Tetra-EU 1.0: a species-level trophic meta-web of European and Mediterranean tetrapods

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ABSTRACT

Motivation

Documenting potential interactions between species represents a major step to understand and predict the spatial and temporal structure of multi-trophic communities and their functioning. The metaweb concept summarises the potential trophic (and non-trophic) interactions in a given speciespool. As such, it generalises the regional species-pool of community ecology by incorporating the potential relationships between species from different trophic levels along with their functional characteristics. However, while this concept is theoretically very attractive, it has rarely been used to understand the structure of ecological network, mostly because of data availability. Here, we provide a continental scale, species-level, metaweb for all tetrapods (mammals, breeding birds, reptiles, amphibians) occurring in Europe and in the Northern Mediterranean basin. This metaweb is based on data extracted from scientific literature, including published papers, books, and grey literature.

Main type of variable contained

For each species considered, we built the network of potential 2-way trophic interactions.

Spatial location and grain

We considered all species occurring in the entire European sub-continent, from Macaronesia (including only the islands politically belonging to Spain and Portugal) to the Ural Mountains (west to east), and from Fennoscandia and UK islands to the Mediterranean (north to south). We included Turkey, geographically part of Asia, to provide a complete picture of the north-eastern Mediterranean coast.

Time period

The data represent information published and/or collected during the last 50 years.

Major taxa studied and level of measurement

We focused our metaweb on terrestrial tetrapods occurring in the study area. Only species introduced in historical times and currently naturalized were considered; novel introductions were excluded. In total we included 288 mammals, 509 regularly breeding birds, 250 reptiles, and 104 amphibians.

Software format

Data are supplied as semi-colon separated text files.

1. INTRODUCTION

Despite centuries of data collection, our understanding of biodiversity remains limited in many aspects (Hortal et al. 2015). Indeed, we still have a limited knowledge on 1) how many different types of organisms exists (the Linnean shortfall, Brown and Lomolino 1998), 2) how different lineages are related (the Darwinian shortfall; Diniz-Filho et al. 2013), 3) where the different species are distributed (the Wallacean shortfall; Whittaker et al. 2005), and 4) the number and types of interactions that exists among species (the Eltonian shortfall; Peterson et al. 2001). Although some progresses has been made on the first three shortfalls (e.g., Mora et al. 2011; Rondinini et al. 2011; Roquet et al. 2013), the Eltonian shortfall is still prevalent, even for relatively simple systems (Morales-Castilla et al. 2015).

Despite this general lack of knowledge, it has been clearly demonstrated that biotic interactions can have a major influence on species distribution and co-occurrence patterns well beyond local scales (Heikkinen et al. 2007; Gotelli et al. 2010, but see Thuiller et al. 2015), potentially influencing and guiding species responses to ongoing and future environmental changes (Araujo et al. 2011; Bateman et al. 2012; Wisz et al. 2013).

In the last years, an increasing number of databases focusing on the ecological traits of animal species have been published in peer reviewed journals (e.g., Jones et al. 2009) but these mostly focused on morphological, functional, and behavioral traits. More recently, a number of different initiatives increased access to species interaction data, often with a marine focus (Mouritsen et al. 2011; Raymond et al. 2011; Planque et al. 2014) or even considering historical resource use by humans (Dunne et al. 2016). While many websites currently provide access to the results of empirical studies on species interactions (<u>http://www.web-of-life.es;</u> <u>https://www.globalbioticinteractions.org; https://www.globalwebdb.com;</u>

http://www.foodwebs.org; https://www.nceas.ucsb.edu/interactionweb/index.html; https://mangal.io/#/), many have a limited geographical scope. When considering terrestrial vertebrates and trophic interactions across vast extents (e.g., regional/continental areas), the information available is often limited to very general diet categories (e.g., species X eats small vertebrates; Wilman et al. 2014; Kissling et al. 2015). Morales-Castilla et al. (2015) recently proposed an analytical framework that can be used to infer interaction networks, and which is complementary to empirical, observational approaches (e.g., Gripenberg et al. 2019). This framework can be used to infer potential interactions among species, and represents a major step to predict the structure of emergent communities and their functioning (Gravel et al. 2013). The idea was originally formulated by Dunne (2006), who proposed the concept of metaweb to refer to the potential interactions among a given set of species, whether at the local or regional scale. A metaweb is a network which aggregates the trophic interactions (or any type of biotic interaction) between all species from the pool that are susceptible to both co-occur and interact at the regional scale. Thus, in the same way local communities are conceptualized as assembling from a regional species pool, local interaction networks are realizations of a particular subset of the regional metaweb. With a metaweb, it is thus possible, for instance, to analyze the impacts of global changes on the potential structure of the communities or the evolutionary history of the interactions.

Here, we built a continental scale, species-level, trophic metaweb for 1151 tetrapods (mammals, breeding birds, reptiles, amphibians) occurring in Europe plus Turkey (Fig. 1). The metaweb of potential trophic interactions is based on data extracted from the scientific literature, including published papers, books, grey literature. For each species, we gathered information on the potential trophic links with all other tetrapods as well as with some general food categories (e.g., invertebrates). Wherever possible, we considered literature sources focusing specifically on species' trophic interactions measured or inferred in our study area. This dataset has recently been used to investigate the environmental drivers of local network structure in Europe (e.g., connectance, Braga et al. 2019) and the functional structure of the different trophic groups and their spatial structure (O'Connor et al. 2020). In the supplementary material, we added an

example of the type of analyses that could be carried out with our dataset and the associated R-script (Appendix S1, S2, S3). In particular, we used the stochastic block model to map, over the entire study area, the diversity of trophic groups, defined as the clusters of species sharing similar sets of prey and predators.

2. METHODS

2.1 Data Sources

The potential trophic links for mammals were compiled from the Handbook of the Mammals of the World composed of nine volumes (Wilson and Mittermeier 2009-2019). Furthermore, we considered multiple books on the mammalian fauna of the single countries (e.g., Italy and Spain) and all volumes of Mammalian Species (published by the American Society of Mammalogists) available for species included in the database. The potential trophic links for breeding birds were compiled from the Handbook of the Birds of Europe, the Middle East and North Africa (9 volumes; Cramp et al. 1977-1994), the Handbook of the Birds of the World Alive website (del Hoyo et al. 2014). The potential trophic links for amphibians and reptiles were compiled from the Handbook of the single countries, and from the Handbouch der Reptilien und Amphibien Europas (Arntzen et al. 1999; Bohme 1984; Fritz 2001; Grossenbacher and Thiesmeier 2003; Thiesmeier et al. 2004) plus multiple books and papers on the herpetofauna specific for the single countries. The complete list of references for all taxa is available as a data table.

2.2 Data Collection

Potential trophic links for each species were compiled by the authors using a standardized data input protocol in MS Excel. For each species in the database, we included all trophic links reported in the publications using the highest possible taxonomic detail. Most of the time, the information on species' prey was available at the level of family or higher; for instance, the food habits of *Falco tinnunculus* (the common kestrel) are described as: "in Europe up to 90% voles, with some mice and shrews; open area passerines normally less important [...]; also lizards and insects [...]". Therefore, we included as potential prey items all mammals of the families Arvicolinae, Muridae, and Soricidae, all birds of the family Alaudidae, and all reptiles of the

family Lacertidae. For each prey species, we indicated the life stage at which the trophic interaction occurred, spanning the entire life from eggs and larvae (if available), to young and adults.

The final database reports the potential trophic links between any possible combination of species, with the following values: 0 = trophic link not reported; 1 = potential trophic link. When no information was available for a given species, all field have been filled with "NA". We draw the attention of the reader to the potential nature of the trophic interactions we are reporting in this data paper. We trimmed the full matrix of possible interactions (e.g., any predator would consume any prey) according to the literature. This could yield false negatives in our dataset (i.e., interactions that exist in nature but that we characterized as non-existent because the literature fails to document those interactions). Using the approach proposed by Morales-Castilla et al. (2015), it is possible to use data on species' ecology (e.g., habitat preferences) and distribution (for example considering the data presented in Maiorano et al. 2013) to distinguish potential trophic links (what we reported) from trophic links actually occurring (see Braga et al. 2019 and O'Connor et al. 2020).

2.3 Variables

For each species, we gathered information on species specific trophic links plus a set of 11 trophic items: mushrooms, mosses/lichens, algae, detritus, seeds-nuts-grains, fruits, other plant parts, invertebrates, fish, domestic animals, coprofagus. These diet items could then be used to have basal food items in the network (see Braga et al. 2019, O'Connor et al. 2020).

2.4 Taxonomy and systematics

The taxonomy used in our database follow Maiorano et al. (2013) and was updated following the data sources considered. All names were checked against the ITIS (<u>https://www.itis.gov</u>) and the Catalogue of Life (<u>http://www.catalogueoflife.org</u>) databases.

2.5 Data verification

Data were entered directly from the literature into the digital file, and values were carefully double checked by the authors. After the complete data entry, a random 20% of the species for each taxonomic group (20 species for amphibians, 102 species for birds, 58 species for mammals, 41 species for reptiles) were randomly selected and checked against the original source materials. On average, we found errors for 6.3% of the species double-checked (0 amphibians, 9 birds, 4 mammals, 1 reptiles), with single entry errors in all cases.

3. DATA STRUCTURE

3.1 Data Table

We provide a total of four data files. A first file contains the taxonomy, ITIS code, Catalogue of Life database number, and our own species code for each species. A second file contains the complete list of publications used to build the database with their code. The bulk of the database is made by two files, one referring to 11 generic trophic items and one representing pairwise trophic links between any possible two-way combination of taxa.

Data file name for species taxonomy and species codes:

TetraEU_Species_Codes_and_Taxonomy.csv

Data file name for the literature list: TetraEU_Complete_Reference_List.csv

Data file name for the generic trophic items: TetraEU_generic_diet.csv

Data file name for trophic links: TetraEU_pairwise_interactions.csv

3.2 Format Type

Each data file is in ASCII text, semi-colon delimited, not compressed.

3.3 Header Information

Header information in all files is self-explanatory. The naming conventions of each column is fully specified in Table 1.

3.4 Row Information

Each row in the TetraEU_generic_diet and in the TetraEU_pairwise_interactions files represents a single pairwise interaction.

3.5 Variable Definition

All variables common to all species are defined in Table 1.

Table 1. Summary of variable information for the different tables. Only one species is shown as

 example of all species-specific trophic links.

Variable	Description	Туре	Possible values
Species ID	Identification code of the species	Character	N/a
ITIS code	Identification code provided by ITIS Version of the catalogue of life	Character	N/a
Catalogue of life	database in which the species is listed	Character	N/a
Class	Taxonomic Class of the species	Character	N/a
Order	Taxonomic Order of the species	Character	N/a
Family	Taxonomic Family of the species	Character	N/a
Species	Scientific Linnean name of the species	Character	N/a
Reference1 (up to 4 per species)	Literature code	Character	N/a
mushrooms	Presence of mushrooms in the diet	Integer	1 = yes
mosses and lichens	Presence of mosses and/or lichens in the diet	Integer	1 = yes
algae	Presence of algae in the diet	Integer	1 = yes
detritus	Presence of detritus in the diet	Integer	1 = yes
seeds nuts and grains	Presence of seeds and/or nuts and/or grains in the diet	Integer	1 = yes
fruit	Presence of fruit in the diet	Integer	1 = yes
other plant parts	Presence of other plant parts in the diet	Integer	1 = yes
invertebrates	Presence of invertebrates in the diet	Integer	1 = yes
fish	Presence of fish in the diet	Integer	1 = yes
domestic animals	Presence of domestic animals in the diet	Integer	1 = yes
feces	Presence of coprophagia in the diet	Integer	1 = yes
Life stage	Life stage for each species	Character	all; eggs; larvae or youngs; adults

4. DATA ACCESSIBILITY

Data will be made available from the Dryad Digital Repository: link to be determined

REFERENCE LIST

Araujo, M. B., Rozenfeld, A., Rahbek, C., & Marquet, P. A. (2011). Using species cooccurrence networks to assess the impacts of climate change. *Ecography*, 34, 897-908.

Arntzen, J. W., Bohme, W., & Grossenbacher, K. (Eds.) (1999). Handbuch der Reptilien und Amphibien Europas. Bd. 4/I. Schwanzlurche (Urodela) I (Hynobiidae, Proteidae, Plethodontidae, Salamandridae I: Pleurodeles, Salamandrina, Euproctus, Chioglossa, Mertensiella). AULA-Verlag, Wiesbaden.

- Bateman, B. L., VanDerWal, J., Williams, S. E., & Johnson, C. N. (2012). Biotic interactions influence the projected distribution of a specialist mammal under climate change. *Diversity & Distributions*, 18, 861-872.
- Bohme, W. (Ed.) (1984). Handbuch der Reptilien und Amphibien Europas, Band 2/I: Echsen (Sauria) II Lacertidae II: Lacerta. AULA-Verlag, Wiebelsheim.
- Braga, J., Pollock, L. J., Barros, C., Galiana, N., Montoya, J. M., Gravel, D., ... Thuiller, W.
 (2019). Spatial analyses of multi-trophic terrestrial vertebrate assemblages in Europe. *Global Ecology and Biogeography*, doi: 10.1111/geb.12981
- Brown, J. H., & Lomolino, M. V. (1998). *Biogeography*, 2nd edn. Sinauer Press, Sunderland, Massachusetts (USA).
- Cramp, S. E., Simmons, K. E. L., Brooks, D. J., & Perrins, C. M. (1977-1994). Handbook of the birds of Europe, the Middle East and North Africa: The birds of the Western Palearctic. Vol. 1-9. Oxford University Press, Oxford.
- del Hoyo, J., Elliott, A., Sargatal, J., & Christie, D. A. (Eds.). (1992-2013). Handbook of the Birds of the World. Vol. 1-16. Lynx Edicions, Barcelona.
- del Hoyo, J., Elliott, A., Sargatal, J., Christie, D. A., & Kirwan, G. (Eds.). (2014). Handbook of the Birds of the World Alive. Lynx Edicions, Barcelona. (available at: <u>http://www.hbw.com/</u>).

- Diniz-Filho, J. A. F., Loyola, R. D., Raia, P., Mooers, A. O., & Bini, L. M. (2013). Darwinian shortfalls in biodiversity conservation. *Trends in Ecology and Evolution*, 28, 689-695.
- Dunne, J. A. (2006). The network structure of food webs. In Pascual M. & J. A. Dunne (Eds.), *Ecological networks: linking structure and dynamics* (pp. 27-86). Oxford University Press, Oxford, UK.
- Fritz, U. (Ed.). 2001. Handbuch der Reptilien und Amphibien Europas, Band 3/IIIA:
 Schildkröten (Testudines) I (Bataguridae, Testudinidae, Emydidae). AULA-Verlag,
 Wiebelsheim.
- Gotelli, N. J., Graves, G. R., & Rahbek, C. (2010). Macroecological signals of species interactions in the Danish avifauna. *Proceedings of the National Academy of Science of the USA*, 107, 5030-5035.
- Gravel, D., Poisot, T., Albouy, C., Velez, L., & Mouillot, D. (2013). Inferring food web structure from predator-prey body size relationships. *Methods in Ecology and Evolution*, 4, 1083-1090.
- Gripenberg, S., Basset, Y., Lewis, O. T., Terry, J. C. D., Wright, S. J., Simon, I., ... & Vesterinen, E. (2019). A highly resolved food web for insect seed predators in a speciesrich tropical forest. *Ecology Letters*, doi: 10.1111/ele.13359.
- Grossenbacher, K., & Thiesmeier, B. (Eds.). 2003. Handbuch der Reptilien und Amphibien Europas. Bd. 4/IIA: Schwanzlurche (Urodela) IIA. AULA-Verlag, Wiesbaden.
- Heikkinen, R. K., Luoto, M., Virkkala, R., Pearson, R. G, & Körber, J. H. (2007). Biotic interactions improve prediction of boreal bird distributions at macro-scales. *Global Ecology and Biogeography*, 16, 754-763.
- Hortal, J., de Bello, F., Diniz-Filho, J. A. F., Lewinsohn, T. M., Lobo, J. M., & Ladle, R. J.
 (2015). Seven shortfalls that beset large-scale knowledge of biodiversity. *Annual Review* of Ecology, Evolution, and Systematics, 46, 523-549.

- Jones, K. E., Bielby, J., Cardillo, M., Fritz, S. A., O'Dell, J., Orme, C. D. L., ... Purvis, A. (2009). PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. *Ecology*, 90, 2648.
- Kissling, W. D., Dalby, L., Flojgaard, C., Lenoir, J., Sandel, B., Sandom, C., ... Svenning, J. C. (2014). Establishing macroecological trait datasets: digitalization, extrapolation and validation of diet preferences in terrestrial mammals worldwide. *Ecology and Evolution*, 4, 2913-2930.
- Maiorano, L., Amori, G., Capula, M., Falcucci, A., Masi, M., Montemaggiori, A., ... Guisan, A. (2013). Threats from climate change to terrestrial vertebrates hotspots in Europe. *PLoS ONE*, 8, e74989.
- Mora, C., Tittensor, D. P., Adl, S., Simpson, A. G. B., & Worm, B. (2011). How many species are there on earth and in the ocean? *PLoS Biology*, 9, e1001127.
- Morales-Castilla, I., Matias, M. G., Gravel, D., & Araujo, M. B. (2015). Inferring biotic interactions from proxies. *Trends in Ecology and Evolution*, 30, 347-356.
- O'Connor, L., Pollock, L.J., Braga, J., Ficetola, G.F., Maiorano, L., Martinez-Almoyna, C., Montemaggiori, A., Ohlmann, M. & Thuiller, W. (2020). Unveiling the food webs of tetrapods across Europe through the prism of the Eltonian niche. *Journal of Biogeography*, in press.
- Peterson, A. T., Soberòn, J., Pearson, R. G., Anderson, R. P., Martìnez-Meyer, E., Nakamura, M., & Araujo, M. B. (2011). *Ecological niches and geographic distributions*. Princeton University Press, Princeton and Oxford.
- Rondinini, C., Di Marco, M., Chiozza, F., Santulli, G., Baisero, D., Visconti, P., ... Boitani, L.
 (2011). Global habitat suitability models of terrestrial mammals. *Philosophical Transactions of the Royal Society B*, 366, 2633-2641.
- Roquet, C., Thuiller, W., & Lavergne, S. (2013). Building magaphylogenies for macroecology: taking up the challenge. *Ecography*, 36, 13-26.

- Thiesmeier, B., Grossenbacher, K., Franzen, M., Teunis, S. F. M., & Schmidt-Loske, K. (Eds.) (2004). Handbuch der Reptilien und Amphibien Europas. Bd. 4/IIB: Schwanzlurche (Urodela) IIB: Salamandridae III: Triturus 2, Salamandra. AULA-Verlag, Wiesbaden.
- Thuiller, W., Pollock, L. J., Gueguen, M., & Munkemuller, T. 2015. From species distributions to meta-communities. *Ecology Letters*, 18, 1321-1328.
- Whittaker, R. J., Araujo, M. B., Jepson, P., Ladle, R. J., Watson, J. E. M., & Willis, K. J.
 (2005). Conservation biogeography: assessment and prospect. *Diversity & Distributions*, 11, 3-23.
- Wilman, H., Belmaker, J., Simpson, J., de la Rosa, C., Rivadeneira, M. M., & Jetz, W. (2014).EltonTraits 1.0: species-level foraging attributes of the world's birds and mammals.*Ecology*, 95, 2027.
- Wilson, D. E., & Mittermeier, R. A. (Eds.). (2009-2019). Handbook of the Mammals of the World. Vol. 1-9. Lynx Edicions, Barcelona.
- Wizs, M. S., Pottier, J., Kisslling, W. D., Pellissier, L., Lenoir, J., Damgaard, C. F., ...
 Svenning, J. C. (2013). The role of biotic interactions in shaping species distributions and realized assemblages of species: implications for species distribution modelling. *Biological Reviews*, 88, 15-30.