled all
178 climatic variables, primary productivity and human footprint data by averaging at each 10x10
179 km cell. We also measured habitat diversity and heterogeneity using, respectively, the Shannon-
180 Weiner and evenness indices applied to the GlobCover V2.2 habitat classification at 300 m cell
181 resolution. See Appendix S2 in Supporting Information for more information about the spatial
182 distribution of the climatic, energetic and habitat variables.

183

184 **Statistical analyses**

185 Our analyses consisted of three sequential steps. 1) We checked if the spatial distribution of
186 each local metric is different from random using a null model, and selected the metrics that
187 differed from null expectations for subsequent analyses. 2) We reduced the complexity of the

188 retained metrics applying a principal components analysis (PCA) and selecting the first two
189 axes of variation. 3) We related these two axes of variation to climate, resource availability,
190 habitat diversity and human disturbance using generalized additive models (GAMs).

191

192 *Is the spatial distribution of food web properties random?*

193 Food web structure may vary with species richness, independently of any other constraints
194 acting upon it (e.g. environment). We thus built a null model to test whether European local
195 food webs and their associated properties could result from a draw from the European species
196 pool, irrespective of their interactions. The null hypothesis is that species are randomly
197 distributed in space, independently of the local environment and of their position in the
198 metaweb. The null model consisted of randomly drawing species from the metaweb for each
199 cell and then extracting the correspondent local food webs. We applied three constraints to the
200 null model, 1) species richness is the same as observed, 2) with respect of the proportion of
201 squamates, birds, mammals and amphibians, 3) non-basal species needed at least one vertebrate
202 prey (excluding diet categories) to be included in the food web (Gravel *et al.*, 2011). We
203 randomly drew and kept food webs that met all three conditions, until we had 999 food webs
204 for each value of each cell (from 10 to 305 species). We then re-calculated the 17 food web
205 metrics to obtain a distribution of metrics under the null hypothesis (Table 1). For each cell, we
206 compared the observed food web metrics to the corresponding null distribution and computed
207 the associated *p-value*. We adjusted *p-values* for multiple comparisons using a false discovery
208 rate method based on Benjamini & Hochberg, (1995), present in the function *p.adjust* in the
209 ‘stats’ R package. We retained food web metrics that had 90% of rejection rate, i.e. 90% of all
210 local food web metrics were significantly different from ones of random assemblages.
211 Considering that we computed one test per cell (total of 78,873 cells), a food web metric should
212 be significantly different from random in approximately 71,000 cells in order to be kept in our

213 analysis.

214

215 *How to reduce the dimensionality in local food web properties?*

216 Many food web metrics are correlated (Vermaat *et al.*, 2009) either because of their
217 mathematical formulation or because of combinatory constraints (Poisot & Gravel, 2014). We
218 applied a PCA on the eight retained variables over the 78,873 cells of Europe (Table 1) to
219 analyze the most insightful axes of variations between these metrics. This allowed not only
220 understanding how food web metrics co-vary with each other, but also summarizing food web
221 structure of European assemblages (as a whole) into a set of meaningful axes. We emphasize
222 that the correlation structure among metrics we analyzed is not only driven by the fundamental
223 constraints linking metrics referred above, but also driven by the effect of spatial variation in
224 food web composition. From the PCA, we kept only the axes that explained each at least 20%
225 of the total variance, hereafter referred as food web structural composite descriptors. This
226 analysis was performed in R using the ‘ade4’ package (Dray & Dufour, 2007).

227

228 *How to statistically relate food web structural descriptors to environmental predictors?*

229 We related positions on the PCA axes to spatial drivers (climate, energetic and habitat
230 variables) using GAMs. GAMs are more flexible than generalized linear models, which are
231 more appropriate given we had no *a priori* expectations regarding the shape of the relationships
232 between response and predictor variables. To avoid fitting overly complex relationships, we
233 constrained the GAMs with a maximum smoothing degree of 3 (i.e. polynomial of degree 2,
234 maximum). All models were fitted using the function *gam* present in the ‘mgcv’ R package
235 (Wood, 2017).

236 Note that both the environmental variables and food web topological metrics inevitably show
237 some level of spatial autocorrelation. To account for spatial dependency unexplained by the

238 spatial drivers, we built an autocovariate variable for each of the composite descriptors to
239 estimate how much the response variable for any site reflects the values of the neighboring sites
240 (Dorman et al. 2007; function *autocov_dist* in ‘spdep’ R package). However, since this
241 autocovariate was unconditional to environmental variation (i.e. the response variable could
242 show a spatial autocorrelation because the environment is itself autocorrelated), we modelled
243 each autocovariate variable (for each structural composite descriptor) to the set of
244 environmental variables using a bootstrap aggregating model (random forest function in
245 ‘randomForest’ R package; Liaw *et al.*, 2002). We then extracted the residuals of the model and
246 used them as spatial variables independent of the spatial predictors in the GAMs. Hereafter,
247 these variables will be referred as spatial residuals variables.

248 We used the permutation accuracy importance method (Strobl *et al.*, 2007, 2009) to estimate
249 the importance of each predictor variable on the spatial distribution of local food web metrics.
250 The predictor in test is randomized so that its original association to the response variable is
251 broken. Then, the randomized variable (through means of permutations) and the remaining
252 unchanged predictors are used to predict the response. A variable importance score is then
253 measured as the Pearson correlation coefficient (ρ) between the original prediction and the
254 prediction after permutation of the selected predictor (Strobl *et al.*, 2009). The lower the
255 correlation, the more important the variable is. This whole procedure was repeated 1000 times.
256 To facilitate the interpretation of results, we reported the average $1 - \rho$. Values close to 1
257 reflected high importance, values close to 0, no importance.

258 In supplementary material S6 we show that using individual food web metrics or the
259 composite descriptors from the PCA yields equivalent results and relationships with the
260 predictors. Hence, we opted to PCA axes as they summarize the main dimensions of food web
261 structure.

262

263 **RESULTS**

264 **Local food web structure**

265 Most of the seventeen food web structural metrics showed a strong spatial structure (Figure 1
266 for a selection of six metrics; see Appendix S3 Fig. S3.2 for all other metrics, and Table 1 for
267 descriptive statistics). Assemblages in northern latitudes (United Kingdom, Denmark and
268 Scandinavian Peninsula) and in mountain ranges (such as Alps and Carpathians) had fewer
269 species, with shorter food chains and higher proportion of basal species than in the rest of
270 Europe. Species in these locations had larger diet breadths (i.e. higher generality) on average.
271 Food webs in central and eastern Europe were more speciose and with longer food chains.
272 Within these food webs, species were more evenly distributed between basal and intermediate
273 species, with top predator species always representing less than 5 % of the community. In
274 southern Europe, along the Mediterranean basin, food webs were the most species rich and had
275 the highest linkage densities and clustering coefficients. In this region, food chains lengths were
276 as high as for continental food webs, while connectance in the Anatolian region (Turkey) and
277 southeast of Spain, was as high as in near arctic assemblages. In other words, assemblages
278 across the Mediterranean basin were the most species rich and highly interacting.

279

280 **Deviation of local food web structure from random assembly**

281 Deviations of local food webs from the null expectation varied between the different metrics
282 and across the species richness gradient (Table 1; see Appendix 4 Fig. S4.3 in Supporting
283 Information). We observed that only seven food web metrics differed at least 90% of the times
284 from what could be expected from random draws from the metaweb (link density, connectance,
285 proportion of intermediate and omnivore species, mean trophic level, characteristic path length
286 and cluster coefficient). However, at low levels of species richness, most of these metrics do
287 not differ from a random assembly (see Fig. S4.3). The remainder food web properties

288 consistently fell within the random intervals irrespective of species richness (e.g. vulnerability,
289 generality, mean and maximum trophic level; Table 1). In other words, the spatial distribution
290 of these metrics could be explained purely by their correlation with the distribution of species
291 richness and its spatial drivers.

292

293 **Composite descriptors of the local realized food webs**

294 Two main axes of variation, explaining approximately 76.6% of the total variance,
295 summarized the co-variation of six food web properties (link density, connectance, proportion
296 of intermediate and omnivore species and characteristic path length; Table 2; Fig. 2). The first
297 axis, hereafter called the *richness* composite descriptor, explained 49.2% of structural variation
298 and was negatively related with species richness, link density (average number of interactions),
299 proportion of intermediate and omnivore species and mean trophic level (Table 2; Fig. 2). This
300 result indicates that food webs with more species have more links per species, a higher
301 proportion of intermediate species (i.e. proportion of species having both prey and predators in
302 local food webs) and more species at higher trophic levels.

303 The second descriptor, hereafter named the *connectance* composite descriptor, explained
304 27.5% of the total variance and was mainly related to food web complexity, through
305 connectance, clustering coefficient and characteristic path length (Table 2; Fig. 2). Along this
306 descriptor, connectance and clustering coefficient were both negatively correlated with
307 characteristic path length, suggesting that food webs with lower connectance were less clustered
308 and had proportionally longer paths between species.

309

310 **Environment drivers of local food web descriptors**

311 Environmental drivers explained a significant proportion of the variance of the two composite
312 descriptors (74.3% of *richness*, and 42.5% for *connectance*; Table 3). The *richness* composite

313 descriptor had a strong, linear and negative relationship with temperature variables (mean
314 annual temperature and temperature seasonality; Fig. 3a), with sites with high temperatures and
315 seasonality supporting richer assemblages, with more intermediate species, higher link densities
316 and trophic levels. Net primary productivity, had a weaker importance relatively to temperature
317 variables, but had a negative correlation with the *richness* composite descriptor. We observed
318 an increase in species richness and link density up to intermediate productivity from lower to
319 intermediate productive areas; however, the contribution of net primary productivity to food
320 web structure was close to zero in intermediate to high productivity areas (Fig. 3a). Human
321 footprint had the smallest effect on the *richness* composite descriptor, which seemed to saturate
322 above intermediate levels of human footprint.

323 Conversely, the variation in the *connectance* composite descriptor was most affected by mean
324 annual temperature and human footprint (Table 3). Food webs had higher connectance and more
325 closely interacting species at higher annual average temperatures, and the showing a clear
326 positive effect of human foot print up to intermediate values, after which the effect stabilizes
327 (Fig. 3b). Finally, total annual precipitation correlated positively with the *connectance*
328 composite descriptor at low to intermediate precipitation, but negatively at larger precipitation
329 levels (Fig. 3b).

330

331 Spatial residuals variables were only relevant for the *connectance* composite descriptor,
332 indicating that other spatial variables not considered here can be affecting the spatial
333 distribution of food web structure.

334

335 **DISCUSSION**

336 Large-scale variation of food web structure is still largely unknown in terrestrial systems.
337 Thanks to the compilation of a large dataset comprising pairwise trophic interactions between

338 European terrestrial vertebrates, their geographical distributions and habitat preferences, we
339 extracted local food webs and successfully explored how they vary across Europe.

340 The latitudinal gradient of diversity is one of the most conspicuous patterns of biogeography.
341 We not only re-visit this relationship for European terrestrial vertebrates (Fig. 1), but also show
342 that it influences food web spatial structure. Most food web metrics, particularly those related
343 to feeding strategies and vertical diversity metrics, did not differ from what would be expected
344 under random assemblages of species, indicating that species richness was the key driver of
345 their variation, especially at species-poor locations. However, species richness failed to explain
346 the spatial distribution of other important features of food web structure, such as mean trophic
347 level, link density and connectance. This reveals that even at large spatial scales and resolutions,
348 the fingerprint of species interactions is visible on biodiversity distribution, but cannot be
349 summarized by species richness alone.

350 The description of ecological networks with reduced dimensions can provide understanding
351 on how they are structured within a community, from a functional (Eklöf *et al.*, 2013) or
352 structural perspective (Baiser *et al.*, 2012). The reduction analysis of food web metrics revealed
353 two major axes of structural variation, one mainly related to species richness and the other to
354 connectance. We expected species richness and connectance to behave independently from each
355 other and form the two major axes of variation in food web structure (Martinez, 1994; Riede *et*
356 *al.*, 2010; Dunne *et al.*, 2013). Indeed, Vermaat *et al.* (2009) showed a similar correlation
357 structure among food web metrics for 14 empirical food webs, and a similar decomposition was
358 also observed by Baiser *et al.* (2012) for North American aquatic food webs. On the other hand,
359 the constant connectance hypothesis (Martinez 1992) poses that the proportion of realized
360 interactions within a food web (i.e. connectance) is independent of species richness if link
361 density increases proportionally with the number of species. Our analyses confirmed these two
362 major dimensions for on European terrestrial vertebrate food webs .

363 Climatic gradients, namely temperature and precipitation, have long been observed as drivers
364 of biodiversity at both local and global scales (Evans *et al.*, 2005). Climate can affect food web
365 structure in several ways. First, it acts as a filter on species assembly (Keddy, 1992), which may
366 affect the functional composition of communities and therefore food web structure (Lurgi *et*
367 *al.*, 2012; Blanchard, 2015). Second, climate variability may directly affect food web structure.
368 A more stable climate may allow for longer food web chains and narrower diet niches (Menge
369 & Sutherland, 1987; Vázquez & Stevens, 2004; Cirtwill *et al.*, 2015),. Interannual temperature
370 variability has also been shown negatively correlated with modularity (Welti & Joern, 2015).
371 Our results show that European variation in food web structure, summarized by two composite
372 descriptors, is mostly related to annual average temperature and its seasonality. While
373 environmental constancy, particularly in climate conditions, is believed to lead to more speciose
374 communities, we find the opposite here, where climate variability was positively associated
375 with species-rich and longer food webs. There could be several reasons for our observations.
376 On the one hand, our measure of climate variability was calculated between 1970 and 2000,
377 which is likely not representative of the past climatic history to which European terrestrial
378 vertebrates were exposed to. Environmental constancy at larger temporal scales may be a more
379 important driver of species richness and food web complexity than seasonal variability. For
380 instance, Dalsgaard *et al.*, (2013) found a link between historical climate change (across the last
381 21,000 years) and present day pollinator network structure at the global scale. On the other
382 hand, the observed gradient in temperature seasonality coincides with important processes that
383 shaped vertebrate distribution across Europe. Baquero & Tellería (2001) suggest that the
384 decreasing mammalian richness from East-central Europe outwards is related to a decrease in
385 available land area (peninsular effect on species distributions), but also to environmental
386 harshness to the north, loss of suitable habitats and population bottlenecks during glacial periods
387 to the west, and human pressure since Neolithic times to the south – regions that coincide with

388 lower temperature seasonality and lower water availability (Hawkins *et al.*, 2003). This is not
389 to be confounded with endemism, which is higher in southern regions of Europe (Baquero &
390 Tellería, 2001). Mouchet *et al.* (2015) have also noted that species richness across terrestrial
391 vertebrates was more driven by land-use covariates than climate covariates toward south and
392 southwestern Europe. Hence, although human footprint did not stand out as an important driver
393 in our models, the combination of long-term and present human intervention and ancient
394 climatic fluctuations, which coincide with the temperature seasonality gradient, could be
395 driving the observed relationship between species richness, trophic food chain length and
396 seasonality.

397

398 Productivity is often hypothesized to drive the latitudinal gradient of species richness, as
399 higher amounts of energy available to primary consumers should support more diverse
400 communities (Hurlbert & Haskell, 2003). Although the overall effect of productivity was
401 weaker than climate, we found an influence on the *richness* composite descriptor at limiting
402 productivity levels (from low to intermediate primary productivity). Unproductive locations
403 were associated with species-poor networks that had lower trophic levels and lower link density
404 (both via the *richness composite descriptor* and by mean trophic level model, as shown in
405 supplementary material). Previous empirical studies have shown similar relationships, with
406 food web structure in terms of trophic level, omnivory, and proportion of top predators co-
407 varying positively with primary productivity (Vermaat *et al.*, 2009). Further, our results agree
408 with the theoretical expectation that higher resource availability and lower trophic levels should
409 propagate up the food web, promoting rich species assemblages with longer trophic chains and
410 supporting species at higher trophic level, and that this relationship should be stronger in the
411 least productive environments (Jenkins *et al.*, 1992; Post, 2002).

412 Human presence may lead to changes in land-use, habitat fragmentation and pollution, which

413 in turn can negatively affect biodiversity (Barnosky *et al.*, 2011; Cardinale *et al.*, 2012) and
414 food web structure (Evans *et al.*, 2013). Accordingly, human footprint was among the most
415 important predictors of vertebrate food web structure. It was strongly related to the *connectance*
416 composite descriptor, with a negative relationship to the proportion of realized links and species
417 proximity in the web (Fig. 3b; Table 3). However, in this case we cannot assume this to be a
418 cause-effect relationship, because the effect of human footprint was only noticeable below
419 intermediate levels, and because there is a strong spatial coincidence between human footprint
420 and climate. Climatic conditions and resource availability may affect the spatial distribution of
421 human density and species diversity alike, which would explain why the two composite
422 descriptors correlate positively with human population densities (Araújo, 2003). Indeed, despite
423 the weak importance of human footprint on the *richness* composite descriptor (Table 3), we
424 observed a positive relationship at low to intermediate levels of human disturbance (Fig. 3a).
425 Also, even though species richness and connectance metrics were nearly orthogonal in our
426 ordination space (Fig. 2), they were negatively correlated at low to intermediate values of
427 richness. The highest connectance was found in northeastern Europe, where both human
428 presence and species richness were lowest (Fig. 1; see also Appendix 3 Table 3.2). In these
429 areas, vertebrate assemblages were mostly composed by lower trophic level species and
430 comprised a few highly generalist predators, leading to highly dense and realized food webs.
431 Hence, the negative relationship between the *connectance* composite descriptor and human
432 footprint is more likely arising from low values of species richness.

433 The importance of the spatial residuals variable on the *connectance* composite descriptor
434 model suggested the presence of other important spatial variables. Since we used species
435 distributions to design European vertebrate assemblages, biogeographical processes, such as
436 barriers to species dispersal, island sizes, presence of peninsulas or even other biotic factors,
437 could lead to spatial similarities and/or dissimilarities in food web structure not explained solely

438 by climate and primary productivity, but rather through compositional turnover (Kortsch *et al.*,
439 2018). Further work is needed to include such processes under a spatial analysis framework of
440 food web structural turnover (Poisot *et al.*, 2012).

441 Here, we focused on terrestrial vertebrates and so, by definition our local food webs were
442 incomplete. To address this issue, we included nodes of general diet categories, such as
443 invertebrates, plants and fish, to represent absent trophic information from the non-vertebrate
444 components of the food webs. More than 70% of our species had their diet composed (entirely
445 or partly) of diet categories, thus we are likely missing a large part of food web complexity and
446 structure associated with the non-vertebrate portion of our food webs. In addition, given that
447 diet categories represented more than one trophic level (primary producers, but also consumers
448 like fish and invertebrates), our analysis overestimated the proportion of basal species,
449 particularly of non-herbivore basal species. Yet, the generality of the hypotheses explored here
450 should still be applicable. The positive effect of resource availability should reverberate from
451 lower to higher trophic levels (Post, 2002), thus being reflected on purely vertebrate webs which
452 are composed of species at generally high trophic levels. Moreover, resource availability has
453 been shown to positively impact taxonomic diversity across the taxa represented in our food
454 webs, and at similar scales (Waide *et al.*, 1999). Therefore, we are confident that the patterns
455 we observe reflect the structuring effects of the environment and resource availability on
456 European terrestrial food webs.

457 Two limitations to our design are the even contribution of each prey to a predator's diet and
458 the fact that trophic interactions were constant in space (i.e. if two species interacted in the
459 metaweb, they always interacted across their intercepted geographical range). The former
460 implied that we did not account for biomass or energetic requirements (in contrast, weighted
461 food webs interactions may be defined by biomass relationships) and as consequence we may
462 have inflated omnivory and connectance. The latter implied that adaptability in species' diets

463 and behaviors was not taken into account (e.g. predator diet shift due to presence of competitors
464 or prey behavioral changes in function of predator presence; Preisser *et al.*, 2009; Van Dijk *et*
465 *al.*, 2008; Poisot *et al.*, 2012) and as a consequence our webs may have an inflated number of
466 trophic interactions. Further, environmental conditions may also influence the realization of
467 interactions, which would affect the spatial distribution of food web structure. In addition,
468 trophic interactions in our metaweb were defined based not only on empirical studies, but also
469 on a potential array of prey for each predator species, which may lead to inflated generality and
470 vulnerability. More work is necessary to quantify the level of uncertainty related to how
471 metaweb and local food webs were defined. For instance, this could be done by using highly
472 resolved empirical food webs and quantifying how their topological properties differ, relatively
473 to food webs obtained using the methodology described here.

474 Nevertheless, this pioneer work sheds light into how food webs are structured across
475 continental scales, and serves as an example for future biogeographical food web studies that
476 seek to understand and predict biodiversity patterns.

477

478 REFERENCES

479 Araújo, M.B. (2003) The coincidence of people and biodiversity in Europe. *Global Ecology*
480 *and Biogeography*, **12**, 5–12.

481 Baiser, B., Gotelli, N.J., Buckley, H.L., Miller, T.E. & Ellison, A.M. (2012) Geographic
482 variation in network structure of a nearctic aquatic food web. *Global Ecology and*
483 *Biogeography*, **21**, 579–591.

484 Baquero, R.A. & Tellería, J.L. (2001) Species richness, rarity and endemism of European
485 mammals: A biogeographical approach. *Biodiversity and Conservation*, **10**, 29–44.

486 Barnosky, A.D., Matzke, N., Tomiya, S., Wogan, G.O.U., Swartz, B., Quental, T.B.,
487 Marshall, C., McGuire, J.L., Lindsey, E.L., Maguire, K.C., Mersey, B. & Ferrer, E.A.

- 488 (2011) Has the Earth's sixth mass extinction already arrived? *Nature*, **471**, 51–57.
- 489 Benjamini, Y. & Hochberg, Y. (1995) Controlling the false discovery rate: a practical and
490 powerful approach to multiple testing. *Journal of the Royal Statistical Society B*, **57**,
491 289–300.
- 492 Blanchard, J.A. (2015) A rewired food web. *Nature*, **527**, 7–8.
- 493 Boucher-Lalonde, V., Morin, A. & Currie, D.J. (2014) A consistent occupancy–climate
494 relationship across birds and mammals of the Americas. *Oikos*, **123**, 1029–1036.
- 495 Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani,
496 A., MacE, G.M., Tilman, D., Wardle, D.A., Kinzig, A.P., Daily, G.C., Loreau, M.,
497 Grace, J.B., Larigauderie, A., Srivastava, D.S. & Naeem, S. (2012) Biodiversity loss and
498 its impact on humanity. *Nature*, **486**, 59–67.
- 499 Cirtwill, A.R., Stouffer, D.B. & Romanuk, T.N. (2015) Latitudinal gradients in biotic niche
500 breadth vary across ecosystem types. *Proceedings Royal Society B*, **282**, 20151589-.
- 501 Csardi, G. & Nepusz, T. (2006) The igraph software package for complex network research.
502 *InterJournal, Complex Systems*, **1695**, 1–9.
- 503 Currie, D.J. (1991) Energy and large-scale patterns of animal and plant species richness. *Am.*
504 *Nat.*, **137**, 27–49.
- 505 Dalsgaard, B., Trøjelsgaard, K., Martín González, A.M., Nogués-Bravo, D., Ollerton, J.,
506 Petanidou, T., Sandel, B., Schleuning, M., Wang, Z., Rahbek, C., Sutherland, W.J.,
507 Svenning, J.C. & Olesen, J.M. (2013) Historical climate-change influences modularity
508 and nestedness of pollination networks. *Ecography*, **36**, 1331–1340.
- 509 Davies, T.J., Buckley, L.B., Grenyer, R. & Gittleman, J.L. (2011) The influence of past and
510 present climate on the biogeography of modern mammal diversity. *Philosophical*
511 *Transactions of the Royal Society B*, **366**, 2526–2535.
- 512 Van Dijk, J., Gustavsen, L., Mysterud, A., May, R., Flagstad, Ø., Brøseth, H., Andersen, R.,

513 Andersen, R., Steen, H. & Landa, A. (2008) Diet shift of a facultative scavenger, the
514 wolverine, following recolonization of wolves. *Journal of Animal Ecology*, **77**, 1183–
515 1190.

516 Dray, S. & Dufour, A.-B. (2007) The ade4 package: implementing the duality diagram for
517 ecologists. *Journal of statistical software*, **22**, 1–20.

518 Dunne, J.A., Lafferty, K.D., Dobson, A.P., Hechinger, R.F., Kuris, A.M., Martinez, N.D.,
519 McLaughlin, J.P., Mouritsen, K.N., Poulin, R., Reise, K., Stouffer, D.B., Thieltges,
520 D.W., Williams, R.J. & Zander, C.D. (2013) Parasites Affect Food Web Structure
521 Primarily through Increased Diversity and Complexity. *PLoS Biology*, **11**, e1001579.

522 Eklöf, A., Jacob, U., Kopp, J., Bosch, J., Castro-Urgal, R., Chacoff, N.P., Dalsgaard, B., de
523 Sassi, C., Galetti, M., Guimarães, P.R., Lomáscolo, S.B., Martín González, A.M., Pizo,
524 M.A., Rader, R., Rodrigo, A., Tylianakis, J.M., Vázquez, D.P. & Allesina, S. (2013) The
525 dimensionality of ecological networks. *Ecology Letters*, **16**, 577–583.

526 Evans, D.M., Pocock, M.J.O. & Memmott, J. (2013) The robustness of a network of
527 ecological networks to habitat loss. *Ecology Letters*, **16**, 844–852.

528 Evans, K.L., Warren, P.H. & Gaston, K.J. (2005) Species–energy relationships at the
529 macroecological scale: a review of the mechanisms. *Biological Reviews*, **80**, 1–25.

530 Gravel, D., Massol, F., Canard, E., Mouillot, D. & Mouquet, N. (2011) Trophic theory of
531 island biogeography. *Ecology Letters*, **14**, 1010–1016.

532 Hagen, M., Kissling, W.D., Rasmussen, C., De Aguiar, M.A.M., Brown, L.E., Carstensen,
533 D.W., Alves-Dos-Santos, I., Dupont, Y.L., Edwards, F.K., Genini, J., Guimarães, P.R.,
534 Jenkins, G.B., Jordano, P., Kaiser-Bunbury, C.N., Ledger, M.E., Maia, K.P., Marquitti,
535 F.M.D., Mclaughlin, Ó., Morellato, L.P.C., O’Gorman, E.J., Trøjelsgaard, K.,
536 Tylianakis, J.M., Vidal, M.M., Woodward, G. & Olesen, J.M. (2012) Biodiversity,
537 Species Interactions and Ecological Networks in a Fragmented World. *Advances in*

538 *Ecological Research*, **46**, 89–210.

539 Hawkins, B.A., Field, R., Cornell, H. V, Currie, D.J., Guégan, J.-F., Kaufman, D.M., Kerr,
540 J.T., Mittelbach, G.G., Oberdorff, T., O’Brien, E.M., Porter, E.E. & Turner, J.R.G.
541 (2003) Energy, water, and broad-scale geographic patterns of species richness.
542 *Ecological Research*, **84**, 3105–3117.

543 Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high
544 resolution interpolated climate surfaces for global land areas. *International Journal of*
545 *Climatology*, **25**, 1965–1978.

546 Hudson, L.N., Emerson, R., Jenkins, G.B., Layer, K., Ledger, M.E., Pichler, D.E., Thompson,
547 M.S.A., O’Gorman, E.J., Woodward, G. & Reuman, D.C. (2013) Cheddar: analysis and
548 visualisation of ecological communities in R. *Methods in Ecology and Evolution*, **4**, 99–
549 104.

550 Hurlbert, A.H. & Haskell, J.P. (2003) The effect of energy and seasonality on avian species
551 richness and community composition. *American Naturalist*, **161**, 83–97.

552 Imhoff, M.L., Bounoua, L., Ricketts, T., Loucks, C., Harriss, R. & Lawrence, W.T. (2004)
553 *HANPP collection: global patterns in net primary productivity (NPP)*, NASA
554 Socioeconomic Data and Applications Center (SEDAC), Palisades, NY, USA.

555 Jenkins, B., Kitching, R.L. & Pimm, S.L. (1992) Productivity, disturbance and food web
556 structure at a local, spatial scale in experimental containers habitats. *Oikos*, **65**, 249–255.

557 Jetz, W. & Fine, P.V.A. (2012) Global gradients in vertebrate diversity predicted by historical
558 area-productivity dynamics and contemporary environment. *PLoS Biology*, **10**.

559 Jetz, W., Thomas, G.H., Joy, J.B., Hartmann, K. & Mooers, A.O. (2012) The global diversity
560 of birds in space and time. *Nature*, **491**, 444–448.

561 Kaunzinger, C.M.K. & Morin, P.J. (1998) Productivity controls food- chain properties in
562 microbial communities. *Nature*, **395**, 495–497.

563 Keddy, P.A. (1992) Assembly and response rules: two goals for predictive community
564 ecology. *Journal of Vegetation Science*, **3**, 157–164.

565 Kitching, R. (2000) *Food Webs and Container Habitats*, Cambridge university press.

566 Kortsch, S., Primicerio, R., Aschan, M., Lind, S., Dolgov, A. V & Planque, B. (2018) Food-
567 web structure varies along environmental gradients in a high-latitude marine ecosystem.
568 1–14.

569 Kortsch, S., Primicerio, R., Fossheim, M., Dolgov, A. V & Aschan, M. (2015) Climate
570 change alters the structure of arctic marine food webs due to poleward shifts of boreal
571 generalists. *Proceedings of the Royal Society B: Biological Sciences*, **282**, 20151546.

572 Ledger, M.E., Brown, L.E., Edwards, F.K., Milner, A.M. & Woodward, G. (2012) Drought
573 alters the structure and functioning of complex food webs. *Nature Climate Change*, **3**,
574 223–227.

575 Liaw, A., Wiener, M. & others (2002) Classification and regression by randomForest. *R news*,
576 **2**, 18–22.

577 Lurgi, M., Lopez, B.C. & Montoya, J.M. (2012) Climate change impacts on body size and
578 food web structure on mountain ecosystems. *Philosophical Transactions of the Royal
579 Society B*, **367**, 3050–3057.

580 MacArthur, R. (1955) Fluctuations of Animal Populations and a Measure of Community
581 Stability. *Ecology*, **36**, 533–536.

582 Martinez, N.D. (1994) Scale-dependent constraints on food-web structure. *The American
583 Naturalist*, **144**, 935–953.

584 Mazel, F., Guilhaumon, F., Mouquet, N., Devictor, V., Gravel, D., Renaud, J., Cianciaruso,
585 M.V., Loyola, R., Diniz-Filho, J.A.F., Mouillot, D. & Thuiller, W. (2014) Multifaceted
586 diversity-area relationships reveal global hotspots of mammalian species, trait and
587 lineage diversity. *Global Ecology and Biogeography*, **23**, 836–847.

588 Mazel, F., Wüest, R.O., Gueguen, M., Renaud, J., Ficetola, G.F., Lavergne, S. & Thuiller, W.
589 (2017) The Geography of Ecological Niche Evolution in Mammals. *Current Biology*, 1–
590 6.

591 Menge, B.A. & Sutherland, J.P. (1987) Community Regulation: Variation in Disturbance,
592 Competition, and Predation in Relation to Environmental Stress and Recruitment. *The*
593 *American Naturalist*, **130**, 730–757.

594 Montoya, J.M. & Galiana, N. (2017) *Integrating Species Interaction Networks and*
595 *Biogeography. Adaptive Food Webs: Stability and Transitions of Real and Model*
596 *Ecosystems*, p. 289. Cambridge University Press.

597 Montoya, J.M., Pimm, S.L. & Solé, R. V. (2006) Ecological networks and their fragility.
598 *Nature*, **442**, 259–264.

599 Mouchet, M., Levers, C., Zupan, L., Kuemmerle, T., Plutzer, C., Erb, K., Lavorel, S.,
600 Thuiller, W. & Haberl, H. (2015) Testing the effectiveness of environmental variables to
601 explain European terrestrial vertebrate species richness across biogeographical scales.
602 *PLoS ONE*, **10**, 1–16.

603 Pascual, M. & Dunne, J.A. (2006) *Ecological networks: linking structure to dynamics in food*
604 *webs*, Oxford University Press.

605 Pellissier, L., Albouy, C., Bascompte, J., Farwig, N., Graham, C., Loreau, M., Maglianesi,
606 M.A., Melián, C.J., Pitteloud, C., Roslin, T., Rohr, R., Saavedra, S., Thuiller, W.,
607 Woodward, G., Zimmermann, N.E. & Gravel, D. (2017) Comparing species interaction
608 networks along environmental gradients. *Biological Reviews*.

609 Poisot, T., Canard, E., Mouillot, D., Mouquet, N. & Gravel, D. (2012) The dissimilarity of
610 species interaction networks. *Ecology Letters*, **15**, 1353–1361.

611 Poisot, T. & Gravel, D. (2014) When is an ecological network complex? Connectance drives
612 degree distribution and emerging network properties. *PeerJ*, **2**, e251.

613 Poisot, T., Guéveaux-Julien, C., Fortin, M.J., Gravel, D. & Legendre, P. (2017) Hosts,
614 parasites and their interactions respond to different climatic variables. *Global Ecology*
615 *and Biogeography*, **26**, 942–951.

616 Post, D.M. (2002) The long and short of food-chain length. *Trends in Ecology & Evolution*,
617 **17**, 269–277.

618 Preisser, E.L., Bolnick, D.I. & Benard, M.E. (2005) Scared to death ? The effects of
619 intimidation and consumption in predator-prey Interactions. *Ecology*, **86**, 501–509.

620 Riede, J.O., Rall, B.C., Banasek-Richter, C., Navarrete, S.A., Wieters, E.A., Emmerson,
621 M.C., Jacob, U. & Brose, U. (2010) Scaling of Food-Web Properties with Diversity and
622 Complexity Across Ecosystems. *Advances in Ecological Research*, **42**, 139–170.

623 Roslin, T., Hardwick, B., Novotny, V., Petry, W.K., Andrew, N.R., Asmus, A., Barrio, I.C.,
624 Basset, Y., Boesing, A.L., Bonebrake, T.C., Cameron, E.K., Dáttilo, W., Donoso, D.A.,
625 Drozd, P., Gray, C.L., Hik, D.S., Hill, S.J., Hopkins, T., Huang, S., Koane, B., Laird-
626 Hopkins, B., Laukkanen, L., Lewis, O.T., Milne, S., Mwesige, I., Nakamura, A., Nell,
627 C.S., Nichols, E., Prokurat, A., Sam, K., Schmidt, N.M., Slade, A., Slade, V.,
628 Suchanková, A., Teder, T., van Nouhuys, S., Vandvik, V., Weissflog, A., Zhukovich, V.
629 & Slade, E.M. (2017) Higher predation risk for insect prey at low latitudes and
630 elevations. *Science*, **356**, 742–744.

631 Safi, K., Cianciaruso, M. V., Loyola, R.D., Brito, D., Armour-Marshall, K. & Diniz-Filho,
632 J.A.F. (2011) Understanding global patterns of mammalian functional and phylogenetic
633 diversity. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **366**,
634 2536–2544.

635 Schleuning, M., Fründ, J., Klein, A., Abrahamczyk, S., Alarcón, R., Albrecht, M., Andersson,
636 G.K.S., Bazarian, S., Böhning-Gaese, K., Bommarco, R., Dalsgaard, B., Dehling, D.M.,
637 Gotlieb, A., Hagen, M., Hickler, T., Holzschuh, A., Kaiser-Bunbury, C.N., Kreft, H.,

638 Morris, R.J., Sandel, B., Sutherland, W.J., Svenning, J.-C., Tschamtkke, T., Watts, S.,
639 Weiner, C.N., Werner, M., Williams, N.M., Winqvist, C., Dormann, C.F. & Blüthgen, N.
640 (2012) Specialization of Mutualistic Interaction Networks Decreases toward Tropical
641 Latitudes. *Current Biology*, **22**, 1925–1931.

642 Strobl, C., Boulesteix, A.L., Zeileis, A. & Hothorn, T. (2007) Bias in random forest variable
643 importance measures: Illustrations, sources and a solution. *BMC Bioinformatics*, **8**.

644 Strobl, C., Malley, J. & Gerhard Tutz (2009) Characteristics of Classification and Regression
645 Trees, Bagging and Random Forests. *Psychological methods*, **14**, 323–348.

646 Vázquez, D.P. & Stevens, R.D. (2004) The Latitudinal Gradient in Niche Breadth: Concepts
647 and Evidence. *The American Naturalist*, **164**, E1–E19.

648 Vermaat, J.E., Dunne, J.A. & Gilbert, A.J. (2009) Major dimensions in food-web structure
649 properties. *Ecology*, **90**, 278–282.

650 Waide, R.B., Willig, M.R., Steiner, C.F., Mittelbach, G., Gough, L., Dodson, S.I., Juday, G.P.
651 & Parmenter, R. (1999) The Relationship Between Productivity and Species Richness.
652 *Annual Review of Ecology and Systematics*, **30**, 257–300.

653 Wallace, A.R. (1876) *The Geographical Distribution of Animals: With a Study of the*
654 *Relations of Living and Extinct Faunas as Elucidating the Past Changes of the Earth's*
655 *Surface: In Two Volumes*, Macmillan and Company, London.

656 Welti, E. a. R. & Joern, A. (2015) Structure of trophic and mutualistic networks across broad
657 environmental gradients. *Ecology and Evolution*, **5**, 326–334.

658 Wildlife Conservation Society, Center for International Earth Science Information Network &
659 Columbia University (2005) *Last of the Wild Project, Version 2, 2005 (LWP-2): Global*
660 *Human Footprint Dataset (Geographic)*, NASA Socioeconomic Data and Applications
661 Center (SEDAC), Palisades, NY, USA.

662 Wood, S.A., Russell, R., Hanson, D., Williams, R.J. & Dunne, J.A. (2015) Effects of spatial

- 663 scale of sampling on food web structure. *Ecology and Evolution*, **5**, 3769–3782.
- 664 Wood, S.N. (2017) Mixed GAM Computation Vehicle with Automatic Smoothness
665 Estimation. 1.8-22. R package.
- 666 Wright, D.H. (1983) Species-energy theory : an extension of species-area theory. *Oikos*, **41**,
667 496–506.
- 668 Zanden, M.J. Vander & Fetzer, W.W. (2007) Global patterns of aquatic food chain length.
669 *Oikos*, **116**, 1378–1388.

670 **Tables**

671 Table 1. Food web properties, respective mean, standard deviation and null rejection rates across Europe. Rejection rates in bold highlight
 672 variables (rejection rate > 90%) that were retained in the subsequent analyses.

Food web property	Definition	Mean (SD)	Rejection rate	
Species richness	Number of species	194.8 (40.14)	N/A	
Connectance	Proportion of realized links that occur in a web.	0.084 (0.01)	0.99	
Link density	Average number of links per species.	17.33 (3.26)	0.99	
Clustering coefficient	Probability of linkage of two species, given that both are linked to a third species.	0.28 (0.03)	0.99	
Characteristic path length	The mean shortest food chain length between species pairs	1.83 (0.03)	0.99	
Vulnerability	Mean and standard deviation of number of predators per species.	1.01 (0.01)	0	
SD of Vulnerability		0.71 (0.08)	0	
Generality	Mean and standard deviation of number of prey per species.	2.33 (0.21)	0.86	
SD of Generality		2.26 (0.23)	0.85	
Maximum trophic similarity	Mean maximum number of links (in- and outward) shared between all pairs of species.	0.75 (0.02)	0.77	
Proportion of basal species	non-herbivores	Proportion of species that prey on non-plant diet categories	0.53 (0.03)	0.53
	herbivores	Proportion of species that prey exclusively of plant diet categories	0.04 (0.01)	0.43
Proportion of intermediate species	Proportion of species with prey and predators.	0.42 (0.03)	0.96	
Proportion of top predator species	Proportion of species without any predators.	0.01 (0.01)	0	
Proportion of omnivores	Proportion of species that feed on more than one trophic level.	0.43 (0.03)	0.96	
Mean trophic level	Mean prey average trophic level	2.35 (0.08)	0.96	
Maximum trophic level	Maximum prey average trophic level	3.58 (0.14)	0	

673

674 Table 2. Correlation between six food web properties and the two major principal components
 675 axes of the PCA (*richness* and *connectance* composite descriptor). In total, both composite
 676 descriptors explained 76.6% of food web spatial variance (measured by this six variables).

Topological metric	<i>Richness composite descriptor</i>	<i>Connectance composite descriptor</i>
Species richness	-0.45	0.14
Connectance	0.13	-0.64
Link density	-0.44	-0.15
Characteristic path length	-0.24	0.48
Cluster coefficient	-0.06	-0.50
Proportion of intermediate species	-0.40	-0.19
Proportion of omnivore species	-0.37	-0.1
Mean trophic level	-0.47	-0.09

677

678

679 Table 3. Variable importance for each structural composite descriptor model based on
 680 “permutation accuracy importance” method. In the *richness* composite descriptor model,
 681 temperature variables (annual average and seasonality) were the most important variables.
 682 Whereas in the *connectance* composite descriptor model, spatial residuals were the most
 683 important variable, suggesting that other spatial processes are acting on this composite
 684 descriptor, not accounted by the other variables. *Richness* descriptor model explained 68.9% of
 685 the variance, while *connectance* composite descriptor model explained 38.0%.

	<i>Richness</i> composite descriptor	<i>Connectance</i> composite descriptor
Spatial residuals	0.11	0.37
Average annual Temp.	0.41	0.35
Temp. seasonality	0.46	0.11
Precipitation	0.00	0.08
Coeff. of var. precip.	0.02	0.03
Shannon index	0.08	0.08
Habitat evenness	0.03	0.00
Primary productivity	0.11	0.11
Human footprint	0.02	0.25

686

687 **Figure captions**

688

689 **Figure 1.** Spatial distribution of six metrics of the European tetrapod food webs: species
690 richness, link density, connectance, characteristic path length, proportion of intermediate
691 species and proportion of omnivore species. For a detailed description of these metrics see
692 Table 1. The distribution of the 16 food web metrics is provided in Appendix S3, Figure S3.2
693 in Supporting Information.

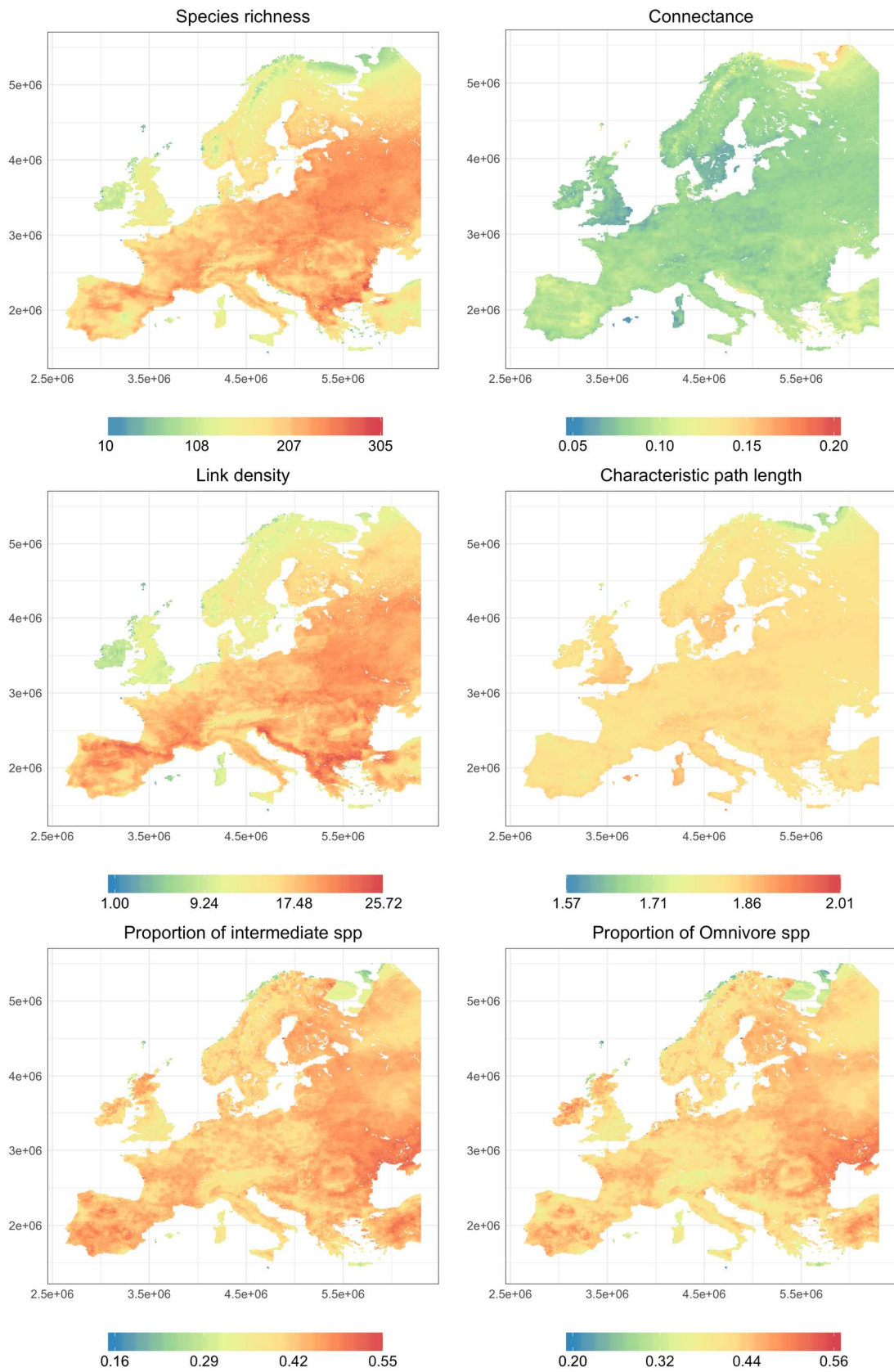
694

695 **Figure 2.** Principal components analysis (PCA) of European food web metrics. Red arrows
696 represent the direction and value of correlations between individual topological metrics and
697 each structural food web descriptors. The first component (*richness* structural composite
698 descriptor) was negatively correlated with species richness (Spp rich.), link density (Link
699 dens.), proportion of intermediate (Prop. int.) and omnivore (Prop. omn.) species and mean
700 trophic level (Mean TL). The second component (*connectance* composite descriptor) was
701 related highly correlated with connectance (Connect.), characteristic path length (Char. path
702 length) and cluster coefficient (Cluster coeff.). The four food webs representing the general
703 typology of food webs in each quadrant, and were drawn from the closest point to the centroid
704 of each quadrant.

705

706 **Figure 3.** Partial response plots of (a) Food web *richness* composite and (b) *connectance*
707 composite descriptor models of the European food web in function of the climatic and landscape
708 predictors. Lines are the estimated effects of each predictor with the respective 95% confidence
709 intervals shaded in grey. Note that these intervals are very narrow. For single food web metrics
710 see supplementary material S6.

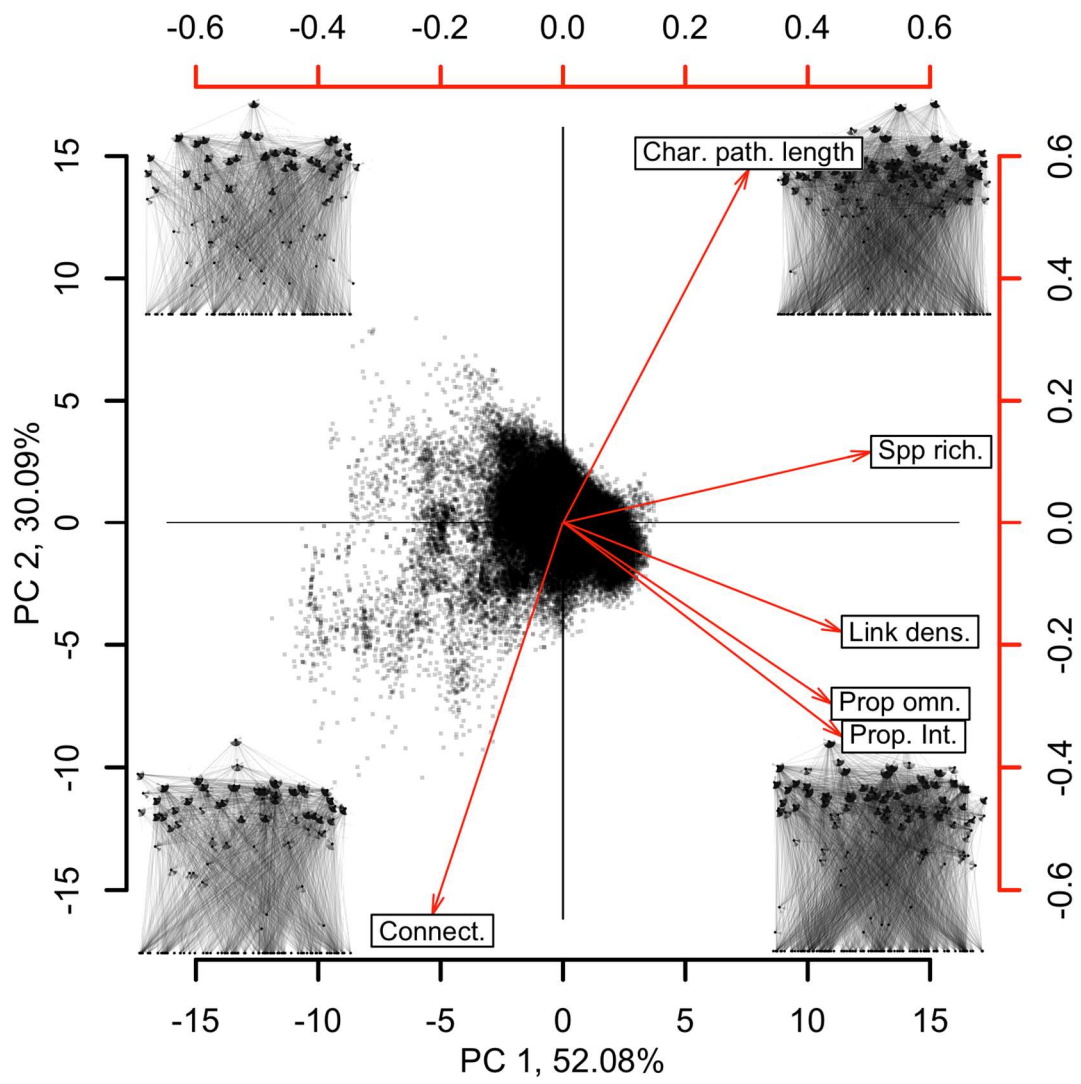
711 Figure 1.

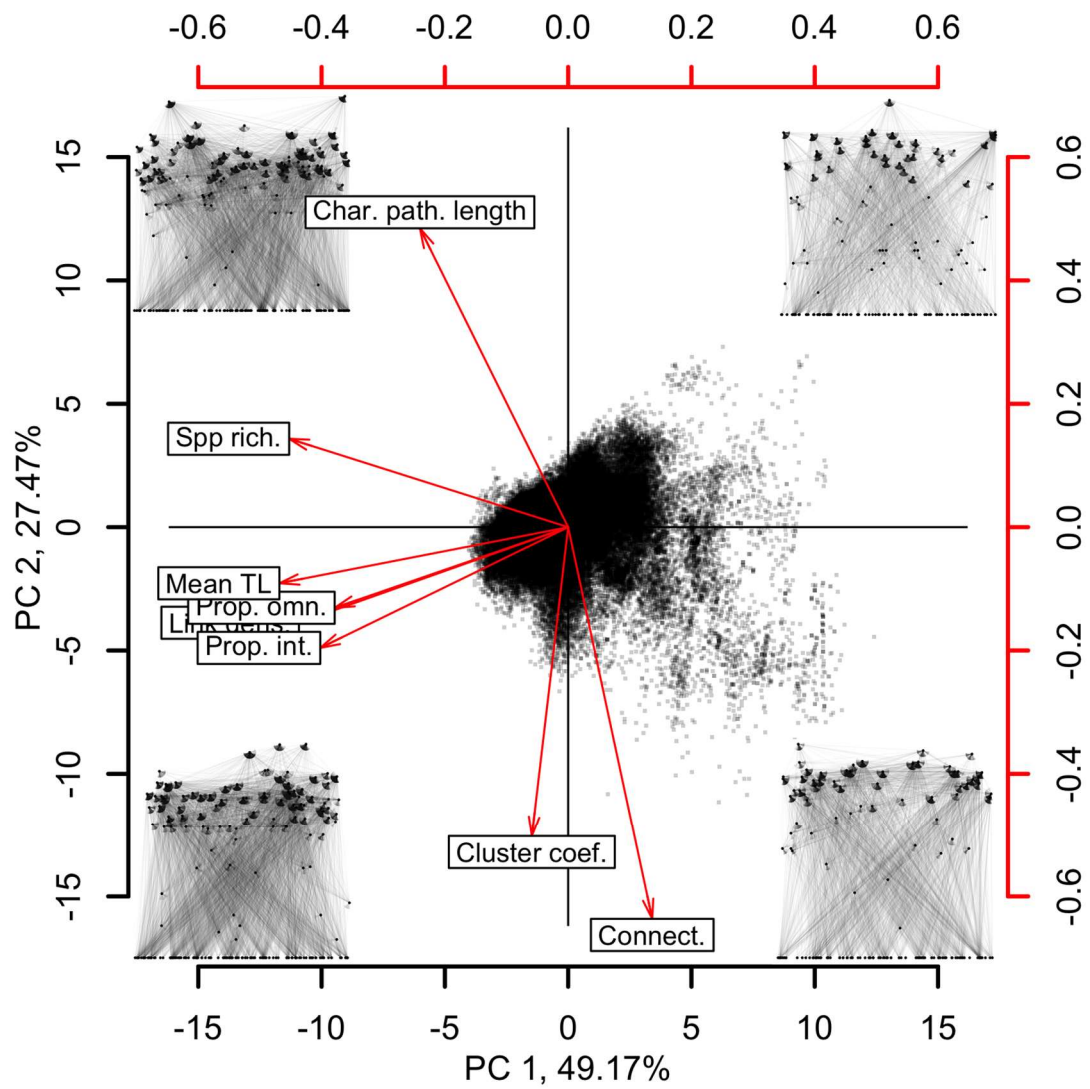


712

713

714 Figure 2.

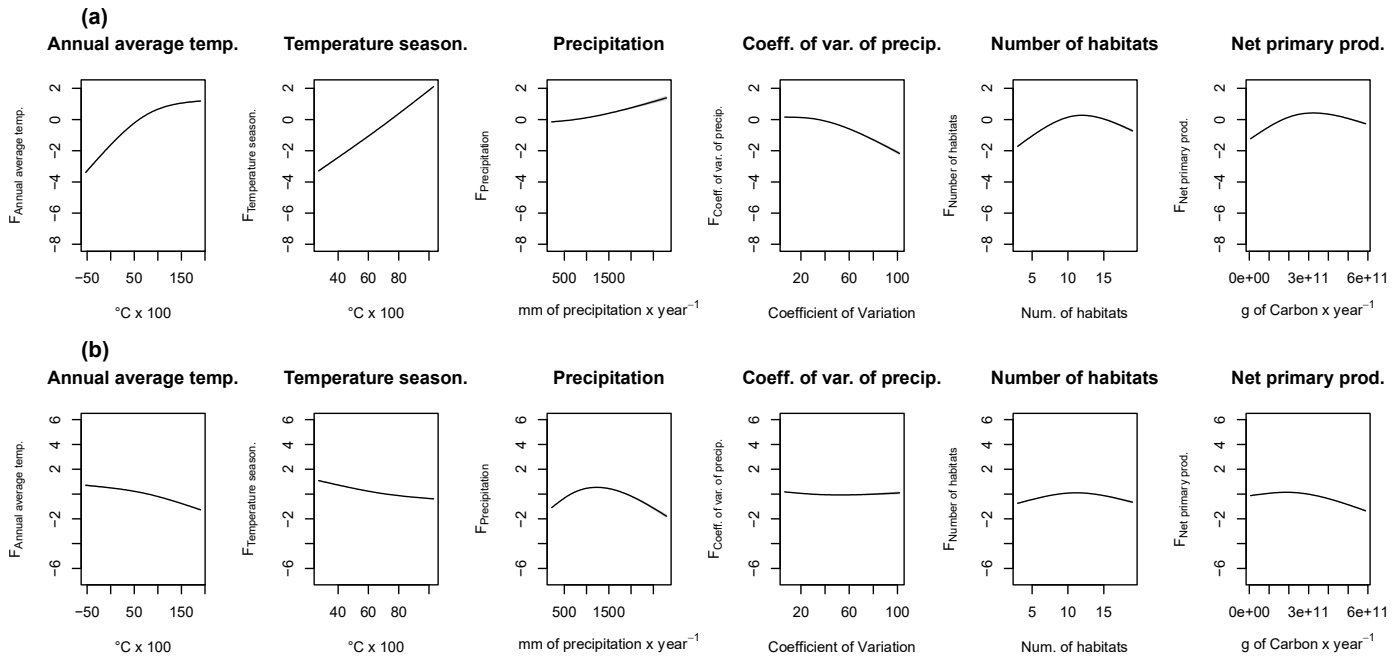




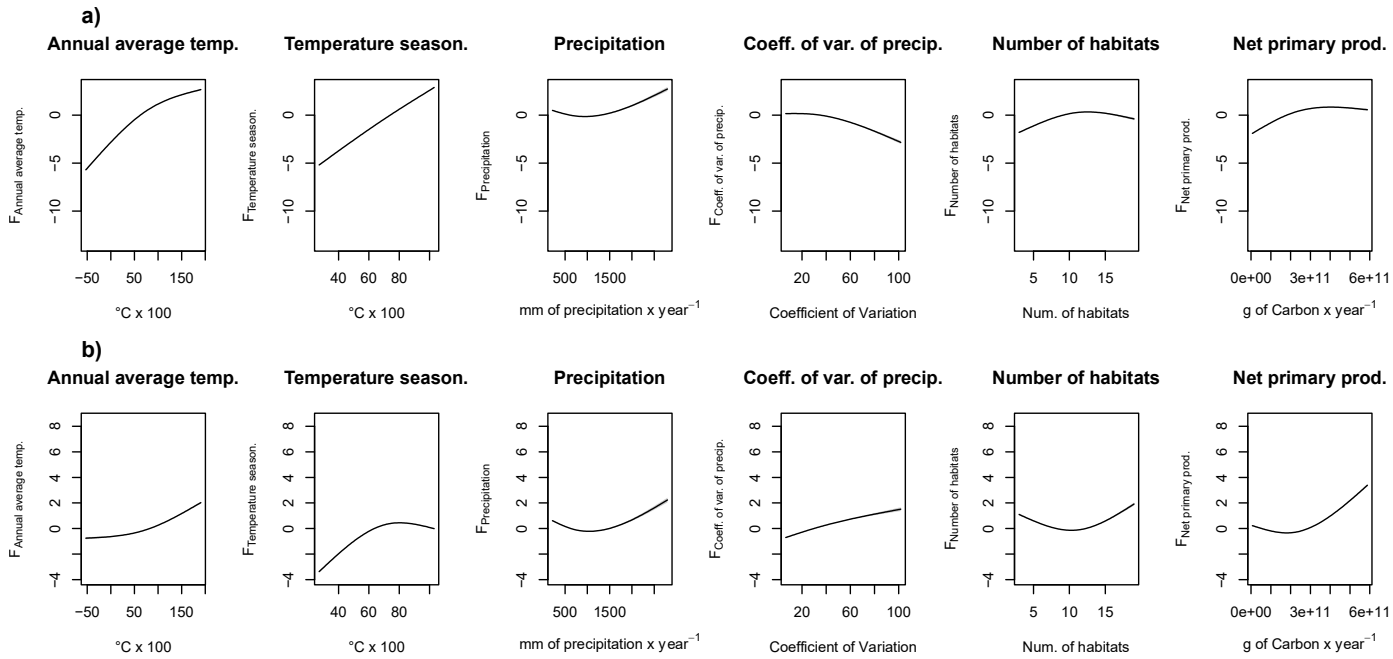
715

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Figure 3.



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718 **Supporting information**

719 Appendix S1 contains: Table S1.1.: List of the tetrapod species considered in the analysis (in
720 XLSX format).

721

722 Appendix S2 contains: Figure S2.1.: Spatial distribution of climatic variable, primary
723 productivity, habitat diversity and human productivity.

724

725 Appendix S3: Suitable habitat threshold sensitivity analysis.

726

727 Appendix S4 contains: Table S4.2.: Pairwise spearman correlation between food web metrics;

728 Figure S4.2.: Spatial distribution of individual food web metrics.

729

730 Appendix S5 contains: Figure S5.3.: Local food web metrics and null distributions.

731

732 Appendix S6: Relationship between individual food web metrics and landscape, climatic

733 descriptors

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