



HAL
open science

Spatial analyses of multi-trophic terrestrial vertebrate assemblages in Europe

Joao Braga, Laura Pollock, Ceres Barros, Núria Galiana Ibañez, José Montoya, Dominique Gravel, Luigi Maiorano, Alessandro Montemaggiori, Gentile Francesco Ficetola, Stéphane Dray, et al.

► To cite this version:

Joao Braga, Laura Pollock, Ceres Barros, Núria Galiana Ibañez, José Montoya, et al.. Spatial analyses of multi-trophic terrestrial vertebrate assemblages in Europe. *Global Ecology and Biogeography*, 2019, 28 (11), pp.1636-1648. 10.1111/geb.12981 . hal-02399915

HAL Id: hal-02399915

<https://hal.science/hal-02399915>

Submitted on 9 Nov 2020

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

1 TITLE

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

3

4

5 AUTHORS

6 João Braga¹, Laura J. Pollock¹, Ceres Barros¹, Núria Galiana², José M. Montoya²,
7 Dominique Gravel³, Luigi Maiorano⁴, Alessandro Montemaggiori⁴, Gentile Francesco
8 Ficetola^{1,5}, Stéphane Dray⁶, Wilfried Thuiller¹

9

10 ¹Univ. Grenoble Alpes, Univ. Savoie Mont-Blanc, CNRS, LECA - Laboratoire d'Écologie
11 Alpine, F-38000 Grenoble, France

12 ²Theoretical and Experimental Ecology Station, CNRS-UPS, 09200 Moulis, France

13 ³Département de biologie, Université de Sherbrooke, 2500 Boul. De l'Université,
14 Sherbrooke, Canada.

15 ⁴Department of Biology and Biotechnologies "Charles Darwin", Università di Roma "La
16 Sapienza", viale dell'Università 32, 00185, Roma, Italia.

17 ⁵Department of Environmental Sciences and Policy, Università degli Studi di Milano. Via
18 Celoria

19 ⁶Univ Lyon, Université Claude Bernard Lyon 1, CNRS, Laboratoire de Biométrie et
20 Biologie Evolutive, F-69100, Villeurbanne, France.

21

22 Corresponding authors – João Braga & Wilfried Thuiller

23 E-mail address: joao.braga@univ-grenoble-alpes.fr / wilfried.thuiller@univ-grenoble-
24 alpes.fr

25

26 ABSTRACT

27 **Aim** While much has been said on the spatial distribution of taxonomic and phylogenetic
28 diversity of large animals, how this diversity interacts in food webs, and especially how these
29 interactions change across space is largely unknown. Here, we analyzed the spatial
30 distribution of terrestrial vertebrate food webs and asked whether the variation in local food
31 web structure is driven by random processes or by natural and anthropogenic factors.

32 **Location** Europe.

33 **Methods** We combined an expert-based food web (1140 species and 76,500 links) of all
34 European terrestrial vertebrates (mammals, breeding birds, reptiles and amphibians) with their
35 respective spatial distributions. We mapped sixteen different food web metrics representing
36 complexity, chain length, proportion of taxa and diet strategy across Europe and tested
37 whether their distribution reflect the spatial structure of species richness using a null model of
38 food web structure. Then, to avoid multi-collinearity issues, we defined composite descriptors
39 of food web structure that we then related to a set of environmental layers summarizing both
40 natural and anthropogenic influences, and tested their relative importance in explaining the
41 spatial distribution of European terrestrial vertebrate food webs.

42 **Results** From the sixteen metrics, six showed a highly structured distribution across Europe
43 and could be summarized along two major axes of variation of food web structure. The first
44 was related to species diversity and proportion of intermediate species and the second was
45 related to connectance and proximity of species within the web. Both descriptors varied with
46 the latitudinal gradient. Mean annual temperature and seasonality was positively correlated
47 with the first axis, while human footprint was positively correlated with the second one.

48 **Main conclusions** We provide the first comprehensive spatial description of the vertebrate
49 food web in Europe, and we demonstrate the importance of climate and anthropogenic
50 pressure in shaping the spatial structure of European terrestrial vertebrate food webs.

51

52 Key words: ecological network, spatial ecology, multi-trophic food webs, topological

53 properties, tetrapod interactions;

54

55 INTRODUCTION

56 Documenting large-scale biodiversity distribution and understanding what drives variation
57 between or within different regions of the world has long fascinated naturalists (Wallace,
58 1876). The recent and ever-increasing rise of large-scale distribution databases (e.g. IUCN,
59 BirdLife, Map Of Life) has led to new comprehensive analyses of biodiversity distribution.
60 Thanks to available data on species traits and phylogenetic relatedness, global and regional
61 patterns of species, traits and phylogenetic diversity are now well documented for terrestrial
62 vertebrates (Jetz & Fine, 2012; Jetz *et al.*, 2012; Mazel *et al.*, 2014, 2017).

63 Such measurements of biodiversity (taxonomic, functional and phylogenetic diversity) focus
64 on a group of species co-occurring in a certain area or region, which can be subsequently
65 compared with measurements of other areas to identify localities with higher or lower
66 biodiversity (e.g. hotspots vs. coldspots, Mazel *et al.* 2014). However, species assemblages
67 are not just only the mere sum of species co-occurring in an area, they share a myriad of biotic
68 interactions (e.g. predation, competition, facilitation, etc.) that form a variety of ecological
69 networks through space. While past biogeographic studies have investigated how species or
70 trait diversity vary in space and the underlying role of environment (e.g. Davies *et al.*, 2011;
71 Safi *et al.*, 2011; Mazel *et al.*, 2017), we know little about the spatial distribution of
72 ecological networks (Pellissier *et al.* 2017).

73 Food webs are representations of communities' trophic interactions, where each node in the
74 network represents a species and each edge is a directional feeding interaction from a prey to
75 a predator species. Previous studies on food web ecology have been focusing on the trophic
76 relationships between species within discrete communities with the goal of inferring the
77 underlying processes acting upon them, such as relation between species diversity and food
78 web structure, community assembly processes and even robustness of those communities to
79 species' extinctions (Montoya *et al.*, 2006). However, since the pioneering work of Kitching

80 (2000) on the latitudinal gradients of aquatic food-web structure, food web ecology has
81 shifted from finding food web structural generalities between communities to search for large-
82 scale spatial distribution of ecological networks, such as latitudinal gradients, relation with
83 climate and resource availability (Post, 2002; Kortsch *et al.*, 2015; Montoya & Galiana, 2017;
84 Pellissier *et al.*, 2017; Poisot *et al.*, 2017; Roslin *et al.*, 2017).

85 Two hypotheses are commonly proposed to explain the large-scale spatial distribution of
86 food webs. The first hypothesis postulates that species niche breadth increases towards the
87 poles, i.e. species are more diet specialists in the tropics and more generalists as we move
88 away from it due to the environmental stability and the amount of energy influencing niche
89 packing (MacArthur, 1955; Schleuning *et al.*, 2012). This hypothesis has been criticized to be
90 inconsistent across different systems (Cirtwill *et al.*, 2015). The second hypothesis states that
91 low resources at the primary consumers level act as a bottom-up control for species richness
92 and food chain length, while at intermediate level of resource availability, disturbances and
93 ecosystem size drive food chain length (Kaunzinger & Morin, 1998; Post, 2002). Yet, again
94 such observations are not ubiquitous (Zanden & Fetzer, 2007). These two hypotheses have,
95 however, never been comprehensively tested over large environmental gradients and for
96 complex (i.e., speciose) food webs.

97 Here, we take this challenge by building the first comprehensive food web of European
98 vertebrates using a combination of expert knowledge and literature. Then, we mapped the
99 food web structures for all vertebrates' assemblages naturally occurring in Europe, west
100 Russia and Turkey using a uniform spatial grid at 10 km resolution. On the one hand, instead
101 of focusing on simple food web metrics to test the above-mentioned hypotheses, we extended
102 the analysis to a large set of descriptors such as complexity metrics (species richness,
103 connectance, number of trophic interactions), taxa composition (proportion of basal,
104 intermediate and top predator species), feeding strategy (generality, vulnerability and

105 omnivory), and trophic level. We contrast observations to a null model in order to reveal the
106 significant associations between metrics and environmental variables. Most network metrics
107 highly co-vary, either through scaling with the number of species or through connectance
108 (Vermaat *et al.*, 2009; Riede *et al.*, 2010; Baiser *et al.*, 2012; Poisot & Gravel, 2014), and
109 therefore we decomposed the food web structure into a set of composite descriptors (Pellissier
110 *et al.*, 2017) . We investigate how the environment, landscape, and anthropogenic pressures
111 influence the spatial distributions of the different topological network properties.

112 We expected annual temperature and precipitation to be good predictors of food web spatial
113 structure because they are major drivers of species sorting and community assembly over
114 large spatial scales (Riede *et al.*, 2010) (Vázquez & Stevens, 2004; Ledger *et al.*, 2012).
115 Likewise, highly productive sites also provide more resources for consumers and thereby
116 support higher trophic levels (Wright, 1983; Post, 2002), therefore we also predicted that
117 habitat fragmentation and disturbance to shape European food webs. High levels of
118 fragmentation may reduce the strength of interactions between species or even prevent species
119 from interacting, which may lead to networks with lower link density (Hagen *et al.*, 2012).

120

121 **MATERIALS AND METHODS**

122 **Study area and species distributions**

123 The study area included Europe (excluding Macaronesia region and Iceland), and the
124 western regions of Turkey and Russia (hereafter referred to as ‘Europe’). We extracted
125 species ranges for terrestrial vertebrates naturally occurring within the study area from
126 Maiorano *et al.*, (2013). In total, our analyses focused on 521 bird, 288 mammal, 251 reptile
127 and 104 amphibian species that naturally occur in Europe (see S1 for full species list). Species
128 range data followed a regular grid of 300 m resolution (WGS84) where Maiorano *et al.*,
129 (2013) classified each cell as zero for unsuitable habitat or one for suitable habitat. All species

130 range maps were up-scaled to a 10x10 km equal-size area grid (ETRS89; total of 78875 cells).
131 We considered a species potentially present in a cell (hereafter referred as local assemblage)
132 when at least one 300 m suitable habitat cell (either as one or two) fell within that same 10x10
133 km cell.

134

135 **European vertebrates metaweb and local food web structure**

136 A trophic metaweb compiles all predator-prey interactions between species for a given
137 regional species pool. Here, we designed the most complete metaweb of European terrestrial
138 vertebrates from expert knowledge, published information and field guides (see references in
139 Supplementary Information). Basically, all obligatory herbivores or insectivores species were
140 assigned to basal species, together with species with fish or any other obligatory diet that does
141 not include other vertebrates. Then, we focused on species feeding upon other vertebrates
142 (including omnivores) and searched for known prey from an exhaustive literature review. We
143 defined a trophic interaction as predation on any life stage of a species (e.g. egg and larval
144 when applicable, juvenile or adult). We considered a trophic interaction potentially feasible
145 between a predator and a prey based on literature review, morphological similarities between
146 potential prey and literature-referenced prey and, in the absence of this information, the diet
147 of predator's sister species. Twelve general diet categories were added to the metaweb, which
148 included detritus, coprophagus, mushrooms, mosses and lichens, algae, fruits, grains, other
149 plant parts, invertebrates, fish, domestic animals and carrion. These categories were used to
150 determine local assemblages and calculate species trophic level (see below).

151 The metaweb comprised 70,600 trophic interactions distributed across 1140 species (60% of
152 basal species, 33% of intermediate species and less than one percent by top predator species)
153 and a connectance of 0.05. Species had on average 61.93 interactions (including prey and
154 predator interactions) and were on average 1.9 interactions away from each other.

155 We extracted local food webs by intersecting the metaweb with local community
156 composition. In the few cases where a given species was present but having neither available
157 prey given the species distribution data, nor any habitat with its resources for predation to be
158 consummated, we considered the species absent for that particular location (i.e. assuming a
159 false positive in the distribution data). Note that diet categories are ubiquitous across the
160 landscape; therefore species that did prey on them always had resources. As a consequence,
161 basal species have always resources within their extent of occurrence.

162 For each local food web, we calculated sixteen food web properties that belong to four
163 groups: complexity, strategy, taxa composition and trophic level. Complexity metrics include
164 number of species, connectance, clustering coefficient, characteristic path length and link
165 density (average distance between species and average number of interactions per species
166 respectively). Strategy metrics refer to dietary niche properties of species, which include
167 generality (mean number of preys) and vulnerability (mean number of predators), their
168 respective standard deviations, proportion of omnivore species and average trophic similarity
169 between species. Taxa composition metrics quantify the proportion of species along three
170 major trophic levels: basal, intermediate and top level. Trophic level metrics refer to vertical
171 trophic position of species within a food web, which included the mean trophic level and the
172 maximum trophic level present. See Table 1 for individual properties definitions.

173

174 **Climatic, energetic and habitat variables**

175 We extracted four climatic variables from the WorldClim database (Hijmans *et al.*, 2005) at
176 30° resolution: annual mean temperature, temperature seasonality (standard deviation of
177 monthly mean temperature), total annual precipitation and coefficient of variation of
178 precipitation. We chose these variables since they correlate with vertebrates species ranges
179 across large spatial scales (Boucher-Lalonde *et al.*, 2014). We approximated the amount of

180 resources available to the primary consumers in each pixel with estimates of net primary
181 productivity (grams of carbon per year at 0.25 decimal degrees spatial resolution; Imhoff et
182 al., 2004). We also represented the anthropogenic influence on natural landscape using the
183 human footprint index from the Last of the Wild database (version 2 at 1 km spatial
184 resolution; WCS & CIESIN, 2005). We resampled all climatic variables, primary productivity
185 and human footprint data by averaging at the 10x10 km resolution data used for the species
186 ranges. We also measured habitat diversity using the richness of distinct habitats within a 10
187 km cell using the GlobCover habitat classification at 300 m resolution.

188

189 **Statistical analyses**

190 Our analyses consisted of three sequential steps. 1) We checked whether the spatial
191 distribution of the local web metrics could result from a purely random process using a null
192 model and only selected the ones that differed from null expectations for subsequent analyses.
193 2) We reduced the complexity of the retained metrics applying a principal components
194 analysis and selecting the first two axes of variation. 3) We related these two axes of
195 variation to climate, resource availability and human disturbance using generalized additive
196 models (GAMs).

197

198 *Are random processes responsible of the spatial distribution of food web properties?*

199 Food web structure may vary with the number of species, independently of any others
200 constrains acting upon it (e.g. environment). We thus built a null model to test whether
201 European local food webs and their associated properties could result from a pure random
202 draw from the European species pool, given the observed local species richness. The null
203 hypothesis is that species are randomly distributed in space, independently of the local
204 environment and of their position in the metaweb. We thus sampled local food webs for each

205 cell by randomly drawing a number of species from the metaweb corresponding to the
206 observed local richness (from 10 to 300 species). We further applied the constraint that every
207 species needed at least one resource to be included in the food web. For each value of species
208 richness, we repeated the random draw 1000 times and calculated the 16 food web metrics for
209 each repetition in order to obtain a distribution of metrics under the null hypothesis. For each
210 cell, we compared the observed food web metrics to the corresponding null distribution and
211 computed the associated *p-value*. We adjusted *p-values* for multiple comparisons using a false
212 discovery rate method based on Benjamin & Hochberg (1995) present in the function *p.adjust*
213 in STATS R package. We retained food web metrics that had 90% of rejection rate, i.e. 90% of
214 all local food web metrics were significantly different from ones of random assemblages.
215 Considering that we computed one test per cell (total of 78,875 cells), a food web metric
216 should be significantly different from random expectation in approximately 71,000 cells in
217 order to be kept in our analysis.

218

219 *How to reduce the redundancy in local food web properties?*

220 Many food web metrics are correlated (Vermaat *et al.*, 2009) either because of their
221 mathematical formulation or because of combinatory constraints (Poisot & Gravel, 2014). We
222 applied a principal components analysis (PCA) on the six retained variables over the 78,875
223 cells of Europe (Table 1) to analyze the most insightful axes of variations between these
224 metrics. This allowed us not only to understand how food web metrics co-vary with each
225 other, but also to summarize the food web structure of European assemblages (as a whole)
226 into a set of meaningful axes. We emphasize that the correlation structure among metrics we
227 analyzed is not only driven by the fundamental constraints linking metrics referred above, but
228 also driven by the effect of spatial variation in food web composition. From the PCA, we kept
229 only the axes that explain each at least 20 % of the total variance, hereafter referred as food

230 web structural composite descriptors. This analysis was performed in R using the ADE4
231 package (Dray & Dufour, 2007).

232

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

234 We related our food web structural composite descriptors to spatial drivers (climate,
235 energetic and habitat variables) with GAMs. GAMs are more flexible than generalized linear
236 models since we did not have any *a priori* expectation regarding the shape of the relationships
237 between the response variable and the predictor variables. To avoid fitting over-complex
238 relationships, we constrained the GAMs with a maximum degree of smoothing of 3, which
239 represents a polynomial of degree 2 maximum. All models were fitted using the function *gam*
240 present in MGCV R package (Wood, 2017).

241 Note that both the environmental variables and the food web topological metrics inevitably
242 show some level of spatial autocorrelation. To account for spatial dependency not explained
243 by the spatial drivers, we first built an autocovariate variable for each of the composite
244 descriptors to estimate how much the response variable for any site reflects the values of the
245 neighboring sites (Dorman et al. 2007; function *autocov_dist* in SPDEP R package). However,
246 since this autocovariate was unconditional to the environmental variation (i.e. the response
247 variable could show a spatial autocorrelation because the environment is itself
248 autocorrelated), we modelled each autocovariate variable (for each structural composite
249 descriptor) to the set of environmental variables using a bootstrap aggregating model (random
250 forest function in RANDOMFOREST R package; Liaw *et al.*, 2002). We then extracted the
251 residuals of the model and used them as spatial variables independent of the spatial predictors
252 (or at least of the predictor variables used here in the study) in the GAMs. Hereafter, such
253 variables will be referred as spatial residuals variables.

254 We used a “permutation accuracy importance” method (Strobl et al. 2007, 2009) to estimate

255 the importance of each predictor variable on the spatial distribution of local food webs
256 metrics. The predictor in test is randomized so that its original association to the response
257 variable is broken. Then, the randomized (through means of permutations) variable and the
258 remaining unchanged predictors are used to predict the response. A “variable importance”
259 score is then measured as the Pearson correlation between the original prediction and the one
260 after permutation of the selected predictor (Strobl et al. 2009). The more the Pearson
261 correlation decreases when the variable is permuted, the more important the variable is. The
262 whole procedure was repeated 1000 times. To ease the interpretation of the results, we
263 reported the average (1 – Pearson correlation). Values close to 1 reflected high importance,
264 values close to 0, no importance.

265

266 **RESULTS**

267 **Local Food web structure**

268 Most of the sixteen food web structural metrics showed a strong spatial structure (Figure 1
269 for a selection of six metrics, Fig S1 for all other metrics, and Table 1 for descriptive
270 statistics). Assemblages in northern latitudes (United Kingdom, Denmark and Scandinavian
271 Peninsula) and in mountain ranges (such as Alps and Carpathians) had fewer species, lower
272 trophic levels and higher proportion of basal species than in the rest of Europe. Species in
273 these locations had larger diet breadths (i.e. higher generality) on average. In continental
274 regions, i.e. in central and eastern Europe, food webs tended to be more speciose and with
275 higher trophic levels. Within these food webs, species were more evenly distributed between
276 basal and intermediate species, with top predator species always representing less than 5 % of
277 the community. In southern Europe, along the Mediterranean basin, food webs were the most
278 species rich and had the highest linkage densities and clustering coefficients. In this region,
279 trophic levels were as high as for continental food webs, while, connectance in some areas,

280 such as Anatolian region (Turkey) and southeast of Spain, was as high as in near arctic
281 assemblages.

282

283 **Deviation of local food web structure to random assembly.**

284 Deviations of local food webs to the null expectation varied between the different metrics
285 and across the species richness gradient (Table 1 and Fig. S.2). We observed that only six
286 food web metrics differed at least 90 % of the times from what could be expected from
287 random draws from the metaweb (link density, connectance, proportion of intermediate and
288 omnivore species and characteristic path length). However, for low species richness, most of
289 these metrics do not differ from a random assembly (Figure S.2). The remainder food web
290 properties consistently fell within the random intervals irrespective of species richness (e.g.
291 vulnerability, generality, mean and maximum trophic level; Table 1). In other words, the
292 spatial distribution of these latter metrics could be explained purely by the distribution of
293 species richness.

294

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

296 Two main axes of variation, explaining approximately 82% of the total variance,
297 summarized the co-variation of six food web properties (link density, connectance, proportion
298 of intermediate and omnivore species and characteristic path length; Table 2; Fig. 2). The first
299 axis, that we hereafter called *richness* composite descriptor, explained 52.02% of structural
300 variation and was related to link density (average number of interactions), proportion of
301 intermediate and omnivore species (Table 2; Fig. 2). This result indicates that food webs with
302 more species have more links per species and higher proportion of intermediate species (i.e.
303 proportion of species having both prey and predators in local food webs).

304 The second descriptor, hereafter named *connectance* composite descriptor, explained

305 30.08% of the total variance and was mainly related to food web complexity (through
306 connectance and characteristic path length; Table 2; Fig. 2). Along this descriptor, food web
307 structure showed a negative correlation between characteristic path length and connectance,
308 suggesting that food webs with lower connectance have proportionally longer paths between
309 species.

310

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

312 Environmental drivers explained a significant proportion of the variance of the two
313 composite descriptors (68.9% of *richness*, and 38% for *connectance*; Table 3). The *richness*
314 composite descriptor of local, realized food webs was strongly related to temperature
315 variables (mean annual temperature and temperature seasonality). In this model, the
316 temperature variables were positively and linearly related with the *richness* composite
317 descriptor (Fig. 3a), i.e. sites with high temperatures and high seasonality supported
318 assemblages with more intermediate species and higher link density than ones in with colder
319 climates and low seasonality. While its importance was weaker than temperature variables,
320 net primary productivity correlated positively with the *richness* composite descriptor, mainly
321 at lower levels of productivity. From lower to intermediate productive areas, we observed a
322 positive relationship with this composite descriptor, i.e. a crescendo in number of species and
323 link density up to intermediate areas; however from intermediate to high productive areas, the
324 contribution of net primary productivity to food web structure was close to zero (Fig. 3a).

325 The human footprint was amongst the most important drivers of variation in the *connectance*
326 composite descriptor (Table 3). The correlation was positive from low to intermediate values
327 of human footprint (Fig. 3b), and it saturated above intermediate human footprint values.
328 Likewise, for the *richness* composite descriptor, but not as important, the temperature
329 variables had also a relevant relationship with the *connectance* composite descriptor (Table

330 3). Food webs had higher connectance with increasing annual average temperature and
331 seasonality, and species tended to be closer (Fig. 3b). Total annual precipitation correlated
332 positively with the *connectance* composite descriptor at low to intermediate precipitation,
333 whereas it correlated negatively at larger precipitation levels (Fig. 3b).

334 Spatial residuals variables were important for both summary descriptors of food web
335 structure (Table 3). The importance was particular higher for the *connectance* composite
336 descriptor than the *richness* composite descriptor, revealing that there are other spatial
337 processes affecting food web metrics along this axis that were not explained by the variables
338 used here.

339

340 **DISCUSSION**

341 The variation of food web structure over broad spatial scales is largely unknown in
342 terrestrial systems. Thanks to the compilation of a large dataset comprising pairwise trophic
343 interactions between European tetrapods, their geographical distributions and habitat
344 preferences, we standardized the design of local food webs, allowing for the analysis of food
345 web structure across broad and continuous spatial scales. By doing so, we were able to
346 explore how food web structure varies across Europe.

347 The spatial distribution of European food webs showed that the variation of several food
348 web metrics is driven mostly by the variation in species richness (Table 1). Furthermore, food
349 web structure was not different from random samples from the metaweb at species poor
350 locations (see supplementary figure. S2). In this case, the relationship between these metrics
351 and the number of species implied a threshold number of species that above which food web
352 structure deviates from the null expectation. Note that our assemblages derive from empirical
353 species distributions; therefore food web structural deviations from null expectancies can be
354 attributed to any selective process acting directly on species.

355

356 Our decomposition of food web structure into composite descriptors revealed two major
357 axes of structural variation, one mainly related to the number of species and another one
358 related to connectance. We had an *a priori* expectation that species richness and connectance
359 would be two orthogonal axes of variation of food web structure (Martinez, 1994; Riede *et*
360 *al.*, 2010; Dunne *et al.*, 2013). The study 14 empirical food webs by of Vermaat *et al.* (2009)
361 showed a similar correlation structure among food web metrics; a similar decomposition was
362 also observed by Baiser *et al.* (2012) for aquatic food webs spread across North America.
363 Further, the constant connectance hypothesis (Martinez 1992) states that the number of links
364 increases at species square rate if connectance is each species interact with a constant fraction
365 of the network, independently of species richness. Our principal components analysis on
366 European local food web metrics was coherent with these studies, as we observed that
367 connectance tended to be independent of the number of species, while link density increases
368 with species richness. However, a more specific analysis is needed to test both hypotheses.
369 Yet, we speculate as empirical evidence has previously shown, the relationship link-species
370 would lay in between the two hypotheses (Ings *et al.*, 2009).

371 Climatic gradients, in particular temperature and precipitation, have long been observed as
372 drivers of biodiversity at both local and global scales (Evans *et al.*, 2005). Climate variables
373 may affect food web structure via several means. First, climate acts as an abiotic filter on the
374 assembly of species (Keddy, 1992), which may affect the functional composition of
375 communities and impact food web structure (Lurgi *et al.*, 2012; Blanchard, 2015). Second, it
376 has been suggested that climate variability may directly affect the vertical structure of the
377 food web, where climate stability allows for longer food web chains and narrower diet niches
378 (Menge & Sutherland, 1987; Vázquez & Stevens, 2004; Cirtwill *et al.*, 2015). Third, climate
379 may affect food web structural properties, where interannual temperature variability can be
380 negatively correlated with modularity (Welti & Joern, 2015). Our study documented that

381 European food web structure, summarized into two descriptors, is related to annual average
382 temperature and its seasonality. The effect of temperature seasonality on food web structure is
383 counter-intuitive, where more climate variability was associated with more species diverse
384 food webs. This result might hide an important structuring effect of landscape structure in
385 Europe. Indeed, most large carnivores, and more generally, top-predators, are mostly present
386 in mountainous areas (the last part of the wild where they were recently re-introduced or
387 protected) where climate variability is the highest. That could explain, in part, this supposedly
388 surprising result.

389 The work from Vermaat *et al.* (2009) contributed to the understanding of how food web
390 structure co-varied with primary productivity, where trophic level, omnivory, proportion of
391 top species co-varied with primary productivity. Here, we raised a similar question, how
392 resource availability may affect European food web structure in space. Hypotheses relating
393 resource availability and food web structure predict that larger basal resource availability
394 should propagate up the food web, promote species richness and increase food chain length;
395 this relationship should be stronger in low productive environments (Jenkins *et al.*, 1992;
396 Post, 2002). Here, we observed that variation of the average trophic level and proportion of
397 basal species was mostly driven by variation in species richness, as revealed by the
398 comparison to the null model. Therefore such hypothesis linking basal species and trophic
399 level with productivity could not be supported here.

400 Human presence may lead to changes in land-use, habitat fragmentation and pollution,
401 which in turn can negatively affect biodiversity (Barnosky *et al.*, 2011; Cardinale *et al.*, 2012)
402 and food web structure (Evans *et al.*, 2013). Here, we used the human footprint index as a
403 measure of anthropogenic pressure to understand its correlation with vertebrate food web
404 structure. We did find a negative relationship between human footprint and the *connectance*
405 composite descriptor (Fig. 4). However, we cannot assume this to be a cause-effect

406 relationship, and it is more likely that it comes from a spatial coincidence between human
407 footprint, species richness and connectance. Climatic conditions and resource availability may
408 affect the spatial distribution of human densities and species diversity alike, which would
409 explain why the two are positively correlated with human population densities (Araújo, 2003).
410 Indeed, despite the weak importance of human footprint on the *richness* composite descriptor
411 (Table 3), its effect peaked at intermediate levels of human disturbance, where we also found
412 food webs with more species (Fig. 3a). On the other hand, even though the two major
413 complexity food web topological properties, species richness and connectance, were nearly
414 orthogonal in our ordination space (Fig. 2), they were negatively correlated at extreme low
415 values of richness. In general, very small food webs had high values of connectance (note in
416 Fig. 1 that areas with low species richness coincide with areas with high connectance).
417 Therefore, areas with low human footprint also had high *connectance* composite descriptor,
418 via low values of connectance.

419 The importance of the spatial residuals variable in *connectance* composite descriptor model
420 suggested the presence of other spatial processes. Since we use species distribution to design
421 European vertebrate assemblages, biogeographical processes, such as barriers to species
422 dispersal or even other biotic factors could lead to spatial similarities and/or dissimilarities in
423 food web structure not explained solely by climate nor resource availability. Further work is
424 needed to include such processes under a beta diversity analysis framework of food web
425 structure (Poisot *et al.*, 2012).

426 A limitation to our design was the even contribution of each prey to the predator's diet and
427 every trophic interaction was constant in space (i.e. if two species interacted in the metaweb,
428 they always interacted across their intercepted spatial range). The former implied that we did
429 not account for biomass or energetic requirements (in contrast, weighted food webs
430 interactions may be defined by biomass relationships) and as consequence we may have

431 inflated omnivory and connectance. The latter implied no species diet or behavioral
432 adaptability (e.g. prey behavioral changes in function of predator presence or predator diet
433 shift due to presence of competitors; Preisser *et al.*, 2009; Van Dijk *et al.*, 2008; Poisot *et al.*,
434 2012) and as a consequence our webs may have an inflated number of trophic interactions.
435 Further, the environment could influence the occurrence of interactions, which could also
436 influence the spatial structure of food webs. In addition, trophic interactions in our metaweb
437 were defined based not only on empirical studies, but also on by defining a potential array of
438 preys for each predator species and this may inflate generality and vulnerability. We are
439 aware of such issues and more work is necessary to quantify the level of uncertainty of our
440 method, for instance, by using highly resolved empirical food webs and quantify the
441 difference in topological properties obtained with the two methods. Nevertheless, this work is
442 a good example of how biogeography may help comprehend terrestrial food webs spatial
443 patterns.

444

445 ACKNOWLEDGEMENTS

446 The author JB was supported by the Communautés de Recherche Académique 3 (ARC 3 -
447 Environment) Auvergne Rhône-Alpes, France. JMM is supported by the TULIP Laboratory
448 of Excellence (ANR-10-LABX-41 and 394 ANR-11-IDEX-002-02), and by a Region Midi-
449 Pyrenees project (CNRS 121090). JB would like to express is gratitude for Julian Renaud for
450 gathering and preparing species distribution to be used in the analysis.

451

452 REFERENCES

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

455 Baiser, B., Gotelli, N.J., Buckley, H.L., Miller, T.E. & Ellison, A.M. (2012) Geographic

456 variation in network structure of a nearctic aquatic food web. *Global Ecology and*
457 *Biogeography*, **21**, 579–591.

458 Barnosky, A.D., Matzke, N., Tomiya, S., Wogan, G.O.U., Swartz, B., Quental, T.B.,
459 Marshall, C., McGuire, J.L., Lindsey, E.L., Maguire, K.C., Mersey, B. & Ferrer, E.A.
460 (2011) Has the Earth’s sixth mass extinction already arrived? *Nature*, **471**, 51–57.

461 Blanchard, J.A. (2015) A rewired food web. *Nature*, **527**, 7–8.

462 Boucher-Lalonde, V., Morin, A. & Currie, D.J. (2014) A consistent occupancy–climate
463 relationship across birds and mammals of the Americas. *Oikos*, **123**, 1029–1036.

464 Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani,
465 A., MacE, G.M., Tilman, D., Wardle, D.A., Kinzig, A.P., Daily, G.C., Loreau, M.,
466 Grace, J.B., Larigauderie, A., Srivastava, D.S. & Naeem, S. (2012) Biodiversity loss and
467 its impact on humanity. *Nature*, **486**, 59–67.

468 Chase, J.M. (2010) Stochastic community assembly causes higher biodiversity in more
469 productive environments. *Science*, **328**, 1388–1389.

470 Cirtwill, A.R., Stouffer, D.B. & Romanuk, T.N. (2015) Latitudinal gradients in biotic niche
471 breadth vary across ecosystem types. *Proceedings. Biological sciences / The Royal*
472 *Society*, **282**, 20151589-.

473 Currie, D.J. (1991) Energy and large-scale patterns of animal and plant species richness. *Am.*
474 *Nat.*, **137**, 27–49.

475 Currie, D.J., Mittelbach, G.G., Cornell, H. V., Field, R., Guégan, J.-F., Hawkins, B.A.,
476 Kaufman, D.M., Kerr, J.T., Oberdorff, T., O’Brien, E. & Turner, J.R.G. (2004)
477 Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic
478 richness. *Ecology Letters*, **7**, 1121–1134.

479 Davies, T.J., Buckley, L.B., Grenyer, R. & Gittleman, J.L. (2011) The influence of past and
480 present climate on the biogeography of modern mammal diversity. *Philosophical*

481 *Transactions of the Royal Society B: Biological Sciences*, **366**, 2526–2535.

482 Van Dijk, J., Gustavsen, L., Mysterud, A., May, R., Flagstad, Ø., Brøseth, H., Andersen, R.,
483 Andersen, R., Steen, H. & Landa, A. (2008) Diet shift of a facultative scavenger, the
484 wolverine, following recolonization of wolves. *Journal of Animal Ecology*, **77**, 1183–
485 1190.

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

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

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

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

496 Hagen, M., Kissling, W.D., Rasmussen, C., De Aguiar, M.A.M., Brown, L.E., Carstensen,
497 D.W., Alves-Dos-Santos, I., Dupont, Y.L., Edwards, F.K., Genini, J., Guimar??es, P.R.,
498 Jenkins, G.B., Jordano, P., Kaiser-Bunbury, C.N., Ledger, M.E., Maia, K.P., Marquitti,
499 F.M.D., Mclaughlin, ??rla, Morellato, L.P.C., O’Gorman, E.J., Tr??jelsgaard, K.,
500 Tylianakis, J.M., Vidal, M.M., Woodward, G. & Olesen, J.M. (2012) *Biodiversity,*
501 *Species Interactions and Ecological Networks in a Fragmented World*, Elsevier Ltd.

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

505 Imhoff, M.L., Bounoua, L., Ricketts, T., Loucks, C., Harriss, R. & Lawrence, W.T. (2004)

506 HANPP Collection: Global Patterns in Net Primary Productivity (NPP).

507 Ings, T.C., Montoya, J.M., Bascompte, J., Blüthgen, N., Brown, L., Dormann, C.F.,
508 Edwards, F., Figueroa, D., Jacob, U., Jones, J.I., Lauridsen, R.B., Ledger, M.E., Lewis,
509 H.M., Olesen, J.M., Van Veen, F.J.F., Warren, P.H. & Woodward, G. (2009) Ecological
510 networks - Beyond food webs. *Journal of Animal Ecology*, **78**, 253–269.

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

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

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

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

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

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

522 Kortsch, S., Primicerio, R., Fossheim, M., Dolgov, A. V & Aschan, M. (2015) Climate
523 change alters the structure of arctic marine food webs due to poleward shifts of boreal
524 generalists. *Proceedings. Biological sciences / The Royal Society*, **282**, 20151546-.

525 Ledger, M.E., Brown, L.E., Edwards, F.K., Milner, A.M. & Woodward, G. (2012) Drought
526 alters the structure and functioning of complex food webs. *Nature Climate Change*, **3**,
527 223–227.

528 Liaw, A., Wiener, M. & others (2002) Classification and regression by randomForest. *R news*,
529 **2**, 18–22.

530 Lurgi, M., Lopez, B.C. & Montoya, J.M. (2012) Climate change impacts on body size and

531 food web structure on mountain ecosystems. *Philosophical Transactions of the Royal*
532 *Society B: Biological Sciences*, **367**, 3050–3057.

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

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

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

541 Mazel, F., Wüest, R.O., Gueguen, M., Renaud, J., Ficetola, G.F., Lavergne, S. & Thuiller, W.
542 (2017) The Geography of Ecological Niche Evolution in Mammals. *Current Biology*, 1–
543 6.

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

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

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

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

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

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

560 Poiset, T., Guéveneux-Julien, C., Fortin, M.J., Gravel, D. & Legendre, P. (2017) Hosts,
561 parasites and their interactions respond to different climatic variables. *Global Ecology
562 and Biogeography*, **26**, 942–951.

563 Post, D.M. (2002) The long and short of food-chain length. *Trends in Ecology & Evolution*,
564 **17**, 269–277.

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

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

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

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

581 2536–2544.

582 Schleuning, M., Fründ, J., Klein, A., Abrahamczyk, S., Alarcón, R., Albrecht, M., Andersson,
583 G.K.S., Bazarian, S., Böhning-Gaese, K., Bommarco, R., Dalsgaard, B., Dehling, D.M.,
584 Gotlieb, A., Hagen, M., Hickler, T., Holzschuh, A., Kaiser-Bunbury, C.N., Kreft, H.,
585 Morris, R.J., Sandel, B., Sutherland, W.J., Svenning, J.-C., Tschardtke, T., Watts, S.,
586 Weiner, C.N., Werner, M., Williams, N.M., Winqvist, C., Dormann, C.F. & Blüthgen, N.
587 (2012) Specialization of Mutualistic Interaction Networks Decreases toward Tropical
588 Latitudes. *Current Biology*, **22**, 1925–1931.

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

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

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

596 WCS, W.C.S. & CIESIN, C.U.-C. for I.E.S.I.N. (2005) Last of the Wild Project, Version 2,
597 2005 (LWP-2): Global Human Footprint Dataset (Geographic).

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

600 Wood, S.N. (2017) Mixed GAM Computation Vehicle with Automatic Smoothness
601 Estimation.

602 Wright, D.H. (1983) Species-energy theory : an extension of species-area theory. *Oikos*, **41**,
603 496–506.

604 Zanden, M.J. Vander & Fetzer, W.W. (2007) Global patterns of aquatic food chain length.
605 *Oikos*, **116**, 1378–1388.