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DATA PAPER

TETRA-EU 1.0: A species-level trophic metaweb of European tetrapods

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Abstract

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

Main type of variable contained: For each species considered, we built the network of potential two-way trophic interactions.

Spatial location and grain: We considered all species occurring in the entire European subcontinent, from Macaronesia (including only the islands belonging politically to Spain and Portugal) to the Ural Mountains (west to east) and from Fennoscandia and U.K. 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; new introductions were excluded. In total, we included 288 mammals, 509 regularly breeding birds, 250 reptiles and 104 amphibians.

Software format: Data are supplied as semicolon-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 of: (a) how many different types of organisms exists (the Linnean shortfall; Brown & Lomolino, 1998); (b) how different lineages are related (the Darwinian shortfall; Diniz-Filho, Loyola, Raia, Mooers, & Bini, 2013); (c) where the different species are distributed (the Wallacean shortfall; Whittaker et al., 2005); and (d) the number and types of interactions that exist among species (the Eltonian shortfall; Peterson et al., 2011). Although some progress has been made on the first three shortfalls (e.g., Mora, Tittensor, Adl, Simpson, & Worm, 2011; Rondinini et al., 2011; Roquet, Thuiller, & Lavergne, 2013), the Eltonian shortfall is still prevalent, even for relatively simple systems (Morales-Castilla, Matias, Gravel, & Araujo, 2015).

Despite this general lack of knowledge, it has been demonstrated clearly that biotic interactions can have a major influence on species distribution and co-occurrence patterns well beyond local scales (Heikkinen, Luoto, Virkkala, Pearson, & Körber, 2007; Gotelli, Graves, & Rahbek, 2010; but see Thuiller, Pollock, Gueguen, & Munkemuller, 2015), potentially influencing and guiding species responses to ongoing and future environmental changes (Araujo, Rozenfeld, Rahbek, & Marquet, 2011; Bateman, VanDerWal, Williams, & Johnson, 2012; Wizs et al., 2013).

In recent 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 most of these have focused on morphological, functional and behavioural traits. More recently, a number of different initiatives have increased access to species interaction data, often with a marine focus (Mouritsen, Poulin, McLaughlin, & Thieltges, 2011; Planque et al., 2014; Raymond et al., 2011) or even considering historical resource use by humans (Dunne et al., 2016). Although many websites currently provide access to the results of empirical studies on species interactions (http://www.web-of-life.es; https://www.globalbioticinteractions.org; https://www.globalwebdb.com; http://www.foodwebs.org; https://iwdb.nceas.ucsb.edu; 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; Kissling et al., 2014; Wilman et al., 2014). Morales-Castilla et al. (2015) recently proposed an analytical framework that can be used to infer interaction networks, 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 towards predicting the structure of emergent communities and their functioning (Gravel, Poisot, Albouy, Velez, & Mouillot, 2013). The idea was originally formulated by Dunne (2006), who proposed the concept of the metaweb to refer to the potential interactions among a given set of species, whether at the local or the regional scale. A metaweb is a network that 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 that 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 analyse 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 1,151 tetrapods (mammals, breeding birds, reptiles and amphibians) occurring in Europe plus Turkey (Figure 1). The metaweb of potential trophic interactions is based on data extracted from the scientific literature, including published papers, books and grey literature. For each species, we gathered information on the potential trophic links with all other tetrapods and with some general food categories (e.g., invertebrates). Wherever possible, we considered literature sources focusing specifically on trophic interactions of species 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 Supporting Information, we have added an example of the type of analysis that could be carried out with our dataset and the associated R script (Supporting Information Appendices S1–S3). In particular, we have 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 & Mittermeier, 2009–2019). Furthermore, we considered many 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 (nine volumes; Cramp, Simmons, Brooks, & Perrins, 1977–1994), the Handbook of the Birds of the World (16 volumes; del Hoyom, Elliott, Sargatal, & Christie, 1992–2013) and the Handbook of the Birds of the World Alive website (del Hoyo, Elliott, Sargatal, Christie, & Kirwan, 2014). The potential trophic links for amphibians and reptiles were compiled from many books and papers on the herpetofauna of the single countries and from the Handbuch der Reptilien und Amphibien Europas (Arntzen, Bohme, & Grossenbacher, 1999; Bohme, 1984; Fritz, 2001; Grossenbacher & Thiesmeier, 2003; Thiesmeier, Grossenbacher, Franzen, Teunis, & Schmidt-Loske, 2004) plus many books and papers on the

FIGURE 1 Study area, including the entire European subcontinent plus Turkey (geographically part of Asia). National boundaries are shown with black lines.

herpetofauna specific to the single countries. The complete list of references for all taxa is available as a data table provided in the database (see the data availability statement).

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. 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 (e.g., considering the data presented by Maiorano et al., 2013) to distinguish potential trophic links (what we reported) from trophic links occurring in reality (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 and faeces. These diet items could then be used as 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 follows Maiorano et al. (2013) and was updated following the data sources considered. All names were checked against the Integrated Taxonomic Information System (ITIS; https://www.itis.gov) and the Catalogue of Life (http://www.catalogueoflife.org) 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 and 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 (no amphibians, nine birds, four mammals and one reptile), with single-entry errors in all cases.

3 | DATA STRUCTURE

3.1 | Data table

We provide a total of four data files. The first file contains the taxonomy, ITIS code, Catalogue of Life database number and our own species code for each species. The second file contains the complete list of publications used to build the database with their code. The bulk of the database is made of 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

TABLE 1 Summary of variable information for the different tables

Variable	Description	Type	Possible values
Species identity	Identification code of the species	Character	N/a
ITIS code	Identification code provided by ITIS	Character	N/a
Catalogue of life	Version of the 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
Faeces	Presence of coprophagia in the diet	Integer	1 = yes
Life stage	Life stage for each species	Character	all; eggs; larvae or young; adults

Note.: Only one species is shown as an example of all species-specific trophic links.
ITIS, Integrated Taxonomic Information System; N/a, not applicable.

3.2 | Format type

Each data file is in ASCII text, semicolon delimited, not compressed.

3.3 | Header information

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

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DATA AVAILABILITY STATEMENT

The database has been deposited in the Dryad Digital Repository: https://doi.org/10.5061/dryad.jm63xsj7b

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BIOSKETCH

The authors are actively participating in understanding and predicting ecological networks through space and time. With the FutureWeb project, they seek to understand the stability and resilience of food webs, how to model them and how they might respond to future changes in climate and land use. Ultimately, they will use conservation planning approaches to improve the protection of species for current and future conditions while accounting for trophic interactions.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the Supporting Information section.

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