

trophich - a national species-level trophic metaweb of 23k species for Switzerland

Authors

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Abstract

Environmental pressures on species can cascade within food webs and even extend beyond individual ecosystems to interconnected systems at large spatial scales. To facilitate the exploration of these dynamics, we construct a data-based national trophic meta-food web (henceforth metaweb), that includes well-documented vertebrates, invertebrates, and vascular plants within Switzerland's national boundaries, and compiles 160 years of ecological knowledge. We additionally use a combination of taxonomic and geographic information to infer further species-level interactions. Our comprehensive dataset catalogues 1,112,073 trophic interactions involving 23,151 species and 125 feeding guilds (e.g. detritivores, fungivores, etc). While explorations of large-scale food webs in space and time have often relied on modelling approaches due to limited data availability, this empirically based metaweb paves the way for data-driven large-scale studies of real-world food webs. By integrating the metaweb with knowledge of local species assemblages, future studies can gain insights into the impact of global change drivers, including climate change and land-use intensification, on food web structures across spatial scales.

Background & Summary

Species responses to perturbations have often led to a modification of their geographical distribution¹ and abundance². Moreover, species are interacting with each other through complex ecological networks in multi-species systems³ and are thus additionally exposed to biotic filters that determine the overall response of an ecosystem to perturbations. Consequently, to study the distribution of biodiversity in space and time and flux-associated ecosystem functions (e.g., pollination, herbivore regulation)⁴, a food web approach is a powerful way to describe complex biological communities, taking into account species richness, composition and the fluxes of biomass and energy between them⁵. Yet, the diversity of these biological communities, their associated ecosystem functions, and the efforts to maintain them operate at different spatial (local, regional and global)^{6–9} and temporal^{10–15} scales.

Recent work has demonstrated that the structure and function of food webs vary across environmental gradients at large spatial scales, e.g. along latitudinal, climatic and resource availability gradients^{16–21}. Additionally, the dynamics of network structure in mutualistic plant-animal interactions has been demonstrated to vary depending on the temporal scale²². Nevertheless, our understanding of how and why ecological networks vary in space and time remains in its infancy, partially due to a shortage of existing interaction datasets and the challenges of comparing differently built food webs¹⁶. One of the primary hurdles in expanding our understanding of food webs beyond the local scale is the inherent difficulty in collecting empirical data on trophic interactions. The collection of occurrence data alone is costly, time-consuming, and requires taxonomic expertise. The added complexity of observing species in their natural habitats and waiting for trophic interactions to occur—possibly across multiple seasons and life stages—complicates the challenge. Designing and implementing a standardised procedure across habitats and regions to document spatial and temporal variability is unrealistic, given the prohibitive requirements for effort and financial costs. This underscores the necessity for innovative methodologies in the study of ecological networks beyond the local scale.

A meta-food web (henceforth metaweb) aggregates all potential trophic interactions between all species that co-occur within a region^{23–25}. Local food webs inferred from the metaweb can be considered subsets, similar to how local communities are assembled from a regional species pool²⁴. While a metaweb approach presents an efficient tool to standardise the comparison of food webs across spatial and temporal scales, exponential growth in computational power and data collection has popularised the approach in the last five years²⁶. Metawebs represent a major step towards understanding complex food web patterns that go beyond the local and the contemporary context²⁶. Yet, this larger scale returns the ecologist to the original problem: data gaps are much more evident when regional pools include potentially thousands of species.

In the face of these large gaps, predictive models based on phylogenetic²⁷ or morphological²⁸ traits may provide an alternative approach. It has long been demonstrated that models based on simple parameters can build complex food webs which are comparable to empirical food webs²⁹. For instance, in aquatic systems, body size can be a strong predictor of feeding interactions, and this relationship has been exploited to create the global marine fish metaweb²⁸. While such models are useful tools to simplify complex ecological systems, they must be calibrated against empirical data²⁶, which can be difficult for already data-deficient regions, taxonomic groups, or interaction types. Additionally, they may not fully capture the complexity, idiosyncrasies, and emergent properties of real-world ecosystems³⁰, presenting a need for an empirically based understanding of food webs across space and time.

Empirical metawebs have been constructed across large scales in Europe^{20,24,31–33} and elsewhere^{34,35}, demonstrating spatial variations in network structure across elevational²⁰, climatic³⁶ and anthropogenic³¹ gradients. These metawebs have been generally limited to bitrophic networks (those including two trophic levels of species, such as plants and their pollinators, or parasitic wasps, and their hosts) or well-studied guilds, such as tetrapods, which only account for a small fraction of trophic links in the web of life. Plant-animal trophic interactions are one of the primary ways taxa are interconnected in ecosystems³⁷, but remain unaccounted for in large-scale studies in Europe—except for some specific taxonomic groups^{31,38}. A metaweb that connects the multiple taxonomic groups co-existing in a region by their trophic interactions enables us to integrate species-habitat dependencies with the additional species-species dependencies. Building such a metaweb requires extensive knowledge of species occurrences and their interactions in a defined geographic region.

Historical records of species occurrences are extensive and well-archived for Switzerland, a small country located in central Europe with an area of approximately 41,000 km². Of the nearly 86,000 multicellular species estimated to occur within the nation, around 56,000 have been identified³⁹, with the spatial distribution of around 10,000 of these species being well-documented⁴⁰. Combining these observations with a method for inferring interaction networks based on geography⁴¹ can allow for the compilation of a comprehensive food web for Switzerland. This approach has already been implemented for some guilds (birds, orthopterans, lepidopterans and plants)²⁰ by making the following assumption: if two species have been observed to interact elsewhere, the interaction is realised if they co-occur within a spatially confined unit. The assumption fixes the diet breadth of a species across the entire metaweb without accounting for intraspecific diet variation driven by biotic^{42–46} and abiotic^{47,48} factors. We emphasise that the nature of the metaweb approach creates a network of all potential links between the target species. This is, in fact, an overestimation of any species' diet breadth at any one point in space and time. We refine this inference approach⁴¹ by only including potential links for documented interactions with known co-occurrence within the region (Switzerland) and by further trimming inferred interactions based on species' habitat associations. Additionally, local food web structure has been demonstrated to be influenced more by the assembly process than local dynamical processes⁴⁹. Thus, by restraining interactions by species ecology (habitat associations), distribution, and the assembly process, local food webs remain within a "realistic boundary" of potential interactions²⁰ while forming comparable local food webs built from the same metaweb.

Here, we provide an empirically based species-level metaweb for multiple taxa (including vertebrates, invertebrates, and vascular plants) in Switzerland containing 1,188,063 links between 26,243 taxa. Of these, 1,107,253 interactions between 23,002 taxa are resolved to the species–species level (Figure 1). This metaweb is based on data extracted from 516 sources of scientific and grey literature (published papers, books, etc.). For some taxa, we additionally used a spatial trait model based on simple parameters (co-occurrence in the same habitats and vertical strata) to infer trophic information from the genus and family levels to the species level. We provide the species list used in this study along with information on the associations of these species with habitats and their vertical strata in those habitats. We provide a dataset including reference metadata, such as the full citation, publication date, location, and data collection methods for each reference.

Our multi-taxa metaweb can facilitate comprehensive large-scale explorations across Switzerland when combined with existing occurrence data⁴⁰. As such, structural and topological properties of food webs (such as connectance⁵⁰, modularity⁵¹, nestedness⁵², etc.) can be compared across environmental gradients (such as precipitation, land-use intensity, temperature, etc.)^{16,25}. This is especially relevant with the recent publication of a 25-m resolution multi-raster dataset covering environmental variables across topographic, bioclimatic, edaphic, land use and vegetation categories, among others⁵³. Moreover, while most existing metawebs have only been used to study spatial variation^{20,28,31,32,35,48,54–58} (with

some exceptions^{21,33}), by incorporating temporally explicit data as such available in Switzerland⁵⁹, it may be possible to study the temporal dynamics of these local networks. In the face of gaps in data needed to infer local networks, the metaweb itself can still provide crucial information on the topography of the regional food web. For example, robustness analyses simulating real-world perturbations (such as the loss of species or of interactions)^{18,60} on threatened habitats across the multi-habitat metaweb could provide an understanding of how habitat-specific losses could influence food web structure and stability. Utilising the entire metaweb could enable us to also consider variations in dietary preferences within species to identify the potential of rewiring the food web, which could lead to new interactions that may only occur in the future as species distributions shift. Metawebs have also been used to predict not only local networks, but also entire metawebs in similar biomes⁶¹, and the Swiss metaweb may be a first step towards a multi-trophic food web for the whole of Europe. Finally, the metaweb can be used for national-scale conservation measures. For example, graph-theoretic topological metrics, such as betweenness or closeness centrality⁶², can be used to identify key species for conservation.

Methods

Checklist of species

We compiled a checklist of animal species based on existing literature for Arachnida^{40,63,64}, Diplopoda⁶⁵, Entognatha (Diplura⁶⁶). Insecta (Coleoptera^{67–87}, Dermaptera⁶⁶, Diptera^{88,89}, Ephemeroptera⁹⁰, Hemiptera^{91–94}, Hymenoptera^{66,95–104}, Lepidoptera^{40,105}, Mecoptera⁶⁶, Megaloptera¹⁰⁶, Mantodea¹⁰⁶, Neuroptera⁶⁶, Odonata¹⁰⁷, Orthoptera¹⁰⁸, Plecoptera⁹⁰, Raphidioptera⁶⁶, Strepsiptera⁶⁶, Thysanoptera⁶⁶, Trichoptera⁹⁰ and Zygentoma¹⁰⁹), Crustacea (Amphipoda^{110–114} and Decapoda¹¹⁵), Mollusca¹¹⁶ and Vertebrata (Hyperoartia¹¹⁷, Actinopterygii¹¹⁷, Amphibia⁴⁰, Aves¹¹⁸, Mammalia¹¹⁹, Reptilia⁴⁰). For plants, we used the Tracheophyta¹²⁰ checklist of Switzerland. We predominantly used national checklists, supplemented by continental checklists where data were lacking, as follows. For a checklist of Swiss aphid parasitoids, we selected a subset of the checklist of the *Aphidiinae of the Czech Republic*¹⁰³, which was validated by a local expert. The existing Chrysididae¹⁰² checklist was similarly validated, as significant changes had been made since the publication of the previous list in 1997. In total, this checklist consisted of 24,039 species. We emphasise that this checklist is not meant to be used as a comprehensive checklist for each family presented here but includes all the species for which trophic and/or occurrence information was available. For example, for some families, such as Chrysomelidae (Coleoptera), we only include an incomplete set of species known to occur in Switzerland (334, in comparison to 399 species according to GBIF records¹²¹, or potentially 86%). Our aim was to include as many well-documented species as possible, especially for groups, such as Chrysomelidae, where validated checklists may be missing, but trophic information is readily available.

Literature-based data search and extraction

We systematically searched for primary literature and datasets using the Google Scholar¹²² and Google Dataset Search¹²³ engines, respectively, and for books using the swisscovery, the Swiss national platform for sharing scientific information between around 500 libraries¹²⁴. We used every combination of the following search queries: taxonomic names at the order, family, and genus level (for vertebrates), the ecological terms trophic, diet, prey, predator, host, and interaction, and the spatial terms Switzerland, France, Germany, Austria, Italy and Europe (the regions surrounding Switzerland). Pairwise species interactions between the resource and consumer taxa were filtered to include only taxa present in our Swiss checklist. After an initial validation (see Technical Validation: Data completeness), we conducted a secondary search for other sources of information, such as amateur entomology websites

and voluntary science (also known as citizen science), for groups lacking data after the preliminary search. Data collection, extraction and archival occurred between January 2021 and October 2023. The temporal range of the covered resources were from 1862-2023.

We extracted digital data, when possible, using an automated pipeline in R¹²⁵ (version 4.3.2) and RStudio¹²⁶ (version 2023.12.1) and saved them as comma-separated files. Books and other analogue data were extracted through manual input into comma-separated files. We primarily recorded resource and consumer names and their taxonomic ranks, then we translated German and English names into scientific names, where applicable. Where available, we gathered additional information on associations to a species' habitat and to a position in the vertical stratification of the ecosystem, on their life stages, and interaction type (Table 1). Broad non-taxonomic diet information (e.g., detritivory) and diet information on non-focal taxa (e.g., fungi) were recorded and standardised into 125 specific feeding guilds. These also included some arthropod families—mostly ill-studied dipterans and beetles—for which higher-resolution data were unavailable. All datasets were merged into one large comma-separated file (henceforth raw dataset)¹²⁷. The raw dataset consisted of 442,599 interactions between 22,862 taxa. Of these, 364,136 interactions were documented between 16,907 species (Figure 1). All references for the interactions are provided as a meta-dataset (Table 3).

Taxonomy-based inference of interactions

While the raw dataset included many species-species interactions, many other interactions were recorded with the consumer taxa at higher taxonomic levels. However, it has been demonstrated that varying node resolution within observational ecological networks can modify network topology metrics¹²⁸. Additionally, our raw dataset included many hierarchically nested interactions, such as genus A and species B eating species C, wherein species B is within the genus A, creating artificial interaction redundancies. Thus, to retain metric reliability in future analyses of the metaweb without losing potential trophic data (as some species only had low-resolution resource information) and to reduce some redundancy of interactions, we implemented further strategies to increase the taxonomic resolution of the metaweb (Figure 2, see below).

We initially followed the approach used by Maiorano et al. (2020)²⁴: if a species was described as consuming species from the family level or higher, all species within the described families were considered as potential prey. While a valid approach for tetrapods, this approach can be problematic when considering interactions between insects and plants. Phenotypic variation within families of insects, which at times include hundreds, if not thousands of species, is higher than within tetrapod families. Thus, we restricted such taxonomy-based inferences to the genus level (Figure 2, link A). Some family-level inferences were allowed for pollinators, but only if empirical records explicitly confirmed the species to be polylectic. The remaining genus-level information was retained in the metaweb at the lower taxonomic resolution.

The species-level interactions within the raw dataset contained a strong bias towards well-studied specialist taxa, especially for primary consumers. In order to better account for the generalist predators in the metaweb, we implemented an empirically based interaction inference strategy based on co-occurrence in the habitat and vertical stratum within ecosystems (see: Habitat and stratum associations). Firstly, all families within the checklist containing only generalist predator species were identified. For species within these families, documented information on their prey at the family level was first used to infer interactions from the predator species to all species within the family. Subsequently, we removed interactions in which the resource and consumer species do not potentially share habitats

and vertical strata within the habitats (see: Habitat and stratum-associations and Figure 2, link B).

In cases where families have been documented to be generalised consumers of taxonomic groups that are absent from the metaweb but present in the form of feeding groups, we inferred links between all species within the family and the feeding groups. For example, all larvae of the Platypezidae fly family feed on fungi¹²⁹. Since we grouped all fungi into the basal feeding group "Fungi" within the metaweb, all Platypezidae species known to occur within Switzerland were thus connected to the node "Fungi" (Figure 2, link C). In this way, information on the predators of Platypezidae species did not have to be aggregated to the family level.

Habitat-association and position in the vertical stratification of the habitat

We define the habitat associations of each species according to nine classes in the broadest of the TypoCH¹³⁰ habitat classifications (Table 2). The habitat information was collected in two different ways. Firstly, we collected it along with interaction data where available. Secondly, we inferred habitat associations by intersecting species occurrence data⁴⁰ with the Habitat Map of Switzerland¹³¹. We used the *st_intersection()* function from the *sf* package^{132,133} (version 1.0-15) in R¹²⁵ to intersect the point data with the polygonal habitat map. The output provided occurrence counts per species and habitat. We retained all habitat associations with at least 100 counts, as well as associations that had also been documented in the literature survey. Then, we classified all species with three or more habitat associations as habitat generalists and all species with less than three as habitat specialists. We justify this as species with two habitat associations may still be specialists, where different life stages may have high habitat specificity. For habitat generalists, only habitat associations with occurrences above the median of total occurrences were retained, others were dropped. For habitat specialists, habitat associations were only retained if the species was documented at least five times within that habitat. We obtained 8,924 habitat associations based on the Habitat Map and 3,325 based on observational data. For the remaining 11,525 species, we inferred habitat associations. Firstly, for species where habitat associations were missing, we first combined all known habitat associations of all species within the same genus. We only retained the habitats shared by the median number of species within the genus or higher and assigned these to the species where habitat data were missing. Thus, we were able to infer habitat associations for all species; 16% of plant species habitat associations were inferred. For animals, this genus-level inference created habitat associations for 19% of all animal species. A similar inference was made for another 36% of the animal species habitat associations, but using aggregated family-level habitat associations, as genus-level inferences were not possible due to gaps in data.

We defined the incidence of each species according to the following strata within a habitat: on ground or in leaf litter, on vegetation, in ground, in water, on host, in dwellings, in air, in host nest, in vegetation, on fungi, in caves. While most of these classes refer to the position in the vertical stratification, some, such as "in vegetation" were included to separate free-living species which can feed on multiple organisms, from species which living within a plant, and thus would not be available as a potential resource for an organism only feeding on the outside of the vegetation. This information was collected along with interaction data for 10,296 animal species (as well as for relevant genera and families if species-level information was not available). All 3,775 plant species were classified according to the Raunkiær plant life-form classifications in *Flora Indicativa*¹³⁴. Plants classified as hydrophytes or pleustophytes were classified as "in water", epiphytes were classified as "on vegetation", and all others were classified as "on ground or in leaf litter", "in ground" and "on vegetation", the latter such that inferences could be correctly made between animals classified as "on vegetation" and vegetation. Where information was unavailable, species-level characteristics

were inferred using the same methods as for the habitats, first at the genus level and then at the family level for 8,047 species. For the remaining 1,626 species, we conducted a broad search of the internet, encyclopaedias or expert knowledge at the family level. Thus, 48% of animal associations to vertical strata in their habitats were inferred from family or genus-level information.

Data Records

Upon acceptance, we will provide all data and scripts¹²⁷ on the following reserved DOI at Envidat (<https://doi.org/10.16904/ENVIDAT.467>), the Swiss data portal for environmental monitoring and research data. We provide six datasets: 1) the metaweb, 2) the taxa checklist, 3) the data source meta-dataset, 4) the list of generalist basal and predator families and polylectic species with citations and 5) a dataset with citations for the inferences of missing predators and 6) a dataset with citations for the parallel inference of diets from similar species (see: Data completeness). The metaweb is a pairwise interaction dataset, with each row representing a potential interaction (see Table 1 for all column information). This dataset includes the taxonomic names, ranks and life stages (where available) of each species in the interaction. Moreover, we provide a numerical identification (ID) for the citation, which relates to the full citation information provided in the resource metadataset. We additionally include information on the level of inference by taxonomic expansion (see: Taxonomy-based inference of interactions), as well as information on further details on the type of interaction, such as predation, parasitism, or pollination, where available. The taxa checklist provides our list of species and feeding groups, upstream taxonomic information, and their associations with habitats and vertical strata within habitats (Table 2). For each ID, the resource meta-dataset contains a full APA-style citation, information about the data source and the methods used to collect the datasets, as well spatial and temporal information about the data collection (Table 3). Additionally, we include a dataset listing the taxa for which the diet breadth was broad, for families of predators and those using feeding guilds as resources, and for polylectic species, along with an ID for the relevant citations (Table 4). We provide a dataset listing the families for which predators were missing, and inferred based on broad data, with accompanying citations (the structure of this dataset is identical to Table 1, except it is missing the column named "Inference"). Lastly, we provide a list of species for which diet information was inferred based on taxonomically similar species, with references validating their similarities in diet (Table 5).

Technical Validation

Data collection

We aimed to estimate the human error arising from manual and automated data extraction (see Figure 3). We first classified the data as originating from either analogue or digital sources. Analogue sources include data gathered from books, manually transcribed into comma separated values. Digital sources include data which were received as data tables or matrices, where the transformation to the standard data table format was automated through scripts in R. Since we processed digital sources automatically, we assumed the error rate to be either very high or close to zero. Thus, five random samples (or the maximal possible number if the data sources included fewer than five samples) were validated for each digital dataset (Figure 3). One error was discovered due to an error in the script, which was corrected, such that the error rate was refactored to be 0 for the digital sources.

For analog sources, we aimed to estimate a (Wilson score) confidence interval of the error rate. To achieve a 95% confidence level ($z = 1.96$), with a margin of error $e=0.01$, and an

estimated error rate $p=7\%$, the required size of the random sample was of $n=2501$, based on the following approach: $n = \frac{z^2 p(1-p)}{e^2}$. The estimated error rate was based on the validation approach of the European tetrapod metaweb²⁴, which estimated a base error rate of 6%. We then randomly sampled 2501 data points and validated them as follows: if the data point had been further confirmed by at least one other data source in the metaweb, it was assumed to be correct (Figure 3). For all other data points in the sample, we manually checked each source and discovered three errors in total, all of them single-entry errors. The error rate for the analogue data sources was thus computed to be between 0.04% and 0.35% (95% CI). This validation was conducted in Python (v. 3.11.4)¹³⁵ using *numPy* (v. 1.25.1)¹³⁶, and *pandas* (v. 2.0.3)¹³⁷.

Data completeness

To assess the extent of data gaps, we checked whether trophic chains were truncated by comparing true basal and apex taxa to those appearing as such within the metaweb. True basal taxa were identified as vascular plants and non-animal groups (such as detritus) within the feeding group classes (3,903 taxa). True apex taxa were classified as apex predators and parasitic arthropods of apex predators (1,018 taxa). We additionally identified taxa for which the only trophic information was a self-loop, in essence, obligate cannibals. The raw network topology revealed that 5,581 species were improperly in an apex predator position (due to missing outgoing links), while another 2,170 species were improperly in a basal position (due to missing incoming links).

We focused on filling these gaps for species for which spatial data are readily available, as many other species for which information is lacking are less well-studied. Moreover, we aimed to cover generally well-studied groups completely, such as tetrapods. To this extent, we conducted broader internet searches to obtain information from secondary and grey literature sources, such as voluntary scientists and insect enthusiasts. For seven species (one slow worm, five orthopterans and one caddisfly), predator information was present while diets were missing. Their diets were inferred based on the diets of ecologically similar species, after confirmation in the literature with regards to the similarities in diets. Additionally, for one species of spider, the predators were inferred based on the predators of an ecologically similar species. Many families of arthropods were additionally missing information on predators. In a few cases, such as with wood beetles, we inferred the predators of the species in these families to generalist predator families such as woodpeckers, or inferred predators of diplopods based on broad information such as, "hedgehogs feed on diplopods", to hedgehog species being connected to all diplopod species within the same shared habitat. Some trichopteran predators were inferred based on the fish predators most commonly shared by other trichopterans. This approach was also applied to amphipods missing predators based on amphipod-eating fishes and birds, as well as decapods based on decapod-eating fishes and birds. In these cases, the interactions were further trimmed by habitat and vertical stratum. Each case is documented by an accompanying citation and classification in the "Inference" column such that this uncertainty can be accounted for in future usage (see also, Code Availability: 02_inferring_interactions_special_cases.R for more detail on all such special cases). After this correction, we recovered diet information for 1,568 species and predator information for 303 species. Nonetheless, 4,013 species are missing diet information, while 1,867 species are missing predator information. This validation thus shines a light towards potential future lines of research to cover these data gaps.

Comparison to other empirical metawebs

We compiled a list of 18 existing empirical metawebs to facilitate a relative comparison to the data coverage of our metaweb. We focus on total degree, which considers the sum of each species' in and out links in a network. We calculated the mean of the sum of all species' total degrees to consider the data coverage, and the standard deviation of the mean. These metrics are likely to depend on the spatial range of the network (some metawebs were limited to one city while others were global) and species richness, as well as random or sampling effects, and therefore cannot be robustly compared across networks¹⁶. To control for these spurious effects, we modelled the co-variation of network properties with linear regression and compared residuals of the metrics^{16,129}. We fit linear mixed effects models to predict relative mean total degree and its standard deviation based on relative species richness, treating the type of network (bitrophic or multitrophic) as a random effect. We used the *lmer()* function from the *lme4* package (v. 1.1-35.1)¹³³ in R¹³⁹. We then compared the mean of residuals to the values of our metaweb to determine whether our residual values were outliers (values outside two standard deviations of the mean). For both metrics, our metaweb remained within two standard deviations (Figure 4). The European tetrapod metaweb was the only outlier for both metrics. Thus, for its size, this metaweb contained relatively more interactions between the species, and a relatively larger variation in the number of links per species. This result is understandable, as this metaweb has a strong bias towards well-studied organisms (tetrapods)¹⁴⁰, in a geographic region where biodiversity had historically been relatively better-studied (Europe) than other parts of the globe¹⁴¹. Although data gaps remain (see Technical Validation: Data completeness), we argue that our trophic data coverage for species is on par with other existing empirical metawebs. To our knowledge, trophiCH represents the largest empirically-based metaweb in existence, both in terms of species richness and trophic levels. In comparison, the next largest metaweb contains a fifth of the species richness and only includes plant-frugivore interactions.

Usage Notes

This work compiles a large empirically based dataset of species interactions along with species-species interactions inferred based on empirical interactions known at lower taxonomic resolution. We emphasise that this is a metaweb, including many interactions that may not be realised at any singular point in space and time. Additionally, when existing metawebs were incorporated into our metaweb, some of the data had already been inferred based on empirical knowledge. For example, the bird-plant interactions in the Swiss bird-lepidoptera-plant metaweb²⁰ were inferred based on expert knowledge of broad diet preferences and habitat-associations. The metaweb serves as an archive that ecologists can use, for example, to create their own local networks – using local occurrence data or simulations. The complete transparency of our metaweb with regard to the derivation of the individual interactions and their data sources enables customization to the individual needs and requirements of the users. Future studies should check the quality of each data point with regards to their research aims before using the dataset in its complete form. Moreover, we note that our metaweb approach does not provide quantitative information about the importance or abundance of each interaction (i.e. weighted interactions). Hence, the derived food webs provide qualitative and not quantitative insights on ecological networks. Future work considering the variation in interaction strengths between species requires new and innovative approaches.

Code Availability

We provide four scripts, accompanying functions, and the raw data required to run these scripts to reproduce the taxonomic expansion and validation of the datasets¹²⁷. In the first script (01_inferring_interactions.R), we infer interactions using genus and family level interactions and for basal feeding groups (see Methods: Taxonomic expansion). In the second script (02_inferring_interactions_special_cases.R), we infer further interactions for a few special cases with detailed explanations. In the third script (03_metaweb_comparisons.Rmd), we provide the statistical comparisons between our metaweb and other empirical metawebs as an R Markdown document (see Technical Validation: Comparison to other metawebs). We additionally provide a final script as a Python Jupyter Notebook, outlining the error validation of the data extraction process (04_error_validation.ipynb and an accompanying .html file).

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M.B.: Resources, Data curation, Writing – Reviewing and Editing

V.B.: Validation, Writing – Reviewing and Editing

F.C.: Visualisation, Data curation, Writing – Reviewing and Editing

W.N.E.: Resources, Data curation, Writing – Reviewing and Editing

F.F.: Conceptualisation, Project administration, Writing – Reviewing and Editing.

M.G.: Resources, Data curation, Writing – Reviewing and Editing

H.H.: Supervision, Methodology, Data curation, Writing – Original draft preparation, Writing – Reviewing and Editing.

A.J.: Resources, Data curation, Validation, Visualisation, Writing – Original draft preparation, Writing – Reviewing and Editing.

P.K.: Data curation, Writing – Reviewing and Editing

F.N.: Resources, Data curation, Writing – Reviewing and Editing

A.P.: Resources, Data curation, Writing – Reviewing and Editing

V.P.: Data curation, Writing – Reviewing and Editing

Z.T.: Resources, Data curation, Writing – Reviewing and Editing

N.Z.: Visualisation, Data curation, Writing – Reviewing and Editing

L.P.: Conceptualization, Methodology, Funding Acquisition, Supervision, Writing – Original draft preparation, Writing – Reviewing and Editing.

Competing interests

There are no conflicts of interest.

Figures

Figure 1.

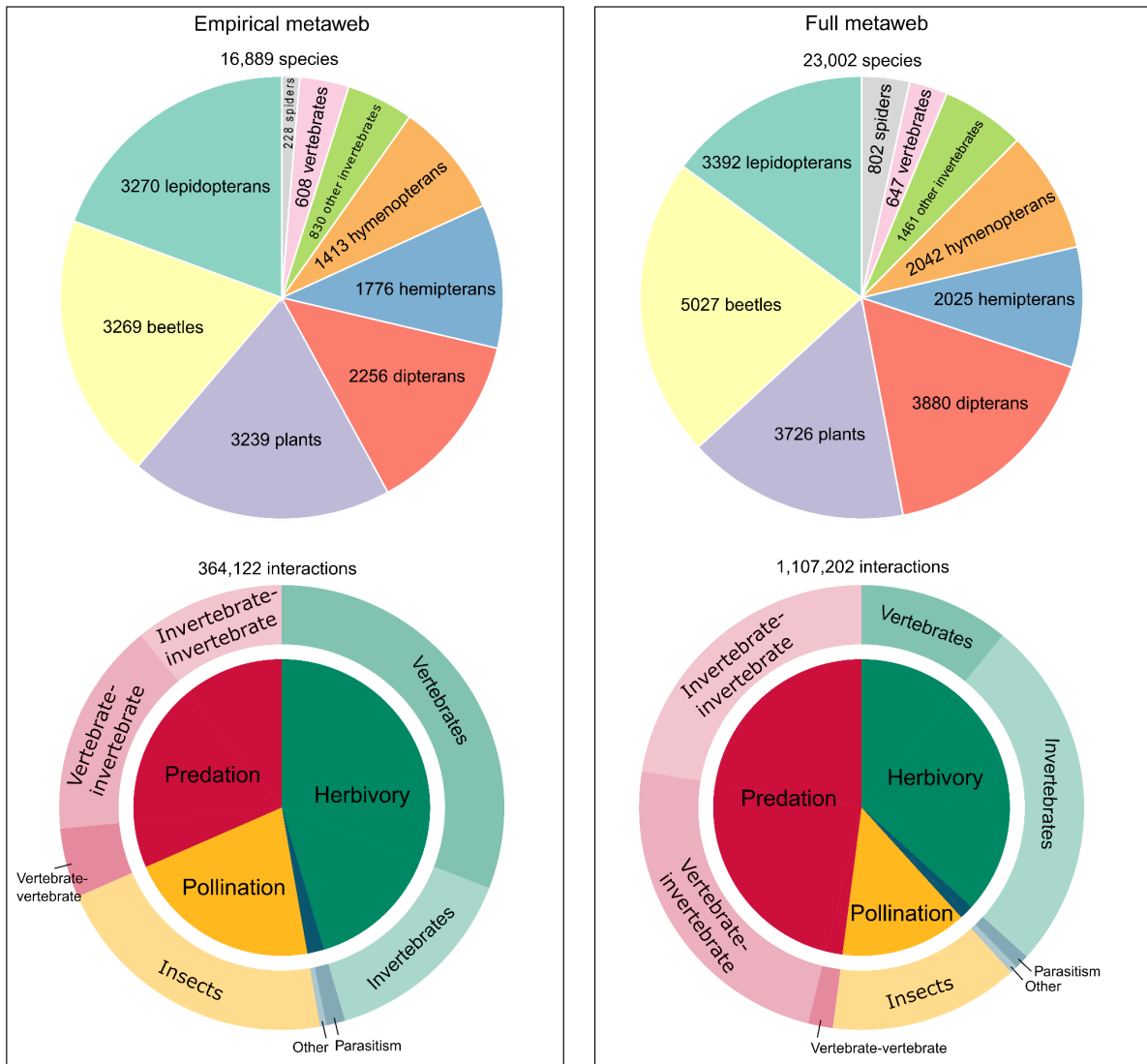


Figure 2.

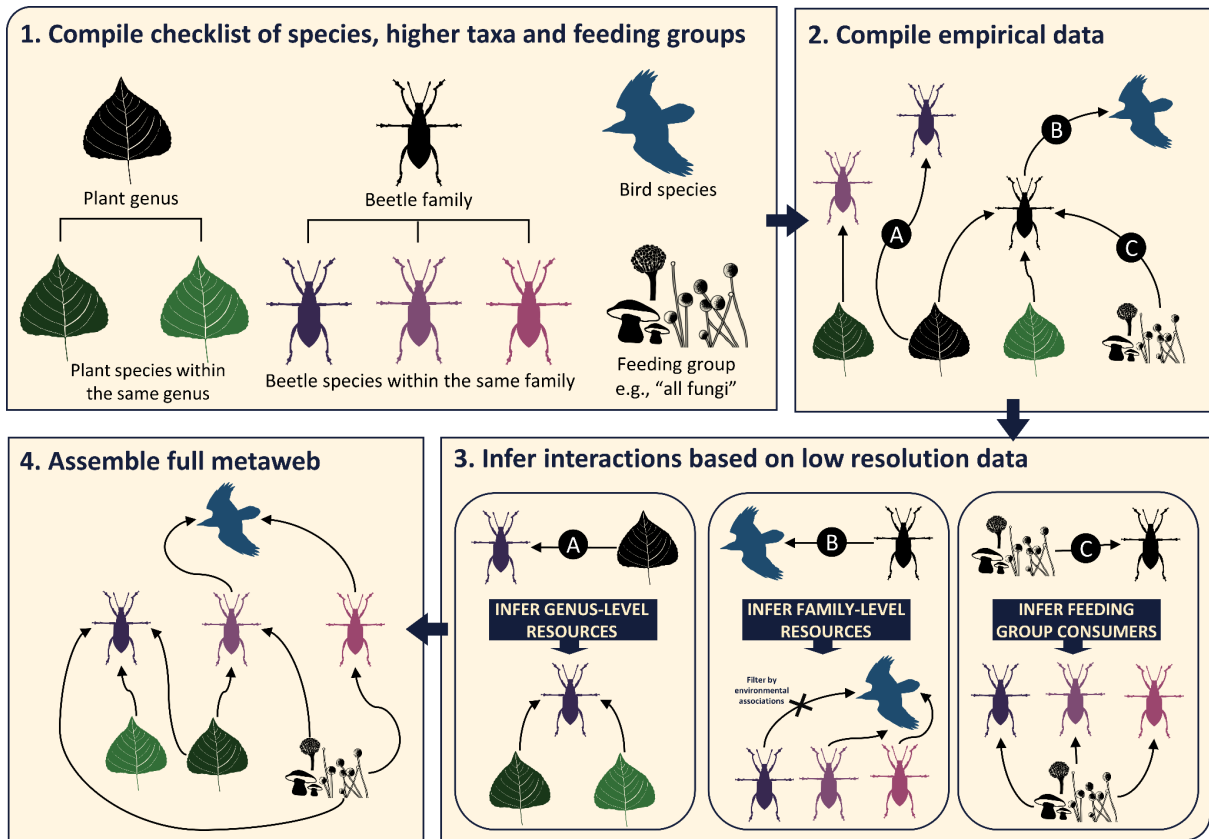


Figure 3

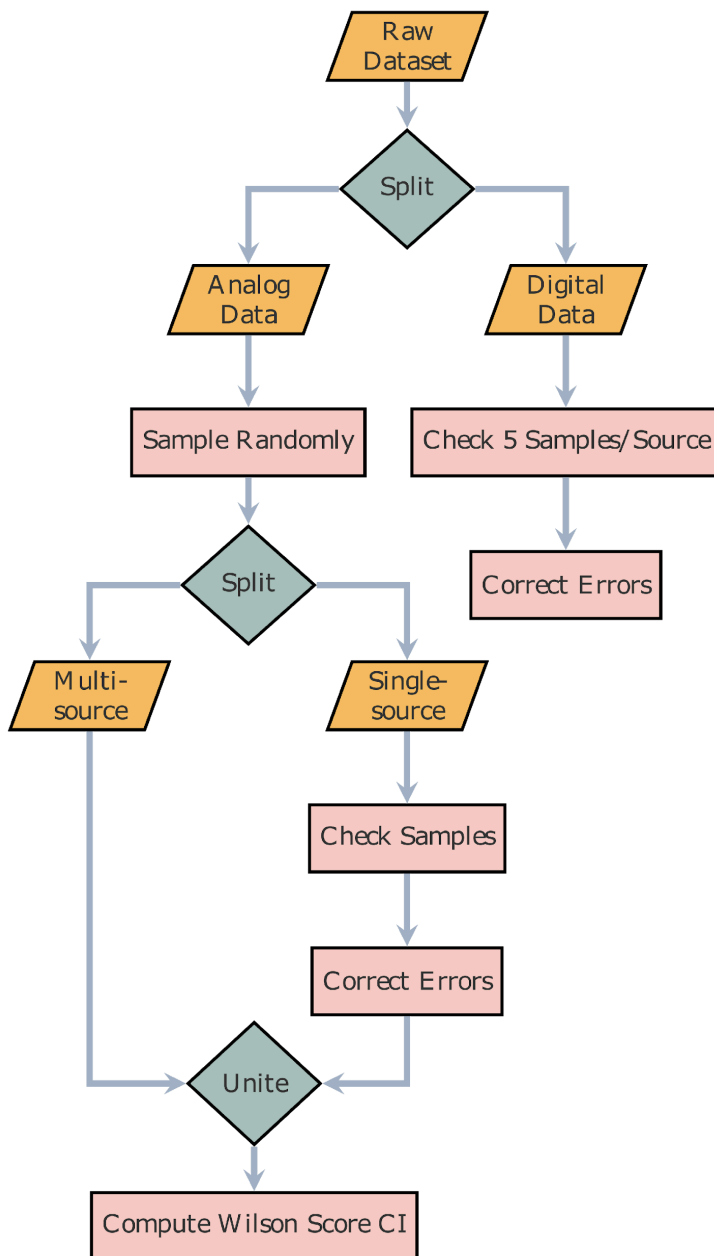


Figure 4

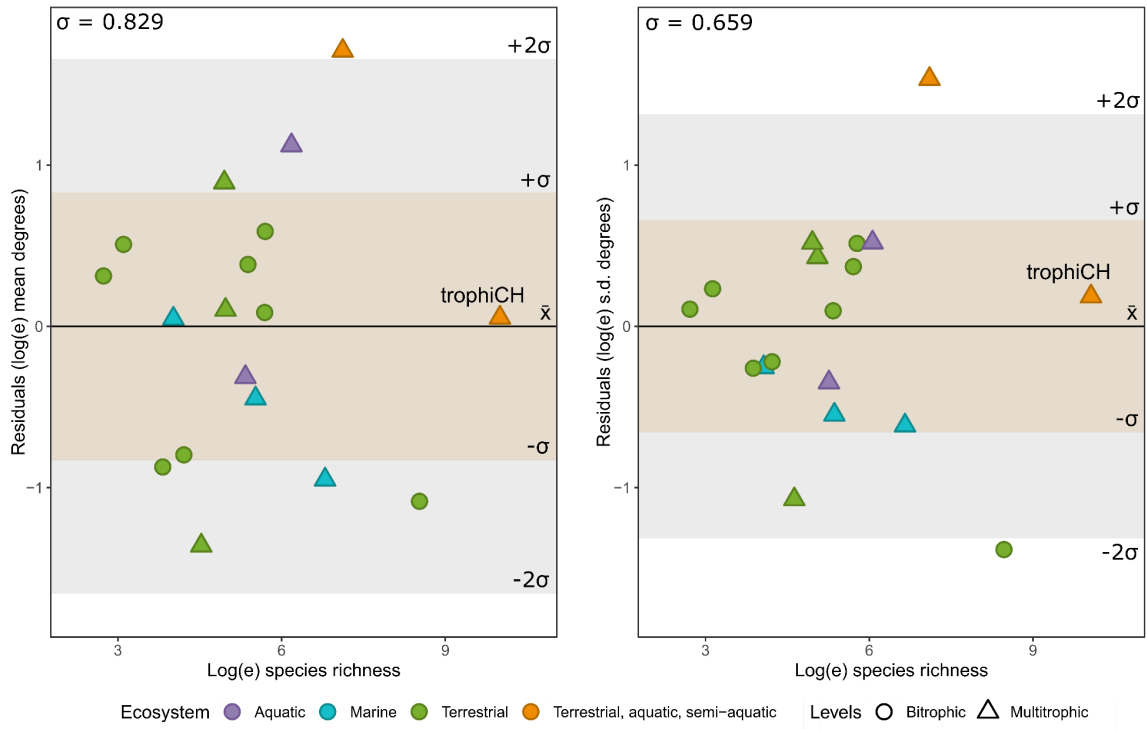


Figure Legends

Figure 1. Distribution of species and interactions within the metaweb. Pie charts depicting the distribution of taxa and interactions in the empirically-based metaweb (left) and the full metaweb (right), when considering only interactions resolved between species.

Figure 2. Construction and expansion of the metaweb. (1) Initial compilation of a species checklist, as well as their upstream taxonomic information for genera and families, and creation of feeding group blocks, such as fungi. (2) Empirical data collection process, focusing on information at the species, genus and family level. (3) We expanded links where species were known to consume an organism at the genus level to include all species within the genus (link A). We additionally inferred links where species were known to consume an organism at the family level, for generalist predators, and filtered by their associations to habitat and vertical stratum within the environment (link B). Links were also inferred where it was explicitly known that a family of organisms were generalist feeders on feeding group blocks, such as fungi (link C). (4) A final metaweb is assembled using all empirical and inferred links.

Figure 3. Validation of the data extraction process. The diagram outlines the sequential steps, beginning with the division of raw datasets into analogue and digital data, then random sampling, error checking, and consolidation across multiple data sources, culminating in the Wilson Score Confidence Interval computation.

Figure 4. Comparison of trophiCH to other metawebs. The scatterplots compare log species richness to the residual variation from mixed linear effects models predicting connectance (left) and node-link ratio (right), treating the type of network as a random effect. The colours of the data points represent the type of ecosystem (aquatic: purple, marine: blue, terrestrial: green and terrestrial, aquatic, semiaquatic: orange). The shapes represent the type of network (circle: bitrophic, triangle: multi-trophic). The dark beige rectangles represent the first($\pm\sigma$) and the light beige rectangles represent the second ($\pm 2\sigma$) standard deviations from the mean(\bar{x}).

Tables

Table 1. The data structure of the metaweb dataset.

Column name	Description	Example(s)
Source_Name	The name of the source taxon, i.e., the consumer	<i>Perca fluviatilis</i>
Target_Name	The name of the target taxon, i.e., the resource	<i>Heptagenia sulphurea</i>
Source_Rank	The taxonomic rank of the source taxon	Species
Target_Rank	The taxonomic rank of the target taxon	Species
Source_Life_Stage	The life stage of the source taxon, if available and/or application. The stages have been summarised into "Young" or "Adult". For insects, "Adult" refers to the imaginal stage, while all larval stages have been summarised into the "Young" stage.	Young and Adult, Young, Adult
Target_Life_Stage	The life stage of the source taxon, if available and/or applicable. The stages have been summarised into "Egg", "Young" or "Adult". For insects, "Adult" refers to the imaginal stage, while all larval stages have been summarised into the "Young" stage.	Egg, Egg and Young, Young and Adult, Egg, Young and Adult, Adult, Young, etc.
Citation	The ID number(s) of the data source(s) documenting the interaction between the source and target taxa. These values correspond with the ID column in the citation meta-dataset.	261, 192, etc.
Inference	Purely empirical interactions are marked NA in this column. For other inferred interactions, this column specifies the degree to which the interaction was inferred. The categories and their explanations are further expanded within the dataset's metadata.	Source_Species_ Target_Family Source_Species_ Target_Genus
Interaction_Type	A more detailed classification of the type of interaction.	Predation, pollination, herbivory, etc.
Interaction	A combination of the Source_Name and Target_Name columns to provide the final interaction	<i>Perca fluviatilis</i> - <i>Heptagenia sulphurea</i>
Interaction_Emp	A combination of the Source_Name and Target_Name according to the original empirical interaction. For empirical interactions, this is identical to the Interaction column.	<i>Perca fluviatilis</i> - <i>Heptagenia</i>

Table 2. The data structure of the taxa checklist.

Column name	Description	Example
Taxon	The name of the taxonomic unit	<i>Dysaphis apiifolia</i>
Rank	The taxonomic rank of the taxon	Species
Kingdom	The taxonomic kingdom within which the taxon resides	Animalia
Phylum	The taxonomic phylum within which the taxon resides	Arthropoda
Class	The taxonomic class within which the taxon resides	Insecta
Order	The taxonomic order within which the taxon resides	Hemiptera
Family	The taxonomic family within which the taxon resides	Aphididae
Genus	The taxonomic genus within which the taxon resides	<i>Dysaphis</i>
Species	The species epithet of the taxon if it is resolved at the species level	<i>apiifolia</i>
Habitat	The habitat association (s) of the taxon	Grassland, Forest, etc.
Stratum	The associations of the taxon to the vertical stratum (or strata) in the habitat	On vegetation, In water, etc

Table 3. The data structure of the reference meta-dataset. Please note that the examples do not all arise from the same Citation ID.

Column name	Description	Example(s)
Citation	The ID number(s) of the data sources(s) documenting the interaction between the source and target taxa. These values correspond with the ID column in the metaweb interactions dataset.	18
Full citation	APA-style full citation of the data source	Benadi, Hovestadt, T., Poethke, H.-J., & Blüthgen, N. (2014). Data from: Specialization and phenological synchrony of plant–pollinator interactions along an altitudinal gradient [dataset]. Dryad. https://doi.org/10.5061/dryad.8mn44
Resource type	Classification of the resource into broad types.	Primary literature, voluntary science, expert opinion, etc.
Resource type comment	Additional comments on the classification of the resources into	This text primarily focuses on species identification, with some information on their biotic interactions.
Methods	When available, classification of the data collection methods into broad types	Molecular methods, morphological analysis, visual observations, etc.
Methods comment	For some method classifications, a more detailed summary of the work	DNA metabarcoding of gut content, DNA metabarcoding of pollen, etc.
Location	The spatial range at which this information was collected	Europe
Year	The publication date of the data source. This was used instead of the data collection date, as the collection dates for larger archived datasets were often unavailable.	1995
Data Type	This category refers to the way the data was extracted, digital for datasets extracted automatically through R scripts and analogue for text or books that required handling by a human.	Digital, Analogue

Table 4. The data structure of the diet range dataset. Please note that the examples do not all arise from the same Citation ID.

Column name	Description	Example(s)
Taxon	The taxonomic name of the potential consumer	Accipitridae
Range	The diet range of the taxon	Basal (if they are generalists feeding on a feeding guild, such as a family of detritivorous insects), Predator, Polylectic (for polylectic pollinators, only if they have explicitly been classified as such in the literature)
Citation	The ID number of the reference(s) documenting this information about their diet and potential diet range	301, 491
Rank	The taxonomic rank of the taxon	Family, Species

Table 5. The data structure of the dataset summarising special cases. Please note that the examples do not all arise from the same Citation ID.

Column name	Description	Example(s)
Taxon	The taxonomic name of the consumer or resource species	<i>Anguis vernonensis</i>
Inference_Taxon	The taxonomic name of the species from which inferences are made	<i>Anguis fragilis</i>
Citation	The ID number of the reference documenting the diet or predator similarities between the two taxa	508
Case	Identification of whether the taxon is missing diet or predator information	Missing diets

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