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TITLE

Spatial analyses of multi-trophic terrestrial vertebrate assemblages in Europe

AUTHORS

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

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

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

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

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

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

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

Corresponding authors – João Braga & Wilfried Thuiller

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

ABSTRACT

Aim While much has been said on the spatial distribution of taxonomic and phylogenetic diversity of large animals, how this diversity interacts in food webs, and especially how these interactions change across space is largely unknown. Here, we analyzed the spatial distribution of terrestrial vertebrate 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.

Methods We combined an expert-based food web (1140 species and 76,500 links) of all European terrestrial vertebrates (mammals, breeding birds, reptiles and amphibians) with their respective spatial distributions. We mapped sixteen different food web metrics representing complexity, chain length, proportion of taxa and diet strategy across Europe and tested whether their distribution reflect the spatial structure of species richness using a null model of food web structure. Then, to avoid multi-collinearity issues, we defined composite descriptors of food web structure that we then 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 From the sixteen metrics, six showed a highly structured distribution across Europe and could be summarized along two major axes of variation of food web structure. The first was related to species diversity and proportion of intermediate species and the second was related to connectance and proximity of species within the web. Both descriptors varied with the latitudinal gradient. Mean annual temperature and seasonality was positively correlated with the first axis, while human footprint was positively correlated with the second one.

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

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

53 properties, tetrapod interactions;

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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 patterns of species, traits and phylogenetic diversity are now well documented for terrestrial vertebrates (Jetz & Fine, 2012; Jetz *et al.*, 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 can be subsequently compared with measurements of other areas to identify localities with higher or lower biodiversity (e.g. hotspots vs. coldspots, Mazel *et al.* 2014). However, species assemblages are not just only the mere sum of species co-occurring in an area, they share a myriad of biotic interactions (e.g. predation, competition, facilitation, etc.) that form a variety of ecological networks through space. While past biogeographic studies have investigated how species or trait diversity vary in space and the underlying role of environment (e.g. Davies *et al.*, 2011; Safi *et al.*, 2011; Mazel *et al.*, 2017), we know little about the spatial distribution of ecological networks (Pellissier *et al.* 2017).

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

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

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

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

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

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 (Riede *et al.*, 2010) (Vázquez & Stevens, 2004; Ledger *et al.*, 2012). Likewise, highly productive sites also provide more resources for consumers and thereby support higher trophic levels (Wright, 1983; Post, 2002), therefore we also predicted that habitat fragmentation and disturbance to shape European food webs. High levels of fragmentation may reduce the strength of interactions between species or even prevent species from interacting, which may lead to networks with lower link density (Hagen *et al.*, 2012).

MATERIALS AND METHODS

Study area and species distributions

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

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

European vertebrates metaweb and local food web structure

A trophic metaweb compiles all predator-prey interactions between species for a given regional species pool. Here, we designed the most complete metaweb of European terrestrial vertebrates from expert knowledge, published information and field guides (see references in Supplementary Information). Basically, all obligatory herbivores or insectivores species were assigned to basal species, together with species with fish or any other obligatory diet that does not include other vertebrates. Then, we focused on species feeding upon other vertebrates (including omnivores) and searched for known prey 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). We considered a trophic interaction potentially feasible between a predator and a prey based on literature review, morphological similarities between potential prey and literature-referenced prey and, in the absence of this information, the diet of predator's sister species. Twelve general diet categories were added to the metaweb, which included detritus, coprophagus, mushrooms, mosses and lichens, algae, fruits, grains, other plant parts, invertebrates, fish, domestic animals and carrion. These categories were used to determine local assemblages and calculate species trophic level (see below).

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

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

For each local food web, we calculated sixteen food web properties that belong to four groups: complexity, strategy, taxa composition and trophic level. Complexity metrics include number of species, 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, which include generality (mean number of preys) and vulnerability (mean number of predators), their respective standard deviations, proportion of omnivore species and average trophic similarity between species. Taxa composition metrics quantify the proportion of species along three major trophic levels: basal, intermediate and top level. Trophic level metrics refer to vertical trophic position of species within a food web, which included the mean trophic level and the maximum trophic level present. See Table 1 for individual properties definitions.

Climatic, energetic and habitat variables

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

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

Statistical analyses

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

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

Food web structure may vary with the number of species, independently of any others 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 pure random draw from the European species pool, given the observed local species richness. The null hypothesis is that species are randomly distributed in space, independently of the local environment and of their position in the metaweb. We thus sampled local food webs for each

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

How to reduce the redundancy 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 principal components analysis (PCA) on the six retained variables over the 78,875 cells of Europe (Table 1) to analyze the most insightful axes of variations between these metrics. This allowed us not only to understand how food web metrics co-vary 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 metrics we analyzed is not only driven by the fundamental constraints linking metrics referred above, but also driven by the effect of spatial variation in food web composition. From the PCA, we kept only the axes that explain each at least 20 % of the total variance, hereafter referred as food

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

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

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

Note that both the environmental variables and the food web topological metrics inevitably show some level of spatial autocorrelation. To account for spatial dependency not explained by the spatial drivers, we first 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 neighboring sites (Dorman et al. 2007; function *autocov_dist* in SPDEP R package). However, since this autocovariate was unconditional to the environmental variation (i.e. the response variable could show a spatial autocorrelation because the environment is itself 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 *et al.*, 2002). We then extracted the residuals of the model and used them as spatial variables independent of the spatial predictors (or at least of the predictor variables used here in the study) in the GAMs. Hereafter, such variables will be referred as spatial residuals variables.

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

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

RESULTS

Local Food web structure

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

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

Deviation of local food web structure to random assembly.

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

Composite descriptors of the local realized food webs

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

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

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

Environment drivers of local food web descriptors

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

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

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

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

DISCUSSION

The variation of food web structure over broad spatial scales is largely 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 standardized the design of local food webs, allowing for the analysis of food web structure across broad and continuous spatial scales. By doing so, we were able to explore how food web structure varies across Europe.

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

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

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

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

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

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 *et al.*, 2013). Here, we used the human footprint index as a measure of anthropogenic pressure to understand its correlation with vertebrate food web structure. We did find a negative relationship between human footprint and the *connectance* composite descriptor (Fig. 4). However, we cannot assume this to be a cause-effect

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

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

A limitation to our design was the even contribution of each prey to the predator's diet and every trophic interaction was constant in space (i.e. if two species interacted in the metaweb, they always interacted across their intercepted spatial 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 may have

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

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