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RESEARCH PAPER

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Spatial analyses of multi-trophic terrestrial vertebrate assemblages in Europe

João Braga[1] | Laura J. Pollock[1] | Ceres Barros[1,2,3] | Núria Galiana[4] | José M. Montoya[4] | Dominique Gravel[5] | Luigi Maiorano[6] | Alessandro Montemaggiori[6] | Gentile Francesco Ficetola[1,7] | Stéphane Dray[8] | Wilfried Thuiller[1]

[1]Laboratoire d'Écologie Alpine (LECA), University Grenoble Alpes, CNRS, University Savoie Mont Blanc, Grenoble, France

[2]Department of Forest Resources Management, Faculty of Forestry, UBC Forest Sciences Centre, Vancouver, British Columbia, Canada

[3]Pacific Forestry Centre, Canadian Forest Service – Natural Resources Canada, Victoria, British Columbia, Canada

[4]Theoretical and Experimental Ecology Station, Moulis, France

[5]Département de biologie, Université de Sherbrooke, Sherbrooke, Quebec, Canada

[6]Department of Biology and Biotechnologies "Charles Darwin", Università di Roma "La Sapienza", Roma, Italy

[7]Department of Environmental Sciences and Policy, Università degli Studi di Milano, Milano, Italy

[8]Laboratoire de Biométrie et Biologie Evolutive, Univ Lyon, Université Claude Bernard Lyon 1, CNRS, Villeurbanne, France

Correspondence
João Braga, Laboratoire d'Écologie Alpine (LECA), University Grenoble Alpes, CNRS, University Savoie Mont Blanc, F-38000 Grenoble, France.
Email: joaofvbraga@gmail.com

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Abstract

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

Location: Europe.

Time period: Present.

Major taxa studied: Tetrapods.

Methods: We combined an expert-based food web (1,140 species and 70,601 links) of all European tetrapods with their respective spatial distributions. We mapped 17 different food web metrics representing complexity, chain length, vertical diversity and diet strategy across Europe and tested whether their distribution reflects the spatial structure of species richness using a null model of food web structure. To avoid multicollinearity issues, we defined composite descriptors of food web structure that we related to a set of environmental layers summarizing both natural and anthropogenic influences and tested their relative importance in explaining the spatial distribution of European terrestrial vertebrate food webs.

Results: Of the 17 metrics, 10 showed a non-random spatial distribution across Europe and could be summarized along two major axes of variation in food web structure. The first was related to species richness, mean trophic level and the proportion of intermediate species, whereas the second was related to the connectance and proximity of species within the web. Both descriptors varied with latitudinal gradient. The best descriptors of food web structure were mean annual temperature and seasonality (negatively correlated with the first axis), and human footprint (positively correlated with the second axis).

Main conclusions: We demonstrate the importance of climate and anthropogenic pressure in shaping the spatial structure of European tetrapod food webs.

KEYWORDS
biodiversity, environmental gradients, food web comparison, metaweb, network properties, null model, tetrapod communities

1 | INTRODUCTION

Documenting large-scale biodiversity distribution and understanding what drives variation between or within different regions of the world has long fascinated naturalists (Wallace, 1876). The recent and ever-increasing rise of large-scale distribution databases (e.g., IUCN, BirdLife, Map of Life) has led to new comprehensive analyses of biodiversity distribution. Thanks to available data on species traits and phylogenetic relatedness, global and regional distributions of species, functional and phylogenetic diversities are now well documented for tetrapods (Jetz & Fine, 2012; Jetz, Thomas, Joy, Hartmann, & Mooers, 2012; Mazel et al., 2014, 2017).

Such measurements of biodiversity (taxonomic, functional and phylogenetic diversity) focus on a group of species co-occurring in a certain area or region, which are subsequently compared with measurements of other areas to identify localities with higher or lower biodiversity (e.g., hotspots versus coldspots; Mazel et al., 2014). However, species assemblages are not merely the sum of species co-occurring in an area; they share a myriad of biotic interactions (e.g., predation, competition, facilitation) that originate a variety of ecological networks through space. Although biogeographical studies have investigated how species or functional diversity vary in space and the underlying role of the environment (e.g., Davies, Buckley, Grenyer, & Gittleman, 2011; Mazel et al., 2017; Safi et al., 2011), we know little about the spatial distribution of ecological networks (Pellissier et al., 2018).

Food webs are representations of the trophic interactions of communities, where each node in the network represents a species and each edge is a directional feeding interaction from a prey to a predator. Food web ecology has focused on the trophic relationships between species within discrete communities, with the goal of inferring the underlying processes acting upon them, such as the relationship between species diversity and food web structure, community assembly processes and even robustness of those communities to species extinctions (Montoya, Pimm, & Solé, 2006). However, since the pioneering work of Kitching (2000) on latitudinal gradients of aquatic food web structure, food web ecology has shifted from finding food web structural generalities across distinct communities to searching for large-scale spatial distribution of ecological networks, such as latitudinal gradients, and relationships with climate and resource availability (Kortsch, Primicerio, Fossheim, Dolgov, & Aschan, 2015; Montoya & Galiana, 2017; Pellissier et al., 2018; Poisot, Guéveneux-Julien, Fortin, Gravel, & Legendre, 2017; Post, 2002; Roslin et al., 2017; Wood, Russell, Hanson, Williams, & Dunne, 2015).

Large-scale spatial distribution of food web structure may be driven by multiple factors. First, food web structure follows both species richness and compositional gradients (Baiser, Gotelli, Buckley, Miller, & Ellison, 2012; Riede et al., 2010), and any process acting upon these features of biodiversity, such as environmental sorting of species, will cause food webs to be spatially structured (Pellissier et al., 2018). Second, food web topology may reflect community adaptations to environmental stability. The latitude–niche breadth hypothesis, for instance, postulates that species have more specialized diets in the tropics and become more generalist towards the poles, because higher environmental stability and amount of energy in the tropics allow for greater species packing (MacArthur, 1955; Schleuning et al., 2012). Nevertheless, this hypothesis does not seem to be verified across different systems (Cirtwill, Stouffer, & Romanuk, 2015) and lacks testing across large spatial scales. Third, resource availability in conjunction with disturbances and environmental variability may also affect food web topology. Low resource availability for primary consumers limits species richness and food chain length, whereas disturbances and ecosystem size drive food chain length at intermediate levels of resource availability (Kaunzinger & Morin, 1998; Post, 2002). Again, such observations are not ubiquitous (Zanden & Fetzer, 2007). This hypothesis has yet to be tested across large environmental gradients and for complex (i.e., species-rich) food webs.

Here, motivated by these hypotheses, we built the first comprehensive food web of European tetrapod species. For this, we used a combination of expert knowledge and literature and mapped the food web structure of all vertebrate assemblages naturally occurring in Europe, western Russia and Turkey, using a uniform spatial grid at 10 km resolution. Given that the above-mentioned hypotheses focus on different facets of food web topology, we analysed a large set of food web properties, such as complexity metrics (species richness, connectance and number of trophic interactions), vertical diversity metrics (proportion of basal, intermediate and top predator species), feeding strategy metrics (generality, vulnerability and omnivory) and trophic level metrics. We compared local observations of food web metrics with a constrained null model to reveal significant associations with environmental variables.

Most network metrics cannot be dissociated from each other because they covary with either the number of species or connectance (Baiser et al., 2012; Poisot & Gravel, 2014; Riede et al., 2010; Vermaat, Dunne, & Gilbert, 2009). Hence, to comprehend and summarize European food web spatial diversity, we applied a principal components analysis (PCA) to decompose the food web structure into two composite descriptors (Pellissier et al., 2018) and investigated how the environment, landscape and anthropogenic pressure influenced their spatial distribution.

We expected annual temperature and precipitation to be good predictors of food web spatial structure because they are major drivers of species sorting and community assembly over large spatial scales (Currie, 1991; Ledger, Brown, Edwards, Milner, & Woodward, 2012; Riede et al., 2010; Vázquez & Stevens, 2004). Likewise, highly productive sites should provide more resources for consumers, therefore supporting higher trophic levels (Post, 2002; Wright, 1983). Thus, we expected higher trophic levels in areas with high productivity. We also anticipated that habitat fragmentation and human disturbance would shape European food webs. High levels of fragmentation might reduce the strength of interactions between species or even prevent species from interacting, ultimately leading to simpler networks with shorter chain lengths and more generalist species (Hagen et al., 2012).

2 | MATERIALS AND METHODS

2.1 | Study area and species distributions

The study area included Europe (excluding Macaronesia region and Iceland) and western regions of Turkey and Russia (hereafter referred to as "Europe"). We extracted species ranges for tetrapods naturally occurring within the study area from Maiorano et al. (2013). In total, our analyses focused on 510 bird, 288 mammal, 239 reptile and 103 amphibian species (for the full species list, see Table S1.1 in Appendix S1 of Supporting Information). Species range data followed a regular grid of 300 m resolution (WGS84), where cells took values of zero for unsuitable habitat, one for secondary habitat and two for primary habitat (Maiorano et al., 2013). We treated secondary and primary habitat equally as "suitable habitat". All species range maps were up-scaled to a 10 km × 10 km equal-size area grid (ETRS89; total of 78,873 cells). We considered species potentially present in a 10 km × 10 km cell (hereafter referred to as local assemblage) when they had least one 300 m suitable habitat cell within it. In the Appendix S2 in Supporting Information, we show that the proportion of suitable habitat needed for a species to be present in each cell did not affect the spatial distribution of species richness or connectance, and thus did not influence the spatial distribution of local food web structure (see below section 2.2).

2.2 | European tetrapod metaweb and local food web structure

A trophic metaweb compiles all predator–prey interactions between species of a given regional species pool (Pascual & Dunne, 2006). Here, we designed the most complete metaweb of European tetrapods from expert knowledge, published information and field guides. As in previous studies (e.g., Lurgi, Lopez, & Montoya, 2012), all tetrapod species whose diet did not include another species of the metaweb (such as herbivores, insectivores, piscivores and detritivores) were defined as basal species. Then, we searched for trophic interactions between species that fed upon other tetrapod species (and omnivores) from an exhaustive literature review. We defined a trophic interaction as predation on any life stage of a species (e.g., egg and larval when applicable, juvenile or adult). Trophic interactions between a predator and a prey were identified from published accounts of their observation, morphological similarities between potential prey and literature-referenced prey and, in the absence of this information, the diet of the sister species of the predator. Twelve general diet categories (i.e., basal resources) were added to the metaweb, which included detritus, coprophagy, mushrooms, mosses and lichens, algae, fruits, grains, other plant parts, invertebrates, fish, domestic animals and carrion.

The metaweb comprised 70,601 trophic interactions distributed across 1,140 terrestrial vertebrate species (66% of basal species, of which 10% were herbivores and 56% non-herbivore basal species, 33% were intermediate species and <1% were top predator species) and a connectance of .05. On average, species had 62 interactions (including prey and predator interactions) and were two interactions away from each other.

We defined local food webs by intersecting the metaweb with local community composition (Gravel et al., 2019). In the few cases where a given species was present in a cell but had no available prey or did not share a common habitat type with any of its prey, the species was considered absent in that particular location (i.e., assuming a false positive in the distribution data; Gravel, Massol, Canard, Mouillot, & Mouquet, 2011). We assumed that diet categories are widely distributed across the landscape and therefore that basal species always have a resource.

For each local food web, we calculated 17 food web properties pertaining to four groups: complexity, strategy, vertical diversity and trophic level. Complexity metrics included species richness, connectance, clustering coefficient, characteristic path length and link density (average distance between species and average number of interactions per species, respectively). Strategy metrics refer to dietary niche properties of species and included the proportion of omnivore species, average trophic similarity between species, the average generality (number of prey per consumer species) and vulnerability (number of predators per resource species). We measure two other strategy metrics, normalized standard deviations of generality and vulnerability, both normalized by link density (Williams & Martinez, 2000). Vertical diversity metrics quantify the proportion of species along three major trophic levels: basal, intermediate and top level. Note that we defined basal species as non-autotroph species without terrestrial vertebrate prey. Trophic level metrics refer to the vertical trophic position of species within a food web and included the mean trophic level and the maximum trophic level. See Table 1 for the list of metrics and their definitions. Food web metrics were calculated using the "igraph" and "cheddar" R packages (Csardi & Nepusz, 2006; Hudson et al., 2013) in R v.3.4.1 (R Development Core Team, 2011).

2.3 | Climatic, energetic and habitat variables

We extracted four climatic variables from the WorldClim database (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005) at 30° resolution: annual mean temperature, temperature seasonality (*SD* of monthly mean temperature), total annual precipitation and coefficient of variation of precipitation. We chose these variables because they are correlated with tetrapod ranges (Boucher-Lalonde, Morin, & Currie, 2014). We approximated the amount of resources available to the primary consumers in each cell with estimates of net primary productivity (in grams of carbon per year at 0.25 decimal degrees spatial resolution; Imhoff et al., 2004). We also represented the anthropogenic influence on natural landscapes using the human footprint index from the Last of the Wild database v.2 (1 km spatial resolution; Wildlife Conservation Society, Center for International Earth Science Information Network & Columbia University, 2005). We resampled all climatic variables, primary productivity and human footprint data by averaging at each 10 km × 10 km cell. We also measured habitat diversity and heterogeneity using, respectively, the Shannon–Weiner and evenness indices applied to the GlobCover v.2.2 habitat classification at 300 m cell resolution. See the Appendix

TABLE 1 Food web properties, respective means, *standard deviations (SD)* and null rejection rates across Europe

Food web property		Definition	Mean (*SD*)	Rejection rate
Species richness		Number of species	194.8 (40.14)	Not applicable
Connectance		Proportion of realized links that occur in a web	.084 (.01)	**.99**
Link density		Average number of links per species	17.33 (3.26)	**.99**
Clustering coefficient		Probability of linkage of two species, given that both are linked to a third species	.28 (.03)	**.99**
Characteristic path length		The mean shortest food chain length between species pairs	1.83 (.03)	**.99**
Vulnerability		Mean number of predators per resource species	16.78 (3.22)	**.99**
SD of vulnerability		Normalized *SD* of number of predators per resource species	.72 (.08)	0
Generality		Mean number of prey per consumer species	38.38 (6.70)	**.94**
SD of generality		Normalized *SD* of number of prey per consumer species	1.88 (1.16)	.89
Maximum trophic similarity		Mean maximum number of links (in- and outward) shared between all pairs of species	.75 (.02)	.77
Proportion of basal species	Non-herbivores	Proportion of species that prey on non-plant diet categories	.53 (.03)	.53
	Herbivores	Proportion of species that prey exclusively on plant diet categories	.04 (.01)	.47
Proportion of intermediate species		Proportion of species with prey and predators	.42 (.03)	**.97**
Proportion of top predator species		Proportion of species without any predators	.01 (.01)	0
Proportion of omnivores		Proportion of species that feed on more than one trophic level	.43 (.03)	**.96**
Mean trophic level		Mean prey average trophic level	2.35 (.08)	**.96**
Maximum trophic level		Maximum prey average trophic level	3.58 (0.14)	0

Note: Rejection rates in bold highlight variables (rejection rate > 90%) that were retained in the subsequent analyses.

S3 in Supporting Information for more information about the spatial distribution of the climatic, energetic and habitat variables.

2.4 | Statistical analyses

Our analyses consisted of three sequential steps. First, we checked whether the spatial distribution of each local metric was different from random using a null model and selected the metrics that differed from null expectations for subsequent analyses. Second, we reduced the complexity of the retained metrics by applying a PCA and selecting the first two axes of variation. Third, we related these two axes of variation to climate, resource availability, habitat diversity and human disturbance using generalized additive models (GAMs).

2.4.1 | Is the spatial distribution of food web properties random?

Food web structure may vary with species richness independently of any other constraints acting upon it (e.g., environment). We thus built a null model to test whether European local food webs and their associated properties could result from a draw from the European species pool, irrespective of their interactions. The null hypothesis is that a given local food web metric is not different from one measured from a random assemblage of species of equal richness. This implies that species are randomly distributed in space, independently of the local environment and of their position in the metaweb, thus breaking any spatial sorting of species patterns. The null model consisted of randomly drawing species from the metaweb and then extracting the corresponding local food webs. We applied three constraints to the null model: (a) species richness was the same as observed (from 10 to 305 species); (b) the observed proportion of reptiles, birds, mammals and amphibians; and (c) species needed at least one prey item to be included in the food web (Gravel et al., 2011). We randomly drew and kept food webs that met all three conditions, until we had 999 food webs for each value of species richness. We then recalculated the 17 food web metrics to obtain a distribution of metrics under the null hypothesis (Table 1). For each cell, we compared the observed food web metrics with their corresponding null distributions and computed the associated *p*-value. We adjusted *p*-values for multiple comparisons using a false discovery rate method based on Benjamini and Hochberg (1995), available in the function *p.adjust* in the "stats" R package. We retained food web metrics that had a rejection rate of 90% (i.e., 90% of all local observed values were significantly different from ones in random assemblages). Considering that we computed one test per cell (total of 78,873 cells), a food web metric should be significantly different from random in *c*. 71,000 cells in order to be kept in our analysis. For a more detailed description of the null model, see the Appendix S4 in Supporting Information.

2.4.2 | How to reduce the dimensionality in local food web properties?

Many food web metrics are correlated (Vermaat et al., 2009) either because of their mathematical formulation or because of combinatory constraints (Poisot & Gravel, 2014). We applied a PCA on the ten retained variables over the 78,873 cells of Europe (Table 1) to analyse the most insightful axes of variations between these metrics. This allowed us not only to understand how food web metrics covary with each other, but also to summarize the food web structure of European assemblages (as a whole) into a set of meaningful axes. We emphasize that the correlation structure among the metrics we analysed is driven not only by the fundamental constraints linking metrics mentioned above, but also by the effect of spatial variation in food web composition. From the PCA, we kept only the axes that each explained ≥20% of the total variance, hereafter referred to as food web structural composite descriptors. This analysis was performed in R using the "ade4" package (Dray & Dufour, 2007).

2.4.3 | How to statistically relate food web structural descriptors to environmental predictors?

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

Is noteworthy that both the environmental variables and food web topological metrics inevitably show some level of spatial autocorrelation. To account for spatial dependency unexplained by the spatial drivers, we built an autocovariate variable for each of the composite descriptors to estimate how much the response variable for any site reflects the values of the neighbouring sites (Dormann et al., 2007; function *autocov_dist* in "spdep" R package). However, given that this autocovariate was unconditional to environmental variation (i.e., the response variable could show a spatial autocorrelation because the environment itself is autocorrelated), we modelled each autocovariate variable (for each structural composite descriptor) to the set of environmental variables using a bootstrap aggregating model (random forest function in "randomForest" R package; Liaw & Wiener, 2002). We then extracted the residuals of the model and used them as spatial variables independent of the spatial predictors in the GAMs. Hereafter, these variables will be referred as spatial residuals variables.

We used the permutation accuracy importance method (Strobl, Boulesteix, Zeileis, & Hothorn, 2007; Strobl, Malley, & Tutz, 2009) to estimate the importance of each predictor variable on the spatial distribution of local food web metrics. The predictor under test is randomized so that its original association with the response variable is broken. Then, the randomized variable (by means of permutations) and the remaining unchanged predictors are used to predict the response. A variable importance score is then measured as the Pearson correlation coefficient (ρ) between the original prediction and the prediction after permutation of the selected predictor (Strobl et al., 2009). The lower the correlation, the more important the variable. This whole procedure was repeated 1,000 times. To facilitate the interpretation of results, we reported the average $1 - \rho$. Values close to 1 reflected high importance, values close to 0, no importance.

In Appendix S6 of the Supporting Information, we show that using single food web metrics or the composite descriptors from the PCA yields equivalent results and relationships with the predictors. Hence, we opt to PCA axes because they summarize the main dimensions of food web structure.

3 | RESULTS

3.1 | Local food web structure

Most of the 17 food web metrics showed a strong spatial structure (for a selection of six metrics, see Figure 1; for descriptive statistics, see Table 1; for all other metrics, see Supporting Information Appendix S5, Figure S5.4). Assemblages in northern latitudes (United Kingdom, Denmark and Scandinavian Peninsula) and in mountain ranges (such as the Alps and Carpathians) had fewer species, with shorter food chains and a higher proportion of basal species than in the rest of Europe. Food webs in central and eastern Europe were more species rich and with longer food chains and larger diet breadths (i.e., higher generality) on average. Within these food webs, species were more evenly distributed between basal and intermediate species, with top predator species always representing <5% of the community. In southern Europe, along the Mediterranean basin, food webs were the most species rich and had the highest link densities and clustering coefficients. In this region, food chains lengths were as high as for continental food webs, and connectance in the Anatolian region (Turkey) and southeast of Spain was as high as in near arctic assemblages. In other words, assemblages across the Mediterranean basin were the most species rich and highly interacting.

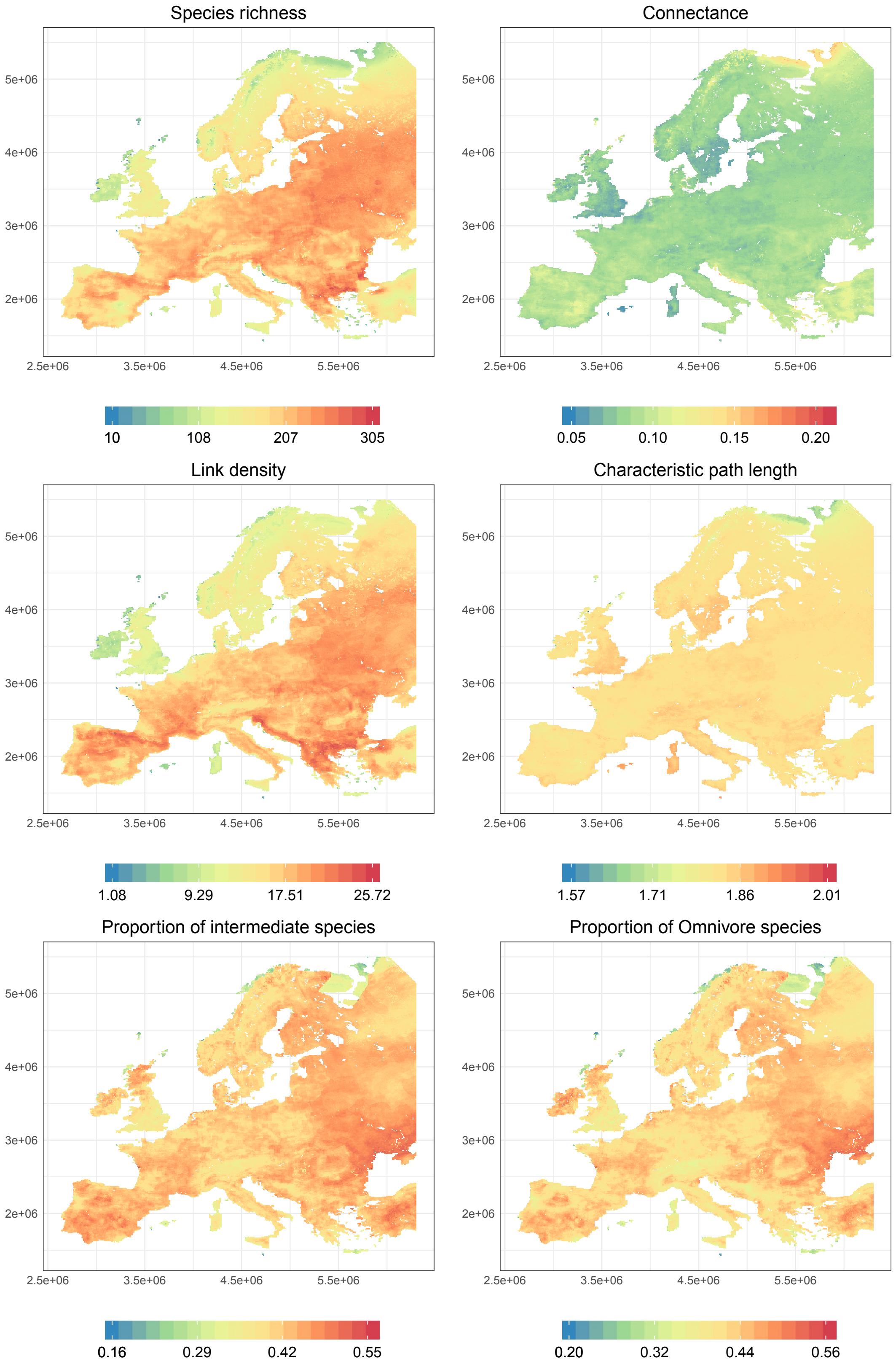

FIGURE 1 Spatial distribution of six metrics of the European tetrapod food webs: species richness, connectance, link density, characteristic path length, proportion of intermediate species and proportion of omnivore species. For a detailed description of these metrics, see Table 1. The distribution of the 17 food web metrics is provided in the Supporting Information (Appendix S5, Figure S5.4)

3.2 | Deviation of local food web structure from random assembly

Deviations of local food webs from the null expectation varied between the different metrics and across the species richness gradient (Table 1; see Appendix S4, Figure S4.3). We observed that only nine food web metrics differed ≥90% of the time from what could be expected from random draws from the metaweb (link density, connectance, proportion of intermediate and omnivore species, mean trophic level, generality, vulnerability, characteristic path length and cluster coefficient). However, at low levels of species richness, most of these metrics do not differ from a random assembly (see Appendix S4, Figure S4.3). The remaining food web properties consistently fell within the random intervals irrespective of species richness (e.g., *SD* of vulnerability and generality, maximum trophic level and maximum trophic similarity; Table 1). In other words, the spatial distribution of these metrics could be explained purely by their correlation with the distribution of species richness and its spatial drivers.

3.3 | Composite descriptors of the local realized food webs

Two main axes of variation, explaining *c.* 76.28% of the total variance, summarized the covariation of 10 food web properties (species richness, link density, connectance, proportion of intermediate and omnivore species, mean trophic level, vulnerability, generality, characteristic path length and cluster coefficient; Table 2; Figure 2). The first axis, hereafter called the *richness* composite descriptor, explained 53.66% of structural variation and was negatively related to species richness, link density (average number of interactions), proportion of intermediate species, vulnerability, generality and omnivore species and mean trophic level (Table 2; Figure 2). This result indicates that food webs with more species have more links per species, a higher proportion of intermediate species (i.e., proportion of species having both prey and predators in local food webs), have on average more prey and predators, and species occupy higher trophic levels.

The second descriptor, hereafter named the *connectance* composite descriptor, explained 22.62% of the total variance and was mainly related to food web complexity, through connectance, clustering coefficient and characteristic path length (Table 2; Figure 2). Along this descriptor, connectance and clustering coefficient were both negatively correlated with characteristic path length, suggesting that food webs with lower connectance were less clustered and had proportionally longer paths between species.

3.4 | Environmental drivers of local food web descriptors

Environmental drivers explained a significant proportion of the variance of the two composite descriptors (74.4% of *richness* and 43.9% of *connectance*; Table 3). The *richness* composite descriptor had a strong, linear and negative relationship with temperature variables (mean annual temperature and temperature seasonality; Figure 3a), with sites

TABLE 2 Correlation between 10 food web properties and the two major principal components axes of the principal components analysis (*richness* and *connectance* composite descriptors)

Topological metric	*Richness* composite descriptor	*Connectance* composite descriptor
Species richness	−.39	.19
Connectance	.05	−.65
Link density	−.42	−.10
Characteristic path length	−.16	.51
Generality	−.36	−.11
Vulnerability	−.42	−.10
Cluster coefficient	−.09	−.49
Proportion of intermediate species	−.30	−.07
Proportion of omnivore species	−.27	0
Mean trophic level	−.41	−.01

Note: In total, both composite descriptors explained 76.28% of food web spatial variance (measured by these 10 variables).

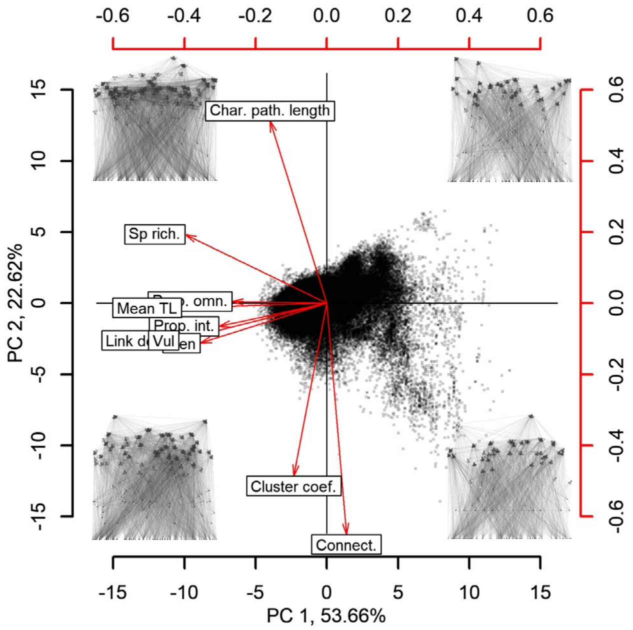

FIGURE 2 Principal components analysis of European food web metrics. Red arrows represent the direction and value of correlations between individual topological metrics and each of the structural food web descriptors. The first component (PC 1; *richness* structural composite descriptor) was negatively correlated with species richness (Sp rich.), link density (Link dens.), the proportion of intermediate (Prop. int.) and omnivore (Prop. omn.) species, mean trophic level (Mean TL), generality (Gen) and vulnerability (Vul). The second component (PC 2; *connectance* composite descriptor) was highly correlated with connectance (Connect.), characteristic path length (Char. path length) and cluster coefficient (Cluster coef.). The four food webs represent the general topology of food webs in each quadrant and were drawn from the closest point to the centroid of each quadrant

TABLE 3 Variable importance for each structural composite descriptor model based on the “permutation accuracy importance” method

	Richness composite descriptor	*Connectance* composite descriptor
Spatial residuals	.12	.32
Average annual temperature	.43	.24
Temperature seasonality	.47	.10
Precipitation	.01	.05
Coefficient of variation for precipitation	.01	.04
Shannon index	.08	.09
Habitat evenness	.03	0
Primary productivity	.18	.13
Human footprint	.01	.30

Note: In the *richness* composite descriptor model, temperature variables (annual average and seasonality) were the most important variables, whereas in the *connectance* composite descriptor model, spatial residuals were the most important variable, suggesting that other spatial processes are acting on this composite descriptor, not accounted for by the other variables. The *richness* descriptor model explained 74.4% of the variance, whereas the *connectance* composite descriptor model explained 43.9%.

that had high temperatures and seasonality supporting richer assemblages, with more intermediate species, higher link densities and trophic levels. Net primary productivity had a weaker importance relative to temperature variables, but had a negative correlation with the *richness* composite descriptor. We observed a nonlinear increase in species richness, generality, vulnerability and link density from lower to highly productive areas, where the contribution of net primary productivity to food web structure was stronger in areas of lower to intermediate productivity (Figure 3a). Human footprint had the least important effect on the *richness* composite descriptor, which seemed to increase slightly above intermediate levels of human footprint (Table 3).

Conversely, the variation in the *connectance* composite descriptor was mostly affected by mean annual temperature and human footprint (Table 3). This descriptor had a negative relationship with annual average temperature, suggesting that food webs had higher connectance and more closely interacting species as annual average temperatures increased. On the contrary, human footprint had a positive correlation with the *connectance* composite descriptor up to intermediate values, after which its effect was near zero. This indicates that food webs became less connected, less clustered and with longer paths from low to intermediate regions of human footprint (Figure 3b). Finally, total annual precipitation was correlated positively with the *connectance* composite descriptor at low to intermediate precipitation, but negatively at higher levels of precipitation (Figure 3b).

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

4 | DISCUSSION

The large-scale variation of food web structure is still mostly unknown in terrestrial systems. Thanks to the compilation of a large dataset comprising pairwise trophic interactions between European tetrapods, their geographical distributions and habitat preferences, we extracted local food webs and successfully explored how they vary across Europe.

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

The latitudinal gradient of diversity is one of the most conspicuous patterns of biogeography. Not only do we revisit this relationship for European tetrapod species (Figure 1), but we also show that it influences food web spatial structure. Food web metrics related to the variability of feeding strategies, vertical diversity and maximum trophic level did not differ from what would be expected under random assemblages of species, indicating that species richness was the key driver of their variation, especially at species-poor locations.

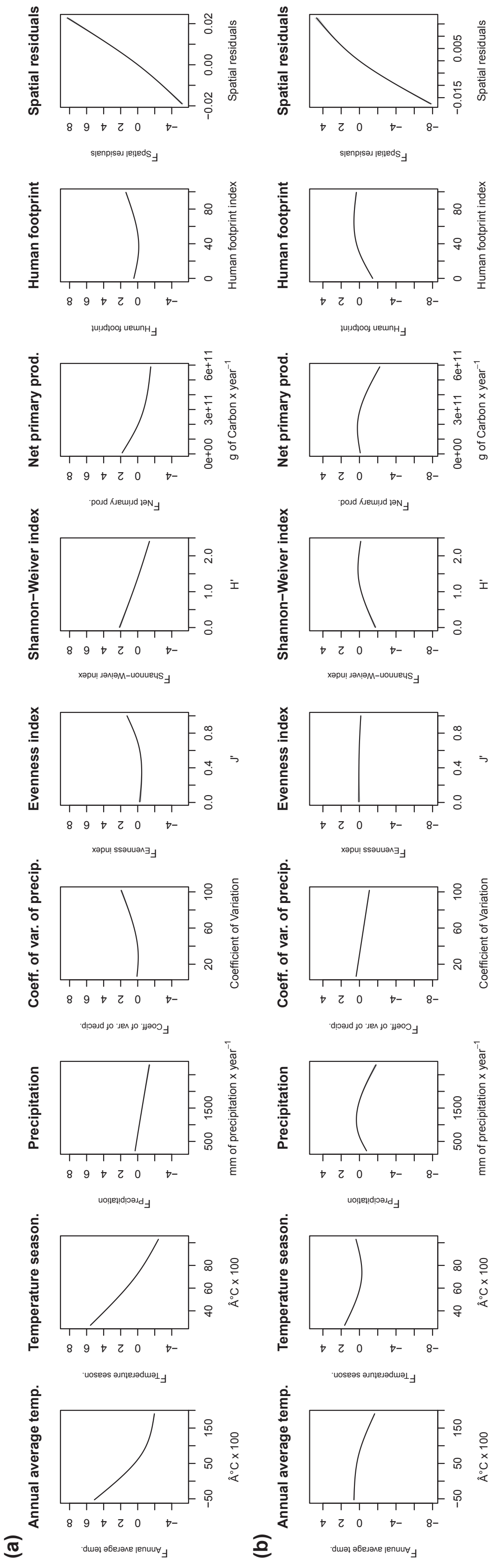

FIGURE 3 Smoother components of food web *richness* composite descriptor (a) and *connectance* composite descriptor (b) generalized additive models of the European food web in the function of the climatic and landscape predictors. Lines are the estimated effects of each predictor, with the respective 95% confidence intervals shaded in grey (note that these intervals are very narrow). For single food web metrics, see the Appendix S6 in Supporting Information.

Nevertheless, species richness failed to explain the spatial distribution of other important features of food web structure, such as mean trophic level, link density, connectance and species niche breadth sizes. This reveals that even at large spatial scales and resolutions, the fingerprint of species interactions is visible on biodiversity distribution but cannot be summarized by species richness alone.

The description of ecological networks with reduced dimensions can provide understanding on how different food web properties covary. The reduction analysis of food web metrics revealed two major axes of structural variation, one related mainly to species richness and the other to connectance. We expected species richness and connectance to behave independently from each other and form the two major axes of variation in food web structure (Dunne et al., 2013; Martinez, 1994; Riede et al., 2010). Indeed, Vermaat et al. (2009) showed a similar correlation structure among food web metrics for 14 empirical food webs, and a similar decomposition was also observed by Baiser et al. (2012) for North American aquatic food webs. Furthermore, the constant connectance hypothesis (Martinez, 1992) poses that the proportion of realized interactions within a food web (i.e., connectance) is independent of species richness if link density increases proportionally with the number of species. Our analyses confirmed these two major dimensions for terrestrial vertebrate food webs.

Climatic gradients, namely temperature and precipitation, have long been observed as drivers of biodiversity at both local and global scales (Evans, Warren, & Gaston, 2005). Climate can affect food web structure in several ways. First, it acts as a filter on species assembly (Keddy, 1992), which may affect the functional composition of communities and therefore food web structure (Blanchard, 2015; Lurgi et al., 2012). Second, climatic variability may directly affect food web structure. A more stable climate may allow for longer food web chains and narrower diet niches (Cirtwill et al., 2015; Menge & Sutherland, 1987; Vázquez & Stevens, 2004). Interannual temperature variability has also been shown to be negatively correlated with modularity (Welti & Joern, 2015). Our results show that European variation in food web structure, summarized by two composite descriptors, is mostly related to the annual average temperature and its seasonality. Although environmental constancy, particularly in climatic conditions, is believed to lead to more species-rich communities, we find the opposite here, where climatic variability was positively associated with species-rich food webs and longer food chains. There could be several reasons for our observations. On the one hand, our measure of climatic variability was calculated between 1970 and 2000, which is likely not to be representative of the past climatic history to which European tetrapods were exposed. Environmental constancy at larger temporal scales might be a more important driver of species richness and food web complexity than seasonal variability. For instance, Dalsgaard et al. (2013) found a link between historical climate change (throughout the last 21,000 years) and present-day pollinator network structure at the global scale. On the other hand, the observed gradient in temperature seasonality coincides with important processes that shaped vertebrate distribution across Europe. Baquero and Tellería (2001) suggest that the decreasing mammalian richness from East-central Europe outwards is related to a decrease in available land area (peninsular effect on species distributions), but also to environmental harshness to the north, loss of suitable habitats and population bottlenecks during glacial periods to the west, and human pressure since Neolithic times to the south; regions that coincide with lower temperature seasonality and lower water availability (Hawkins et al., 2003). This is not to be confounded with endemism, which is higher in southern regions of Europe (Baquero & Tellería 2001). Mouchet et al. (2015) also noted that species richness across terrestrial vertebrates was more driven by land-use covariates than climate covariates towards south and southwestern Europe. Hence, although human footprint did not stand out among the important drivers in our models, the combination of long-term and present human intervention and ancient climatic fluctuations, which coincide with the temperature seasonality gradient, could be driving the observed relationship between species richness, trophic food chain length and seasonality.

Support for the latitudinal niche breadth gradient has so far been mixed (e.g., Cirtwill et al., 2015; Krasnov, Shenbrot, Khokhlova, Mouillot, & Poulin, 2008). We found a strong relationship (through the *richness* composite descriptor) between species richness and more variable climates, which generally agrees with the well-known relationship between species richness and latitude. Although generality and vulnerability are known to scale with species richness (Riede et al., 2010), here, we also showed that vulnerability and generality increase more than can be explained by species richness alone (Supporting Information Appendix S4, Figure S4.3), meaning that for a given number of species, we observed relatively more predators and prey than would be expected under a random assemblage of an equal number of species. This finding adds some support to the hypothesis that species might have wider niche breadth (both generality and vulnerability) in more seasonal climates (MacArthur, 1955; but see Vázquez & Stevens, 2004).

Productivity has been hypothesized to drive the latitudinal gradient of species richness and chain length, because greater amounts of energy available to primary consumers should support more diverse communities (Hurlbert & Haskell, 2003; Young et al., 2013). However, this has been debated, with some suggesting an opposite effect (Ward & McCann, 2017) or other factors coming into play, such as ecosystem size (Post & Takimoto, 2007; Takimoto & Post, 2013; Tunney, McCann, Lester, & Shuter, 2012) and productive space (Schoener, 1989). Most of this research has been focused on freshwater systems, where ecosystem boundaries are more easily defined and relatable to their respective food web structure. Our study design (study area divided into regular grid) did not allow us to test the ecosystem size and productive space hypotheses. Our landscape was divided with no regard for ecosystem boundaries, and in terrestrial environments these boundaries are not as clearly definable. Furthermore, in a tropical terrestrial island system, Young et al. (2013) showed a linear relationship between productivity and food chain length, but no effect of ecosystem size (area of the isles) or productivity space (product of productivity and ecosystem size). We show that the overall effect of productivity was weaker than that of climate, yet we found a relationship with the *richness* composite descriptor at limiting levels of productivity (from low to intermediate primary productivity). Unproductive locations were associated with species-poor networks that had lower trophic levels and lower link density (both via the *richness* composite descriptor and by the mean trophic level model, as shown in Appendix S6). Previous empirical studies have shown similar relationships, with food web structure in terms of trophic level, omnivory and the proportion of top predators covarying positively with primary productivity (Vermaat et al., 2009). Hence, our results support the theoretical expectation that higher resource availability at lower trophic levels should propagate up the food web, promoting richer species assemblages with longer trophic chains and higher trophic levels, and that this resource availability relationship should be stronger in the least productive environments (Jenkins, Kitching, & Pimm, 1992; Post, 2002; Young et al., 2013).

Human presence may lead to changes in land use, habitat fragmentation and pollution, which in turn can negatively affect biodiversity (Barnosky et al., 2011; Cardinale et al., 2012) and food web structure (Evans, Pocock, & Memmott, 2013). Accordingly, human footprint was among the most important predictors of vertebrate food web structure. It was strongly related to the *connectance* composite descriptor, with a negative relationship to the proportion of realized links and species proximity in the web (Figure 3b; Table 3). However, in this case we cannot assume this to be a cause–effect relationship, because the effect of human footprint was noticeable only below intermediate levels and because there is a strong spatial coincidence between human footprint and climate. Climatic conditions and resource availability may affect the spatial distribution of human density and species diversity alike, which would explain why the two composite descriptors are positively correlated with human population densities (Araújo, 2003). Indeed, despite the weak importance of human footprint on the *richness* composite descriptor (Table 3), we observed a positive relationship at low to intermediate levels of human disturbance (Figure 3a). Also, although species richness and connectance metrics were nearly orthogonal in our ordination space (Figure 2), they were negatively correlated at low to intermediate values of richness. The highest connectance was found in northeastern Europe, where both human presence and species richness were lowest (Figure 1; see also Appendix S3, Figure S3.2). In these areas, vertebrate assemblages were mostly composed by lower trophic level species and comprised a few highly generalist predators, leading to highly dense foods webs. Hence, the negative relationship between the *connectance* composite descriptor and human footprint is more likely to be attributable to low values of species richness.

The importance of the spatial residuals variable in the *connectance* composite descriptor model suggested the presence of other important spatial variables. Given that we used species distributions to design European vertebrate assemblages, biogeographical processes, such as barriers to species dispersal, island sizes, the presence of peninsulas or even other biotic factors, could lead to spatial similarities and/or dissimilarities in food web structure not explained solely by climate and primary productivity, but rather through compositional turnover (Kortsch et al., 2019). Further work is needed to include such processes under a spatial analysis framework of food web structural turnover (Poisot, Canard, Mouillot, Mouquet, & Gravel, 2012).

Two limitations to our design are the even contribution of each prey to the diet of a predator and the fact that trophic interactions were constant in space (i.e., if two species interacted in the metaweb, they always interacted across their intercepted geographical range). The former implied that we did not account for biomass or energetic requirements (in contrast, weighted food webs interactions may be defined by biomass relationships), and as consequence, we might have inflated omnivory and connectance. The latter implied that adaptability in the diets and behaviours of species was not taken into account (e.g., predator diet shift owing to the presence of competitors or prey behavioural changes as a function of predator presence; Poisot et al., 2012; Preisser et al., 2005; Van Dijk et al., 2008), and as a consequence, our webs might have an inflated number of trophic interactions. Furthermore, environmental conditions might also influence the realization of interactions, which would affect the spatial distribution of food web structure. In addition, trophic interactions in our metaweb were defined based not only on empirical studies, but also on a potential array of prey for each predator species, which might lead to inflated generality and vulnerability. More work is necessary to quantify the level of uncertainty related to how metaweb and local food webs were defined. For instance, this could be done by using highly resolved empirical food webs and quantifying how their topological properties differ, relative to food webs obtained using the methodology described here.

Exploration of the food web structure of assemblages over continental scales offers a new facet for biodiversity that is still largely uncharted. Inherently, food web structure contains more information on species assemblages than mere species diversity alone. Although food web structure is correlated with species diversity, we show that other important large-scale covariates of biodiversity, such as climate, productivity and anthropogenic pressure are also linked to the spatial diversity of European food webs. We hope that this pioneering work serves as an example for future biogeographical food web studies that seek to understand and predict biodiversity patterns.

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DATA AVAILABILITY STATEMENT

The data that support the findings will be available in the form of a data publication currently being prepared by the authors. All code used in the analyses in this manuscript is available through the GitHub repository: https://github.com/JfvBraga/FoodwebSpace

ORCID

João Braga https://orcid.org/0000-0003-4153-8475
Núria Galiana https://orcid.org/0000-0001-7720-0615

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BIOSKETCH

Joao Braga is mostly interested in macroecology and biotic interactions. His work mainly focuses on describing and understanding the spatial variability of trophic interactions and the trophic structure of communities.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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