Metaweb and its applications in understanding ecological interactions

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Abstract

Understanding the dynamics of ecological interactions is an essential initial step in acquiring a comprehensive understanding of the ecosystem structure and functions. Such knowledge is pivotal in effective conservation planning, sustainable development, and ecosystem management. However, the limited availability of information on ecological interactions, commonly referred to as Eltonian shortfalls, presents a significant challenge in moving beyond taxonomic diversity.

The concept of a metaweb, which encompasses all species and their interactions in a specific region, has greatly contributed to our understanding of macroecology. This helps bridge the gap between static ecological networks and the dynamic nature of real ecosystems. Therefore, we aimed to comprehensively review various approaches to constructing metawebs and analyze both the metaweb and its constituent local webs.

Metawebs can be improved through link prediction to overcome the issue of data availability for ecological interactions. Different predictive approaches for ecological interactions can be categorized based on the data requirements. Some methods rely solely on existing databases and predict links based on observed interaction patterns within the web. Other methods incorporate additional information about the nodes, such as phylogenetic or trait data, to predict the links. While predicting interactions, it is crucial to ensure the model's performance and validate the predicted links.

The metaweb helps develop a local web according to the available information on local biodiversity at different spatiotemporal scales. This allowed us to study the structural properties of local webs and their dynamics at the spatiotemporal scale with minimum data requirements. This knowledge is essential for obtaining insights into how ecological interactions change in response to various factors such as climate and habitat changes. Furthermore, with increasing data availability, it may be possible to integrate biomass, abundance, and energy flow to explore the functional aspects of ecosystems.

Our review highlights the existing metawebs and suggests future research directions. Harnessing the power of the metaweb enhances our understanding of ecological communities and their responses to various drivers.

Keywords: ecological network; metaweb development; prediction model; machine learning; species interactions; functional traits; phylogeny; biodiversity

Contents

I. INTRODUCTION

A thorough understanding of the intricate web of species interactions within and between ecological communities is indispensable for devising effective conservation plans (Stork, 2010). This knowledge is essential for overcoming one of the four major gaps in our understanding of biodiversity: the Linnaean shortfall (lack of knowledge about different kinds of organisms), the Wallacean shortfall (limited understanding of the geographic distribution of different species), the Darwinian shortfall (limited knowledge about the evolutionary relationships between species), and the Eltonian shortfall (limited understanding of the ecological interactions between different species) (Morales-Castilla *et* *al.*, 2015). By addressing the Eltonian shortfall and understanding species interactions holistically, we can better protect biodiversity from the growing threats posed by human activities and climate change.

Ecological networks, also known as ecological webs, are powerful tools for studying the interactions between different ecological entities (Wulff, Field & Mann, 1989). These interactions take many forms, including trophic, mutualistic, and parasitic. In network science, entities interacting with one another are referred to as nodes, whereas the interactions between them are called edges (Kay, Graham & Ulanowicz, 1989). Depending on the research question, nodes can represent individuals, species, functional groups, or entire ecosystems (Poisot, Stouffer & Kéfi, 2016). The study of ecological networks is greatly influenced by the field of network science (Barabási, 2013; Newman, 2018), which provides many concepts, models, and tools for investigating ecological questions (Poisot *et al.*, 2016). Using graph theory, researchers can analyze various topological properties of a network, such as connectance, linkage density, degree distribution, motif distribution, diameter, clustering coefficients, modularity, nestedness, intervality, and centrality (Delmas *et al.*, 2019). These properties help uncover the underlying ecological and evolutionary mechanisms that shape the network. For example, centrality is a node-level measure that can help identify the most well-connected nodes in a food web (Dunne, Williams & Martinez, 2002; Martín González, Dalsgaard & Olesen, 2010). The extinction of such nodes may have drastic consequences, making it important to understand the functional traits that make nodes central (Dallas *et al.*, 2019; Hui *et al.*, 2021). Nestedness, conversely, is a network-level measure that reflects the presence of more specialist species in the network, which can increase biodiversity by minimizing competition between species (Bastolla *et al.*, 2009). Furthermore, several other indices for ecological network analysis, such as generality, vulnerability, and average trophic length, are described in this review.

Ecological networks have been a subject of interest among ecologists; however, initial efforts toward understanding these networks have been limited owing to data unavailability (Delmas *et al.*, 2019). However, with the increasing availability of data, there is growing interest in understanding the spatiotemporal variability of ecological networks (Pilosof *et al.*, 2017; Strydom *et al.*, 2021). The main challenge in understanding the spatiotemporal dynamics of a network is its static nature (McCann & Rooney, 2009; Poisot, Stouffer & Gravel, 2015). Some modeling frameworks with a multilevel hybrid modeling approach have been developed, such as “Ecopath with Ecosim and Ecospace (EwE)” (Christensen & Walters, 2004; Colléter *et al.*, 2015; Subramaniam *et al.*, 2022; Ren *et al.*, 2023), “AQUATOX” (Park, Clough & Wellman, 2008; Zhang *et al.*, 2013; Zhang & Liu, 2014), and “Atlantis” (Tarnecki *et al.*, 2016; Ortega-Cisneros *et al.*, 2018; Audzijonyte *et al.*, 2019; Nilsen *et al.*, 2022), to address this challenge. These models enable the spatiotemporal simulation of static food webs.

However, these models require information on many parameters, which limits their application to data-rich contexts. For example, the EwE approach requires a static mass-balance model of the food web (Ecopath) to be developed using a diet matrix and three (out of four) basic parameters. It requires essential inputs, such as a base map, along with habitat properties, dispersal rate of each species, habitat preference of each species, and migration of each species. Although the EwE approach focuses on developing a more realistic model, several parameter requirements restrict its application. Moreover, EwE is limited to aquatic food web development and simulations (Walters, 1999).

In this regard, the “metaweb” concept serves as a solution for the dynamic spatiotemporal analysis of ecological networks with comparatively fewer data requirements. The term “metaweb” (gr. μετά= comprehensive) first appeared in literature in a very different context than network science in 1982 (Briskman, 1982) and was then introduced in ecology (Dunne, 2006), who referred to a metaweb as a master web that includes all species that occurred in similar habitats and their interactions as if they co-occur in a single habitat (Fig. 1). It is synonymously referred to as the “metanetwork” (Tylianakis & Morris, 2017).

Therefore, the species pool and interactions in a metaweb are largely the consequences of long-term evolutionary and biogeographical processes (HilleRisLambers *et al.*, 2012; Saravia *et al.*, 2022). In contrast, local biodiversity results from subsampling the regional metaweb by a metacommunity process influenced by environmental conditions, dispersal ability, stochastic events, and biotic interactions (Tylianakis & Morris, 2017; Saravia *et al.*, 2022). All potential interactions between nodes in the metaweb may not be present in the local web, owing to the variability in species abundance and the physical structure of the habitat (Tylianakis & Morris, 2017).

The concept of metawebs in ecology has emerged as a significant study area over the past five years. This review aims to comprehensively summarize the extensive research conducted on the metaweb, encompassing its conceptual development and applications in understanding spatiotemporal variations within networks and proposing future directions for metaweb research.

II. HOW TO DEVELOP A METAWEB?

(1) Classical approach

The metaweb concept (Dunne 2006) refers to the collection of all species in similar habitats and their potential interactions. However, more recent studies have applied the metaweb concept to an entire biogeographical region across all types of habitats rather than just similar habitats from a region (Gravel *et al.*, 2019; Albouy *et al.*, 2019; Braga *et al.*, 2019; Strydom *et al.*, 2022) (Table 2). Typically, the development of a metaweb involves the following five steps: first, the geographical and ecological boundaries of the metaweb were defined (1 in Fig. 2). Second, a list of available target species in that region was prepared (2 in Fig. 2) by collecting data from direct surveys, scientific literature, and gray literature. Organisms can be categorized into taxonomic categories (species, genus, etc.), trophospecies, and functional groups. Species can be further subdivided into age stages when ontogenic differences in ecological interactions are considered. Third, the species were tabulated into an adjacency matrix to enter their interactions (3, Fig. 2). The presence or absence of species interactions can be found in direct observations, literature, and several online open-access databases (Supporting information: Appendix A). Fourth, if there are any species without any known interactions, two approaches can be considered: (i) those species can be removed from the matrix (4A, Fig. 2), or (ii) those species can be clumped with other similar species based on functional traits or phylogeny (4B, Fig. 2) (Albouy *et al.*, 2019). Finally, the interaction matrix is presented as a graph (5, Fig. 2) (Dunne, 2006).

Several metawebs have been developed using classical approaches, including the European tetrapod metaweb (Braga *et al.*, 2019), German Blight metaweb (Olivier *et al.*, 2019), and Barents Sea metaweb (Kortsch *et al.*, 2019) (Table 2). The WebBuilder function in R can be used to construct a metaweb for a region at different taxonomic resolutions given a regional node list, a database of interactions, and their taxonomic information (Gray *et al.*, 2015).

(2) Predictive approach

(a) Background of predictive approach in metaweb development

Finding species that do not interact with others (4 in Fig.2) is a common problem encountered during classical metaweb development (Rohr *et al.*, 2010). In reality, a species cannot exist without interacting with other species, except in the very early stages of ecological succession. Defining the interactions between species is challenging, particularly when the actual interactions are unknown. The difficulty of collecting ecological interaction data compared to species occurrence data is due to the higher number of interactions in an ecosystem than the number of species and the need for more time and expertise to documenting species interactions (Jordano, 2016).

Interactions between species develop through natural selection and coevolution as they adapt to their environment (Thompson, 1999). This reciprocal adaptation leads to reciprocal phenotypic plasticity, enabling species pairs to modify their interactions in changing environments (Agrawal, 2001). Bartomeus *et al.* (2016) highlighted how species traits shape ecological network structures. Habitat filtering (Grinnellian niche), which is determined by traits related to environmental tolerance, plays a key role in structuring the network (Lima-Mendez *et al.*, 2015). Phenology also restricts the interactions between species that share the same location (Encinas-Viso, Revilla & Etienne, 2012). Life history traits influence species abundance and response to disturbances, thereby affecting the possibility of interactions (Woodward *et al.*, 2005; White *et al.*, 2007; Laughlin *et al.*, 2012). The combination of life-history traits, phenology, and environmental tolerance determines the likelihood of a species coexisting in the same spatiotemporal space. However, the morphological, physiological, and behavioral traits of a species ultimately determine potential interactions (Bartomeus *et al.*, 2016).

Species interactions and traits co-evolve, often showing phylogenetic relationships that can be utilized to predict missing links in networks (Gray *et al.*, 2015; Elmasri *et al.*, 2020). Traits (or phylogenetic relationships) determine the probability of interactions, whereas the probability of interactions among potentially interacting species is influenced by neutral mechanisms linked to their local abundance (Olito & Fox, 2015; Pomeranz *et al.*, 2019; Pichler *et al.*, 2020). Therefore, these relationships in species interactions can be used to estimate unknown species interactions using a predictive modeling approach. However, validation of the prediction results is essential for its application. The core of the predictive model relies on understanding how species interact with each other.

Several different types of predictive approaches have been used to predict the non-randomness of ecological networks, primarily focusing on food webs (Cohen & Newman, 1985). These methodologies are broadly categorized into three groups based on the inputs required to develop the models: niche-, interaction matrix-, phylogeny-, and supervised learning-based predictions (Table 1).

(b) Niche-based predictions

Niche-based prediction models, also known as the "trait-matching" model (Bartomeus *et al.*, 2016; Brousseau, Gravel & Handa, 2018), are commonly used to predict interactions based on a predefined niche of the interacting species. These models can be classified into two categories: intervality property models and intervality problem models (Table 1). The former includes cascade, niche, and mechanistic diet breadth models. The top-down approach is used in both **cascade** (Cohen & Newman, 1985) and **niche** (Williams & Martinez, 2000) models to infer the network with basic parameters such as network size (represented by the number of species), desired connectance, and niche value for each species. The cascade model does not allow for the cannibalism and predation of species with higher niche values, whereas the niche model considers both cannibalism and predation for a more realistic model. Gravel *et al.* (2013) inferred a food web for Mediterranean fish using this approach. Bartomeus *et al.* (2016) modified the niche model by incorporating the effect of abundance and applied it to predict prey-predator, grasshopper-leaf dry matter content, and plant-pollinator interactions. They also developed an R package called 'traitmatch' (Gravel *et al.*, 2013) with examples to serve the same purpose, which can be downloaded from GitHub (https://github.com/ibartomeus/traitmatch). The **mechanistic diet-breadth model** predicts niche and connectance to develop a network with a mechanistic approach using the optimal foraging theory and allometric feeding relationships (Beckerman, Petchey & Warren, 2006; Petchey *et al.*, 2008). Although the mechanistic approach is praised for the process-based formulation, it requires a large amount of information that is difficult to gather (e.g., searching time and handling time) and does not perform well.

The intervality problem models included four models to predict the non-interval links of the natural ecosystem in a concise duration: nested hierarchy, generalized cascade, generalized niche, and minimum potential niche models (Table 1). The **nested-hierarchy model** (Cattin *et al.*, 2004), which modifies the *niche model*, assumes that if a predator shares prey with one predator, it can share more prey with that predator from its niche space defined by niche value [see (Dunne, 2009) for a brief understanding of niche space and niche value]. After fulfilling the above criterion, if more links are needed to form the desired network, random links are created with any species, preferably with species of a lower niche value. The **generalized cascade model** (Stouffer *et al.*, 2005) assumes that a predator randomly selects prey from a niche space. The niche space is defined as a cascade model. However, the probability of forming a link with prey for any predator is species-specific. The **generalized niche model** reduces the niche space to make it an interval and then selects some prey randomly from the remaining unreduced niche space (Stouffer, Camacho & Amaral, 2006). Finally, the **minimum potential niche model** (Allesina, Alonso & Pascual, 2008) uses the inverse approach of the generalized niche model. After ordering the matrix to obtain the maximum intervality, the model scales the niche with two extreme interactions defined by their niche values (for example, the smallest and largest prey). The number of prey not consumed by the predators was counted to calculate the probability of forbidden links within the extended niche space. Therefore, they predict the number of interactions within the niche space by deleting random prey depending on the probability of forbidden links within the niche space (Allesina *et al.*, 2008).

The original cascade and niche models operated in a single niche dimension. However, a multidimensional niche leads to non-intervality within a single niche dimension (Cattin *et al.*, 2004; Allesina *et al.*, 2008; Allesina & Pascual, 2009). Modified cascade and niche models were developed to address this issue. Eklöf *et al.* (2013) attempted to solve the multidimensional niche problem by analyzing 200 ecological networks, including food webs, mutualistic networks, and antagonistic networks. They found that less than ten traits were sufficient to predict most of the links in the ecological network, with model selection favoring fewer than five traits. The authors also suggested that phylogeny could be a good proxy for multiple traits.

(c) Interaction matrix-based prediction

Interaction matrix-based prediction models have been developed as alternatives to niche-based models to handle large and emerging ecological networks more effectively. These models require an input–interaction matrix that predicts the output matrix by understanding the statistical properties of the input matrix. There were four specific interaction matrix-based prediction models: stochastic block, latent trait, matching centrality, and coverage deficit (Table 1).

The **stochastic-block model**, also known as the group-based model (Allesina & Pascual, 2009), utilizes the modular properties of an ecological network. The model groups interact similarly with species, and if one node of a group interacts with a node from another group, the other nodes of that group will also have similar interactions (Guimerà & Sales-Pardo, 2009). Model performance was determined by the number of groups with the lowest value for the Akaike information criterion.

The **latent trait model** (Rohr *et al.*, 2010) introduced the concept of "latent trait" in social network research (Hoff, Raftery & Handcock, 2002). Here, the latent trait serves as a proxy to explain certain aspects of the web, rather than representing an actual trait. This additional dimension explains the unexplained aspects of the niche model. The latent trait can be a single trait or a combination of different traits, even a phylogeny, with each having different contribution levels, such as an ordination axis, and can be compared with the real trait to understand what explains most latent traits. The **matching-centrality model** (Rohr *et al.*, 2016) is an extension of the latent trait model, which considers the concept of degree distribution. The model predicts the number of links that each node can make by adding a centrality property to each node. The matching part helps us understand which pairs can be linked to the latent trait. Finally, the **coverage deficit model** (Terry & Lewis, 2020) is based on the concept that ecologists often miss interactions between rare species. The model used the Chao1 (Chao & Jost, 2012) estimator to understand the sampling completeness of ecological interactions.

The R package 'cassandRa' (Terry, 2019) provides a basic framework for using the aforementioned models for interaction prediction in bipartite networks.

(d) Phylogeny-based predictions

As a proxy for traits, phylogeny effectively predicted ecological networks as traits co-evolved during evolution. Two purely phylogeny-based prediction models were proposed: a generalized linear model and a latent score network model. The **phylogeny-based generalized linear model** (Pearse & Altermatt, 2013) predicts interactions with a generalized linear model formulation using the number of documented interaction partners of a node in the observed matrix and the phylogenetic distance as the dependent variable. While the **latent score network (LS-net)** model (Elmasri *et al.*, 2020) combines phylogenetic distances and interaction affinity (similar to 'centrality' term in matching-centrality model) between groups to predict the network with a Bayesian model. Phylogeny can improve network prediction, as it is a good predictor of the potential interactions between species.

Another recent study, Brousseau *et al.* (2018) used a hybrid approach by modifying the matching-centrality model using real traits and phylogeny with a generalized additive modeling approach and found better predictive performance when using phylogeny as a predictor.

(e) Supervised machine learning-based prediction

Recently, machine-learning algorithms have been used to predict ecological networks, driven by the availability of large datasets. Supervised learning, which requires explanatory variables to predict interactions, has gained popularity. The explanatory variables used in these models include niche, functional traits, and phylogenetic information. This approach can be divided into two categories:

simple supervised learning and graph embedding, followed by supervised learning. Desjardins-Proulx *et al.* (2017) used k-nearest neighbor (kNN) and random forest algorithms to predict interactions using traits and phylogeny as explanatory variables. Pichler *et al.* (2020) used seven supervised machine-learning algorithms (random forest, boosted regression trees, kNN, support vector machines, deep neural networks, convolutional neural networks, and naïve Bayes) under three different circumstances: binary networks, weighted networks, and networks sampled with different observation times. Strydom *et al.* (2021) proposed a graph-embedding approach that involved reducing the dimensionality of the interaction matrix and using the resulting lower-dimensional space to predict a network using a supervised learning algorithm. This method was recently applied to predict Canadian mammalian metawebs (Strydom *et al.*, 2022).

(f) Comparison of performance of different models

The performance of different models was mostly measured with binary classification test measures, such as accuracy, sensitivity, specificity, precision, True Skill Statistic (TSS), and Area Under Receiver Operating Characteristic Curve (AUROC), discussed in Supporting information: Appendix B. However, initial studies used measures such as mean normalized error and the likelihood of producing links.

Williams & Martinez (2000) showed that the niche model (mean normalized error 0.22±1.8) was superior to the cascade model (mean normalized error -3.0±14.1) in the prediction of species interactions. Although the nested hierarchy model has the advantage of breaking the interval rules compared to the cascade and niche models, its predictive performance has not improved (Cattin *et al.*, 2004). Dunne (2009) criticized the nested hierarchy and generalized cascade models for their poor performance in representing several network structural properties compared with the niche model.

Allesina *et al.* (2008) introduced a novel approach by comparing different network models (niche, cascade, and nested hierarchy) based on their ability to predict observed links in empirical networks. This approach is ecologically superior to previous attempts because accurately predicting desired links is of paramount importance. They found that the prediction of the niche model was more accurate than those of the cascade and nested hierarchy models; however, it showed the lowest performance in terms of irreproducible connections. In contrast, the minimum potential niche model was the best-performing model for the likelihood of predicting correct links.

Gravel *et al.* (2013) evaluated the fitness of food webs generated by a niche model based on TSS (Allouche, Tsoar & Kadmon, 2006). The TSS is based on the number of correctly and falsely predicted links and the number of correctly and falsely predicted absences of links. The TSS approach is considered ecologically sound for model assessment because it considers link identities. Petchey *et al.* (2008) revealed that the mechanistic model correctly predicted observed links in 5–65% of 15 analyzed food webs. However, the model performance was worst in the case of a highly non-interval network. Allesina and Pascual (2009) found that the stochastic block model performed better than the minimum potential niche model in predicting the structures of six of ten tested food webs. Notably, these six food webs were larger than the four better-predicted networks obtained using the minimum potential niche model.

Introducing the latent trait concept improves the prediction of ecological networks considerably. Rohr *et al.* (2010) found that the inclusion of latent traits alone could predict 29–87% of the links in the empirical food web, whereas the inclusion of both body size and latent traits could predict 44–93% of the links. Additionally, the matching-centrality model displayed a 50–100% fit to the empirical data, which was improved by incorporating two matching latent traits. In contrast to the latent trait model, the matching-centrality model does not include body size in combination with the latent traits. The main advantage of these latent trait-based models is the identification of correlations between latent and ecological traits by exploring their relationships (Rohr *et al.*, 2016).

Terry and Lewis (2020) showed that stochastic block, latent trait, and matching-centrality models outperform the coverage-deficit model. However, the coverage deficit model can predict poorly sampled interactions. Therefore, combining the coverage deficit model with other models sometimes improves the model's predictability.

In phylogenetic models, a phylogeny-based generalized linear model was used to predict the interactions between lepidopterans and non-native plants using an observed network of lepidopteran-native plants (AUROC 0.93, (Pearse & Altermatt, 2013). In a study comparing LS-net, another phylogenetic model, with the machine learning-based approach kNN, researchers found that LS-net exhibited slightly better predictability based on AUROC and the percentage of true interactions recovered in a host-parasite interaction network (Elmasri *et al.*, 2020). However, the nearest neighbor method, which relies solely on the interaction matrix, also demonstrated good predictive power. Consequently, the researchers suggested using the nearest-neighbor approach when phylogenetic data are unavailable, as it provides insight into the extent and nature of interactions between entities, which is influenced by phylogeny.

Brousseau *et al.* (2018) formulated a general additive model by combining a matching-centrality model (using real traits) and phylogenetic information with different combinations of functional traits, both including and excluding phylogenetic information. They found that phylogeny, with an accuracy of 74% and a TSS of 0.46, alone could better predict interactions than the best trait-matching combinations, which have an accuracy of 71.5% and a TSS of 0.37. They also found that combining both phylogenetic and trait combinations greatly improved model predictions, resulting in an accuracy of 83.4% and a TSS of 0.65.

The predictability of the nearest-neighbor approach exhibited variability across studies, with one study (Elmasri et al., 2020) reporting good predictability and another one (Desjardins-Proulx et al., 2017) reporting unclear results. Among the supervised machine-learning algorithms, random forests, boosted regression trees, and deep neural networks are the most suitable for predicting ecological networks (Pichler et al., 2020; Desjardins-Proulx et al., 2017). Strydom *et al.* (2022) used graph embedding followed by machine learning and reported that their model correctly predicted 92% of interactions.

(g) Which method to use for metaweb development?

As the metaweb is a collection of all species and their interactions in a region, we recommend employing any random yet accurate method to analyze and study the data effectively. Unlike local-scale ecological networks, metawebs often contain an overwhelming number of species. Data on the functional traits and environmental tolerance of such a large number of species belonging to diverse taxonomic groups are often challenging to gather. However, many emerging databases exist (see Supporting information: Appendix A). Therefore, our recommendation is based on the amount of data available (Fig. 3). Firstly, interaction matrix-based predictive models, especially the matching-centrality model, as per its superior predictive ability, are recommended for metaweb development because this kind of model only needs the interactions matrix to predict the metaweb. Our second choice was phylogeny-based models because of their superior predictive ability and ease of collecting phylogenetic data compared to trait data. Phylogenetic information reflects the effects of multiple traits (Brousseau *et al.*, 2018). Supervised learning can be used if trait or phylogeny data are available. random forests, boosted regression trees, and deep neural networks can be used in this case.

III. INFERRING LOCAL WEBS USING METAWEB APPROACH

The decomposition of the metaweb into local food webs facilitates the examination of spatiotemporal variations in ecological networks. This, in turn, establishes a research domain for comprehending the factors accountable for the differences in ecological communities and their structural organization. In local web development, two scenarios could arise: (i) presence of empirical data on local species, and (ii) absence of local species data (Fig. 4). In the first case, locally available species form the nodes of the local web and interactions are assigned from the metaweb. Nodes without any interactions were removed from the local web and were considered *false positives* (Braga *et al.*, 2019). This method was followed in all existing studies, where local webs were developed from a metaweb for further analysis (Kortsch *et al.*, 2019; Albouy *et al.*, 2019; Braga *et al.*, 2019; Olivier *et al.*, 2019; Ho *et al.*, 2022). However, these local webs overestimate actual interactions because co-occurrence does not always result in interactions (neutral mechanisms) (Olivier *et al.*, 2019). Metawebs can also be developed from regional-level species occurrence data, such as checklists of different species in a country. In the second case, the local data are unavailable for metaweb inference. Recently, Strydom *et al.* (2021) proposed a method to overcome the issue of data unavailability; however, this method is yet to be tested.

The probability of occurrence of different species across space and time can be inferred from species distribution models using bioclimatic data. Such data can also be used to infer local networks. However, the co-occurrence of these two species does not always imply that they interact. In this regard, we suggest including a neutral mechanism to infer the local web from the metaweb. Therefore, generalist nodes have stronger interactions with nodes with higher abundances than with those with lower abundances. If the interaction matrix is binary, there should be an ecologically sound limit to the minimum abundance with which a generalist can interact. However, this condition should not be applied between specialist nodes; otherwise, it would result in fewer interactions on the local web.

Another concern is the removal of species that do not interact with the local web. The presence of this kind of species in the local checklist indicates undersampling of biodiversity, that is, other taxa with which it should have ecological interactions are not reported because of inadequate sampling. This type of species must be reported in research publications to highlight the gap in knowledge regarding local biodiversity and missing interactions.

IV. ANALYSIS OF METAWEB AND ITS LOCAL CONSTITUENT WEBS

Metaweb and its local constituent webs should be analyzed to obtain ecological insights into network properties at the local and regional scales, along with their temporal and spatial variability. The metaweb represents the gamma (γ) diversity of species interactions in a region, which is a combination of all species and their interactions. However, local constituent webs are local subsets of the metaweb and represent alpha (α) diversity. The difference between a metaweb and its local constituent webs represents beta (β) diversity (Luna *et al.*, 2020).

(1) Metrics to describe a network

These metrics can be used to understand the properties of both local webs and metaweb; thus, they can provide an overview of α and γ interaction diversity, respectively. The inferred local web matrix developed from a metaweb is usually binary. Therefore, graph theory-based indices are generally used to describe networks. The **richness** of the interactions is simply the number of links in the network. The number of network links was determined by the species count. Therefore, **connectance** is considered an accurate measure of community interaction richness (Tylianakis *et al.*, 2010). Connectance is emphasized as one of the most important descriptors of an ecological network because of its robustness (Dunne *et al.*, 2002), invasiveness (Baiser, Russell & Lockwood, 2010; Smith-Ramesh, Moore & Schmitz, 2017), and correlation with most ecological properties (Dunne *et al.*, 2002; Poisot & Gravel, 2014). Connectance decreases with increasing species richness in a network (Kay & Schemske, 2004). **Degree distribution**, which counts the number of nodes with a particular number of edges, can also be a good indicator of network properties. It helps understand the number of specialists or generalists in a network (Memmott, Waser & Price, 2004). In the case of a directed network, the degree distribution can be further divided into in-degree and out-degree, corresponding to vulnerability and generality in the food web, respectively (Schoener, 1989). **Modularity**, another important network property, can be measured to compare networks (Girvan & Newman, 2002; Poisot, 2013). Modularity measures the extent of network distribution to subsystems of densely connected nodes called modules. Modularity increases the persistence of a network by restricting perturbations in the module (Stouffer & Bascompte, 2010, 2011). Measuring **nestedness** (Almeida-Neto, R. Guimarães Jr & M. Lewinsohn, 2007; Bastolla *et al.*, 2009) is essential for comparing networks. This measures the extent to which specialist edges are a subset of generalist edges in the network. This is the tendency of nodes to interact with subsets of interaction partners of better-connected nodes. Nested structures promote greater biodiversity by minimizing competition within the community (Bastolla *et al.*, 2009). The **diameter of the network**, which is the longest of the shortest distances between every pair of nodes, is also an ecologically interpretable network property (Delmas *et al.*, 2019). A small diameter indicates the presence of densely connected nodes in a network, which makes the network sensitive to perturbations (Minor *et al.*, 2008). Other commonly used indices to compare networks concerned with chain lengths, which are mainly applicable to the food web, including the **maximum chain length, average chain length, median chain length,** and **standard deviation of chain lengths** (Bersier, Banasek-Richter & Cattin, 2002).

Ohlmann *et al.* (2019) developed three Hill numbers (Hill, 1973) based on indices to understand the average alpha diversity across local webs generated from meta-webs using a single metric. They developed three matrices for node (weighted or unweighted) diversity (A_P), link diversity (A_L), and weighted link diversity (A_π) (Table 2). Similar indices were also developed to calculate the diversity at γ-level, i.e., G_P, G_L, and G_π representing the γ-level indices for nodes (weighted or unweighted), links and weighted links, respectively. These indices can be calculated with the R package 'metanetwork' (Ohlmann, Garnier & Vuillon, 2022).

Some other indices for alpha diversity are used for comparing local webs derived from metaweb (Kortsch *et al.*, 2019; Olivier *et al.*, 2019) as follows: **VulSD**, **GenSD** (Williams & Martinez, 2000; Bersier *et al.*, 2002), **level of omnivory** (Sprules & Bowerman, 1988; Goldwasser & Roughgarden, 1997), **mean trophic level** (Williams & Martinez, 2004), **mean maximum trophic similarity** (Williams & Martinez, 2000) and **proportion of basal, intermediate, top, cannibals and omnivores in a food web** (Claessen, de Roos & Persson, 2000; Bersier *et al.*, 2002; Thompson *et al.*, 2007). A brief description of the metrics used to understand the network properties of ecological interactions and their usage in different meta-web analysis studies is provided in Table 2. The R package 'UNODF' (Cantor *et al.*, 2017) can calculate nestedness while 'Netindices' (Soetaert, Kones & Dick, 2022) for calculating other indices.

(2) Metrics to understand interaction turnover

The species composition of an ecological network varies spatially and temporally depending on the ecosystem. Different measures of diversity exist to estimate interaction turnover with a single measurement, including various formulations for use with presence-absence data (Koleff, Gaston & Lennon, 2003). However, interactional diversity differs from species diversity; in many cases, these measures are not correlated and are more complex (Poisot *et al.*, 2011, 2017). Consequently, most studies differentiate between networks by performing multivariate ordination analyses with network measures (Vermaat, Dunne & Gilbert, 2009; Baiser *et al.*, 2012; Kortsch *et al.*, 2015; Braga *et al.*, 2019). Kortsch *et al.* (2019) used the popular index $\boldsymbol{\beta_W}$ (Whittaker, 1960) to understand the interaction differences between local networks. However, this analysis focuses more on the mathematical perspective of dissimilarity than the ecological perspective (Poisot *et al.*, 2012).

The diversity of ecological networks (β_{WN}) results from the variation in species composition ($\boldsymbol{\beta_{ST}}$), as well as variation in the interaction between shared species ($\boldsymbol{\beta_{OS}}$) (Canard, 2011; Poisot *et al.*, 2012). The first β diversity index developed in the perspective of metaweb is $\boldsymbol{\beta'_{OS}}$, which measures how the local network interactions differ from the interactions between the same species in a metaweb. The β'_{OS} index was further used in many studies to understand how locally realized interactions differ from potential interactions in metaweb at a spatial scale (Poisot *et al.*, 2017; Dáttilo & Vasconcelos, 2019). However, the β'_{OS} index is not applicable if the local web is subsampled from the metaweb without considering local abundance, as this results in the interaction in the metaweb and local web being precisely the same between the same set of species (Olivier *et al.*, 2019). Therefore, measuring interaction variability due to species turnover (β_{ST}) is the only alternative in this case. R package 'betalink' (Poisot *et al.*, 2012) is available to calculate the above beta diversity indices.

Luna *et al.* (2020) argued that β'_{OS} is not a measure of β diversity because it compares the local network with the regional metaweb, comparing α diversity with γ diversity. They also argued that β'_{OS} does not represent the presence of unique interactions because finding a locally unique interaction requires subtracting the focal network from the metaweb. They proposed two indices along with an R function to calculate these: **Local Network Uniqueness (LNU)** and **Shared Interactions Frequency (SIF)**. For comparison, these indices require the development of a quasi-metaweb, which is the metaweb minus the local focal web. Subsequently, the local web was compared with the quasi-metaweb to compare the indices. In contrast to β'_{OS}, LNU and SIF can be applied in cases where the local food web is developed by subsampling the regional metaweb, making them better measures of β-diversity than others.

Ohlmann *et al.* (2019) proposed three β-diversity indices by dividing the γ diversity indices with the α-diversity indices for node diversity (B_P), unweighted (B_L), and weighted link diversity (B_π). These β diversity indices can be calculated with the 'Metanetwork' (Ohlmann *et al.*, 2022) R package.

Recently, a couple of indices ($\beta_{co\text{-}pres}$ & $\beta_{co\text{-}abs}$) were proposed and integrated into the R package 'econetwork' (Miele *et al.*, 2022) to understand the co-presence and co-absence of different nodes across the environmental gradients. These two indices jointly signify the effects of biotic interactions and environmental variables on the organization of ecological networks along environmental gradients.

V.OVERVIEW OF RESEARCH ON METAWEBS

Among the ten metawebs developed thus far (Table 3), only one metaweb was analyzed for temporal variations in local webs using the metaweb approach (Olivier *et al.*, 2019), and one metaweb has not yet been analyzed (Strydom *et al.*, 2022), whereas others were analyzed for spatial variations. Global marine metawebs are the largest metawebs ever made (Albouy *et al.*, 2019). They investigate the influence of heterogeneous species distribution across latitudinal gradients and trophic interactions of marine fishes on their networks globally. They also studied whether the metaweb-exhibit modules corresponded to spatial species distribution across biogeographic regions. Ho *et al.* (2022) inferred aquatic and terrestrial food webs from a metaweb using empirically sampled local community composition data and examined how these webs have different structural and ecological properties along elevational gradients and various land use patterns. Grünig *et al.* (2020) studied the effects of climate change on the metawebs of managed plants and their novel pests. Maiorano *et al.* (2020) evaluated the effects of climatic and anthropogenic factors on the spatial structure of European tetrapod food webs using a metaweb. Metawebs were also analyzed for changes in trophic groups in response to environmental variations across European ecoregions. Trophic groups were formed by applying a stochastic block model to a metaweb (O'Connor *et al.*, 2020). In Brazil, a metaweb was developed to understand the variation in network properties, beta diversity, and latitudinal variation in the ant-plant interaction network (Dáttilo & Vasconcelos, 2019). The Eurasian rodent-ectoparasite metaweb was developed to study the climatic impacts of these interactions (Poisot & Gravel, 2014).

Most meta-webs are constructed using observed literature-based data. However, the predictive approach is applied to two metawebs: the Canadian Mammal metaweb (Strydom *et al.*, 2022) using a machine learning algorithm (Brownian motion) with graph embedding and the global marine metaweb (Albouy *et al.*, 2019), using niche-based prediction with body size as a measure of niche.

As a descriptor of α diversity, the following measures are used in different studies: species richness, interaction richness, link density, connectance, generality (weighted, non-weighted, standard deviation), vulnerability (weighted, non-weighted, standard deviation), clustering coefficient, the proportion of different species (basal, intermediate, predator, cannibal and omnivore), maximum trophic similarity, mean trophic level, maximum trophic level, Horn's index, nestedness, and modularity. Dáttilo and Vasconcelos (2019) used the H_2' index (Blüthgen, Menzel & Blüthgen, 2006) to measure the interaction diversity, which can only be used if local-level abundance data are available. β_{WN}, β_{ST}, β_{W}, β_{OS}, β'_{OS}, and ordination methods are used to understand network turnover (Table 2).

A null model of the network was developed mathematically using certain parameters and conditions to test the hypotheses. Kortsch *et al.* (2019) used a null model to test whether an ecological network was formed randomly or influenced by environmental constraints. It was also used to test the evidence for the effects of colonization, extinction, habitat filtering, and dynamical constraints that result in the formation of local webs from a metaweb (Saravia *et al.*, 2022). Multivariate analyses, such as principal component analysis, have been applied to define differences in different local networks (Braga *et al.*, 2019). Various methods, such as correlation (Albouy *et al.*, 2019; Braga *et al.*, 2019), redundancy analysis (Poisot *et al.*, 2017; Kortsch *et al.*, 2019), principal component analysis (Braga *et al.*, 2019), generalized additive modeling (Braga *et al.*, 2019), structural equation modeling (Ho *et al.*, 2022), probabilistic modeling (Gravel *et al.*, 2019), generalized dissimilarity modeling (Dáttilo &

Vasconcelos, 2019), and permutation accuracy importance (Braga *et al.*, 2019) were used to understand the influence of environmental drivers on network structure.

VI.CONCLUSION

(1) The study of metawebs is essential for understanding spatiotemporal variations in communities and how they react to environmental changes, including climate change and anthropogenic disturbances.

(2) One of the primary limitations of metaweb approach is the lack of information on species abundance and interaction strength, which are critical factors in developing local food webs. This knowledge is crucial for moving beyond mere structural analyses of the network and delving into its functional aspects. Recently, citizen science projects, such as eBird (https://www.ebird.org) (Sullivan *et al.*, 2009), have greatly improved our ability to collect abundance data. However, there are still limits to public participation and expertise in the sampling and identification of lesser-known taxa; and methods to collect data on the interaction strength with citizen science initiatives remain unclear. Incorporating abundance data into the development of local food webs can help to better understand the variation of intra- and inter-network diversity using indices such as H2′ and d′ index. Furthermore, different ecosystem health-based and keystone indices can be calculated using as much data as possible in Ecopath.

(3) The behavior of animals significantly affects ecological interactions, and collecting this information can help develop better metawebs and local subsets.

(4) Metawebs faced the challenge of “false positives” in local webs, where certain species are included despite lacking interactions with other species in the metaweb. Although this issue can be addressed by removing these species from the matrix, they cannot exist without interacting with others unless the ecosystem is at an early successional stage. Better

methodologies must be developed to overcome this problem. Environmental DNA and metabarcoding have recently emerged as promising approaches for improving species occurrence data (Saccò *et al.*, 2022). However, there is still no method for revealing undersampled ecological interactions, except for predictive models.

(5) Recent effort toward understanding the patterns of ecological networks along the environmental gradients through the ordination method or recently developed β-diversity indices ($\beta_{\text{co-pres}}$ & $\beta_{\text{co-abs}}$) is quite encouraging. However, research in this area is still in its infancy. Future research should be conducted to understand how environmental variables function and affect network structure and predict network properties using environmental variables.

(6) Furthermore, having a metaweb and a local food web is better than not having anything because no model is perfect. Therefore, a future approach should be taken to develop a metaweb for regions where no metaweb has been developed, by taking a predictive approach incorporating a species distribution model, climatic model, niche model, phylogenetic model, and mechanistic model. This can help us understand how interactions change spatially and temporally on local and regional scales. It is also possible to verify whether the metaweb changes over time.

(7) We believe incorporating this future direction is essential for a better macroecological understanding. Wildlife conservation is incomplete without the proper knowledge of species interactions. A realistic ecological network will ultimately help policymakers find an answer to one of the most crucial questions about wildlife conservation: which species should be protected to enhance ecological interactions and ultimately save other species within the ecosystem.

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Table 1. Summary of the different predictive models.

Category		Model	Characteristics	Advantage	Disadvantage
Niche-based	Intervality property model	Cascade Model (Cohen & Newman, 1985)	Each species has a fixed probability of consuming other species with lower niche value	This first model to predict ecological interactions.	Does not allow cannibalism and feeding on the node with higher niche values.
		Niche Model (Williams & Martinez, 2000)	Species interact within a niche range determined by beta distribution, with the center of the niche having either equal or lower niche value than the concerned species.	Allows cannibalism and feeding on species with higher niche values.	Most accurate in this category model but criticized for generating false interactions.
		Mechanistic diet-breadth model (Beckerman *et al.*, 2006)	This model mechanistically predicts niche size and connectance of nodes using optimal foraging theory.	The niche and connectance are mechanistically calculated in this method.	Needs information about many parameters compared to other models. Also, the predictive performance is low.
	Intervality problem model	Nested-hierarchy model (Cattin *et al.*, 2004)	The model is based on the niche model and follows two rules: (i) predators with shared prey in their niche space will form more links with each other, (ii) additional links are formed randomly to reach the desired connectance.	First attempt to break the intervality issue and create modularity, as seen in the real ecological network.	Predictive performance is poor compared to the niche model.
		Generalized cascade model (Stouffer *et al.*, 2005)	It follows the rule of the cascade model. Niche distribution follows either exponential or beta distribution.	The model addresses intervality issues through random link	Model performance is not as good as the niche model.

		Predator selects prey randomly from niche space.	formation within the niche space.	
	Generalized niche model (Stouffer *et al.*, 2006)	It attempted to modify the niche model by reducing the niche space to make it interval, then selecting some preys randomly from the remaining unreduced niche spaces.	The model tries to overcome the intervality issue by creating random interactions outside the niche space.	The predictive performance is not as good as the niche model.
	Minimum potential niche model (Allesina *et al.*, 2008)	The model creates a maximum niche space, then randomly forbids some nodes to develop interactions based on observed data.	The model tries to overcome the intervality problem by randomly making some interactions forbidden from the niche space.	This model produces fewer non-reproducible links compared to the niche model, although its predictive performance is not better.
Interaction matrix-based	Stochastic block model (Allesina & Pascual, 2009)	The model uses network modularity properties to group similarly interacting nodes by organizing the interaction matrix.	The model is capable of predicting large networks accurately.	Performance to predict small-sized network is not good.
	Latent-trait model (Rohr *et al.*, 2010)	It predicts the interaction with the help of one or more imaginary trait	Capable of predicting large networks and has good predictive performance. The latent trait can be compared to functional traits.	Predictive performance is not always good (29% correct prediction in one network).

	Matching-centrality model (Rohr *et al.*, 2016)	It combined the latent trait model with the concept of degree distribution.	Model performance is better than the latent-trait model.	Sometimes the performance can be poor (50% correct prediction).
	Coverage deficit model (Terry & Lewis, 2020)	The model is based on the Chao1 estimator to understand the incompleteness of the sampling of interactions in the network.	The model tries to focus on a genuine issue of incomplete sampling of interactions.	The predictive performance is worst in this category.
Phylogeny-based	Phylogeny-based generalized linear model (Pearse & Altermatt, 2013)	This model predicts interaction with generalized linear model formulation with number of interaction partner of a node and phylogenetic distance.	Predictive performance is good	Requires phylogenetic data.
	LS-net (Elmasri *et al.*, 2020)	It combines phylogenetic distances and interaction affinity between groups to predict the network with Bayesian model	Predictive performance is good.	Requires phylogenetic data.
Supervised learning-based	Simple supervised learning (Desjardins-Proulx *et al.*, 2017)	This model learns from observed interactions and explanatory variables to predict missing links.	Capable of handling large data. Predictive performance is good.	Requires large data and information about explanatory variables.

	Graph embedding (Strydom *et al.*, 2021)	This model reduces the dimension of the ecological network and uses supervised learning to predict interactions.	This model reduces the problem of the very high dimension of the ecological network.	Requires large data and information about explanatory variables.

869 Table 2. Summary of network metrics and their previous application in different research.

Category	Metric	Definition	Applications
Metrics to describe a network (α-diversity and γ-diversity) General indices	Interaction richness	Number of interactions in a community	(Kortsch *et al.*, 2019; Albouy *et al.*, 2019; Olivier *et al.*, 2019; Grünig *et al.*, 2020)
	Linkage density	Average number of links per node	(Kortsch *et al.*, 2019; Gravel *et al.*, 2019; Albouy *et al.*, 2019; Braga *et al.*, 2019; Olivier *et al.*, 2019)
	Connectance	Proportion of links realised out of the maximum possible links.	(Kortsch *et al.*, 2019; Gravel *et al.*, 2019; Albouy *et al.*, 2019; Dáttilo & Vasconcelos, 2019; Braga *et al.*, 2019; Olivier *et al.*, 2019; Ho *et al.*, 2022)
	Degree distribution	Probability that the number of species having a particular number of interactions	
	Clustering coefficient	Probability that two linked species are also linked with a third species.	(Kortsch *et al.*, 2019; Braga *et al.*, 2019)
	Modularity	Measures how much the network is distributed to subsystems of densely connected nodes.	(Kortsch *et al.*, 2019; Albouy *et al.*, 2019)
	Nestedness	Measures how much the specialist edges are a subset of generalist edges in the network.	(Dáttilo & Vasconcelos, 2019; Ho *et al.*, 2022)
	Diameter of the network	Longest of the shortest distances between every pair of nodes	
	A_P	Overall α-diversity at for weighted or unweighted nodes.	(Ohlmann *et al.*, 2019)
	G_P	Overall γ-diversity at for weighted or unweighted nodes.	(Ohlmann *et al.*, 2019)
	A_L	Overall α-diversity at for links in binary interaction matrix.	(Ohlmann *et al.*, 2019)
	G_L	Overall γ-diversity at for links in binary interaction matrix.	(Ohlmann *et al.*, 2019)
	A_π	Overall α-diversity at for weighted interaction matrix.	(Ohlmann *et al.*, 2019)
	G_π	Overall γ-diversity at for weighted interaction matrix.	(Ohlmann *et al.*, 2019)

Food web specific indices	Maximum chain length	Longest of the maximal food chain (a chain linking top and basal species)	
	Average chain length	Average of the maximal food chain	(Kortsch *et al.*, 2019; Braga *et al.*, 2019)
	Median chain length	Median of the maximal food chain	
	Standard deviation of chain lengths	The standard deviation of the maximal food chain	
	Vulnerability	Mean number of consumers per resource	(Kortsch *et al.*, 2019; Albouy *et al.*, 2019; Braga *et al.*, 2019; Olivier *et al.*, 2019)
	Generality	Mean number of resources per consumer	(Kortsch *et al.*, 2019; Albouy *et al.*, 2019; Braga *et al.*, 2019; Olivier *et al.*, 2019)
	VulSD	Standard deviation of vulnerability	(Kortsch *et al.*, 2019; Albouy *et al.*, 2019; Braga *et al.*, 2019; Olivier *et al.*, 2019)
	GenSD	Standard deviation of generality	(Kortsch *et al.*, 2019; Albouy *et al.*, 2019; Braga *et al.*, 2019; Olivier *et al.*, 2019)
	Mean trophic level	Mean of the prey-averaged trophic level	(Kortsch *et al.*, 2019; Albouy *et al.*, 2019; Braga *et al.*, 2019; Olivier *et al.*, 2019)
	Maximum trophic level	Maximum of the prey averaged trophic level	(Braga *et al.*, 2019)
	Level of omnivory	Level of omnivory of each species is the standard deviation of the trophic level of its resources.	(Kortsch *et al.*, 2019; Albouy *et al.*, 2019; Braga *et al.*, 2019)
	Mean maximum	Mean maximum similarity of two nodes in terms of shared resources and consumers, based on Jaccard similarity	(Olivier *et al.*, 2019)

	trophic similarity		
	Proportion of basal species	Proportion of nodes with no prey	(Kortsch *et al.*, 2019; Albouy *et al.*, 2019; Braga *et al.*, 2019)
	Proportion of intermediate species	Proportion of nodes with both prey and predator	(Kortsch *et al.*, 2019; Albouy *et al.*, 2019; Braga *et al.*, 2019)
	Proportion of top species	Proportion of nodes with no predator	(Kortsch *et al.*, 2019; Albouy *et al.*, 2019; Braga *et al.*, 2019)
	Proportion of omnivores	Proportion of nodes that consumes other nodes belongs to more than one trophic level	(Kortsch *et al.*, 2019)
	Proportion of cannibals	Number of nodes having self-edge	(Kortsch *et al.*, 2019)
Metrics to understand interaction turnover (β-diversity)	β_W	Overall dissimilarity of interaction between two networks	(Kortsch *et al.*, 2019)
	β_{ST}	Variation of interaction between two networks due to variation in their species composition	(Olivier *et al.*, 2019)
	β_{OS}	Variation of interaction between shared species of two networks	
	β'_{OS}	Difference between the interaction of two species in local network and metaweb	(Poisot *et al.*, 2017; Dáttilo & Vasconcelos, 2019)
	LNU	The proportion of unique interaction in a local network with its quasimetaweb	
	SIF	Mean of occurrence of shared interactions of local networks with quasimetaweb	
	B_P	Overall β-diversity of weighted/unweighted nodes between the local webs	(Ohlmann *et al.*, 2019)
	B_L	Overall β-diversity of links between the local webs for binary interaction matrix.	(Ohlmann *et al.*, 2019)

Bπ	Overall β-diversity of links between the local webs for weighted interaction matrix.	(Ohlmann *et al.*, 2019)
$\beta_{co\text{-}pres}$ & $\beta_{co\text{-}abs}$	Measures co-presence and absence of different nodes along the environmental gradients	

Table 3. List of different metawebs developed so far. For the metaweb construction method, 'classical' and 'predictive' corresponds to section 2 of this article. In the local web construction method, 'predicted' means interactions are predicted from metaweb, whereas 'observed' means interactions are observed locally. The column 'analysis method' indicates how the metawebs were analysed. Here, spatial and temporal indicates that local webs were analysed for spatial and temporal changes, respectively; ‘α’ indicates that α diversity was analysed. While in the case of β diversity, ‘β_1’ indicates that indices are estimated to understand β diversity, ‘β_2’ indicates ordination used to understand the turnover, and ‘β_3’ indicates both indices & ordination are used to understand the β diversity.

Metaweb	**Ecosystem**	**Taxa**	**Method of network construction**		**Analysis method**	**Reference**
			Metaweb	**Local web**		
European Tetrapod metaweb	Terrestrial	Mammals (288), birds- (509-510), Reptiles (239-250), Amphibians (103-104)	Classical	Predicted	Spatial α β_1	(Braga *et al.*, 2019; Maiorano *et al.*, 2020)
German Blight Metaweb	Marine	Benthic epifaunal invertebrates (21), fish (27)	Classical	Predicted	Temporal α β_1	(Olivier *et al.*, 2019)
Barent sea metaweb	Marine	233 trophospecies belong to planktons and benthos	Classical	Predicted	Spatial α β_3	(Planque *et al.*, 2014; Kortsch *et al.*, 2019)
Canadian mammals metaweb	Terrestrial and semi-aquatic ecosystem	-	Predictive	-	-	(Strydom *et al.*, 2022)
Global Marine	Marine	Fishes (11,365)	Predictive	Predicted	Spatial α	(Albouy *et al.*, 2019)

Ecosystem metaweb						
Northern Europe Host-parasite metaweb	Terrestrial (agricultural)	Plants (52), herbivores (96), Parasitoids (127)	Classical	Observed	Spatial α	(Gravel *et al.*, 2019)
European crop-forest pest metaweb	Terrestrial	Pest (89), Host plant (126)	Classical	Predicted	Spatial	(Grünig *et al.*, 2020)
Eurasian rodent-flea metaweb	Terrestrial	Rodents (121), ectoparasites (206)	Classical	Observed	Spatial β_2	(Poisot *et al.*, 2017)
Brazilian ant-tree metaweb	Terrestrial	Ants (100) and tree (177)	Classical	Observed	Spatial α β_1	(Dáttilo & Vasconcelos, 2019)
Swiss Blue and Green metaweb	Terrestrial and Freshwater	Plant (2016), butterfly (191), grasshopper (109), bird (155), stream invertebrate (248), stream fish (78)	Classical	Predicted	Spatial α β_2	(Ho *et al.*, 2022)

Figure legends

Figure 1. Concept of the metaweb. A, B and C are three bipartite undirected ecological networks documented from a region. Here, circles represent nodes, and lines represent edges. The metaweb (M) is a combination of all nodes and potential interactions documented from that region ($M=A \cup B \cup C$)

Figure 2: Classical approach of developing metaweb. (1) Defining the ecological and geographical boundary of the metaweb, (2) preparing a list of species from the defined area, categorizing them by trophospecies or functional groups or clumping them to a higher taxonomic level, (3) developing an interaction matrix of the species, where in this figure, A-F and P-U are two groups of species with only intergroup interactions possible, (4) resolving the problem of species that do not interact with other species (in this case, P) by (A) either merging it with another similar species or (B) removing it from the matrix, and (5) presenting the resulting matrix as a graph, which is the metaweb.

Figure 3. A recommended method for metaweb development. See section 2.2.7 for the elaboration.

Figure 4. A suggested guideline to develop local web from the metaweb. See section 3 for the detailed description.

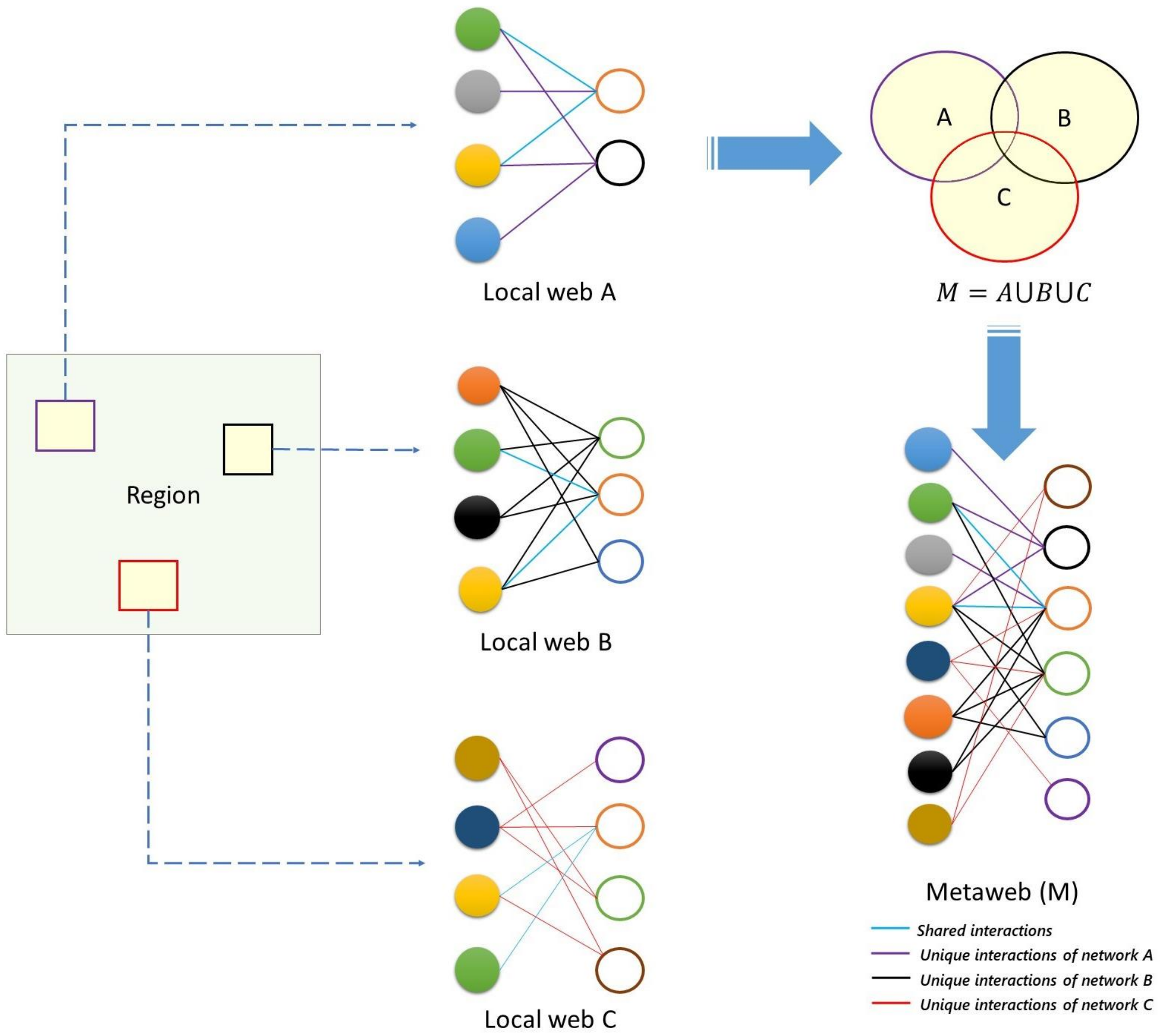
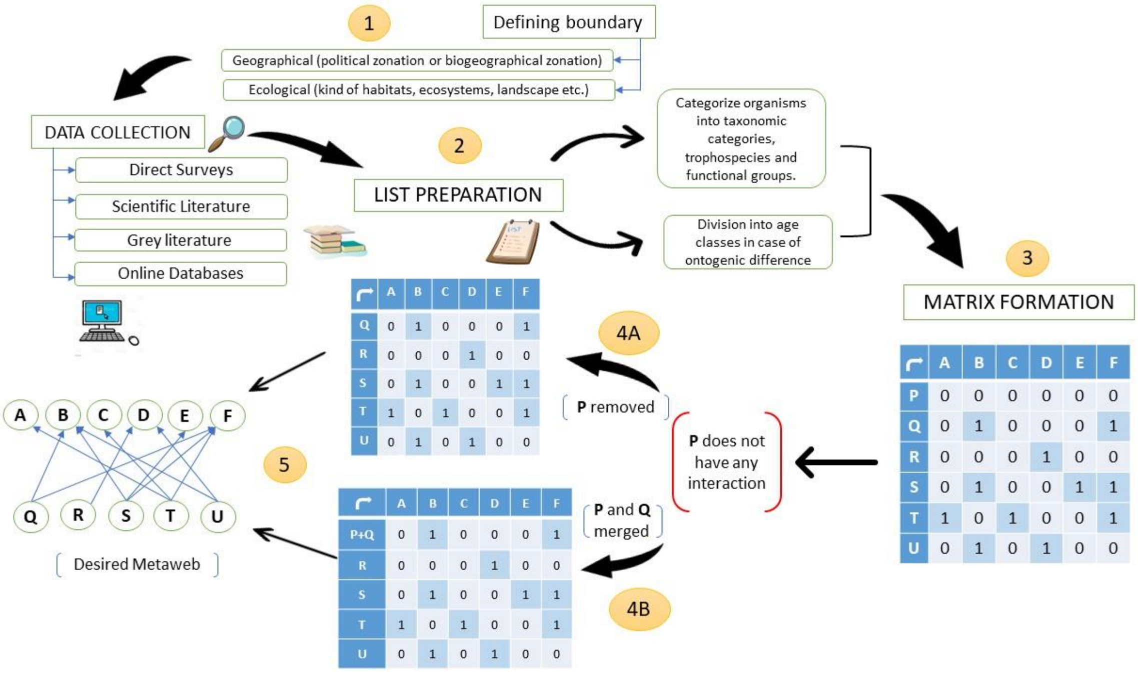

Local web A
A
B
C
$M = A \cup B \cup C$
Region
Local web B
Local web C
Metaweb (M)
Shared interactions
Unique interactions of network A
Unique interactions of network B
Unique interactions of network C

Figure 1.

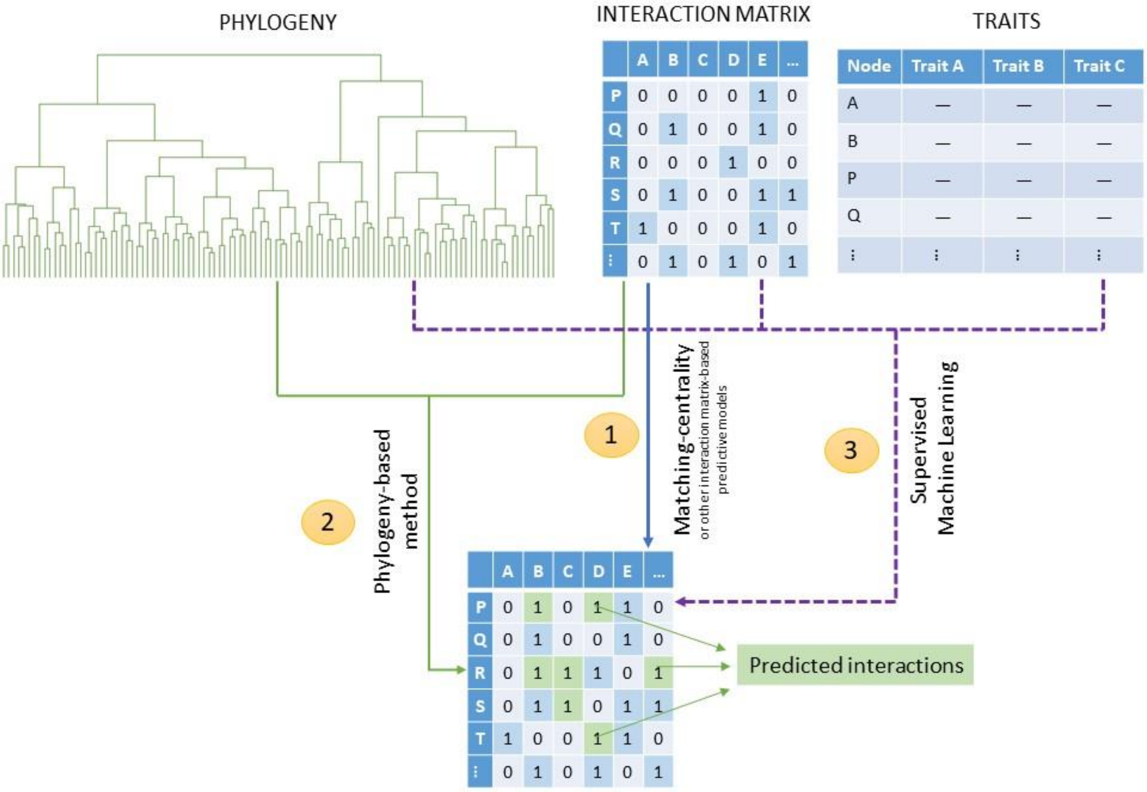


	A	B	C	D	E	F
P	0	0	0	0	0	0
Q	0	1	0	0	0	1
R	0	0	0	1	0	0
S	0	1	0	0	1	1
T	1	0	1	0	0	1
U	0	1	0	1	0	0

	A	B	C	D	E	F
Q	0	1	0	0	0	1
R	0	0	0	1	0	0
S	0	1	0	0	1	1
T	1	0	1	0	0	1
U	0	1	0	1	0	0

	A	B	C	D	E	F
P+Q	0	1	0	0	0	1
R	0	0	0	1	0	0
S	0	1	0	0	1	1
T	1	0	1	0	0	1
U	0	1	0	1	0	0

Figure 2.

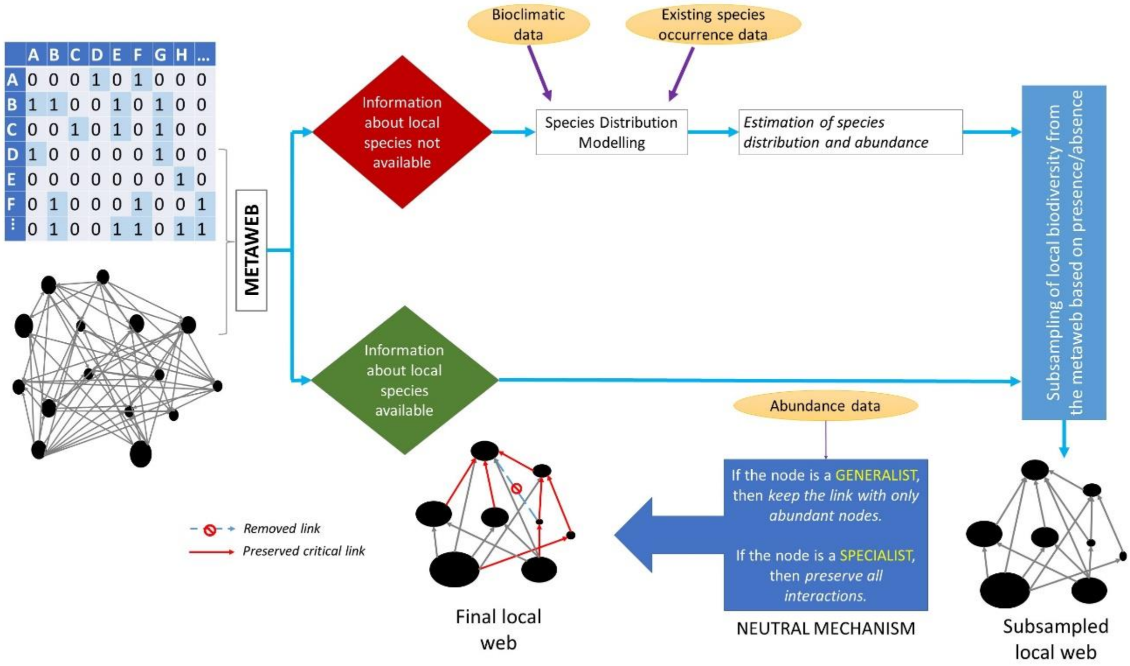


	A	B	C	D	E	...
P	0	0	0	0	1	0
Q	0	1	0	0	1	0
R	0	0	0	1	0	0
S	0	1	0	0	1	1
T	1	0	0	0	1	0
⋮	0	1	0	1	0	1

Node	Trait A	Trait B	Trait C
A	—	—	—
B	—	—	—
P	—	—	—
Q	—	—	—
⋮	⋮	⋮	⋮

	A	B	C	D	E	...
P	0	1	0	1	1	0
Q	0	1	0	0	1	0
R	0	1	1	1	0	1
S	0	1	1	0	1	1
T	1	0	0	1	1	0
⋮	0	1	0	1	0	1

Figure 3.



	A	B	C	D	E	F	G	H	...
A	0	0	0	1	0	1	0	0	0
B	1	1	0	0	1	0	1	0	0
C	0	0	1	0	1	0	1	0	0
D	1	0	0	0	0	0	1	0	0
E	0	0	0	0	0	0	0	1	0
F	0	1	0	0	0	1	0	0	1
⋮	0	1	0	0	1	1	0	1	1

If the node is a GENERALIST, then *keep the link with only abundant nodes.*

If the node is a SPECIALIST, then *preserve all interactions.*

Figure 4.