Metaweb approaches for understanding complex ecological interactions: A Review

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Abstract

A metaweb is the regional pool of potential interactions, capturing the gamma diversity of species and interactions. A metaweb enables the generation of local webs from species occurrence data by subsampling contained interactions, thereby allowing insights into alpha and beta diversities with minimal data requirements. Moreover, understanding ecological interactions is critical for a complete ecological perspective and enhancing knowledge of ecosystem structure and function beyond species diversity alone. However, the Eltonian Shortfall—limited species interaction data—impedes this holistic view. Thus, predictive approaches utilising interaction matrices or additional node information (traits, phylogeny) have emerged to address this gap. This review explores the applications and methodologies in metaweb studies, detailing methods for metaweb construction, applying metawebs for generating local webs, and analysing both local webs and metawebs across alpha, beta, and gamma levels. This review further examines existing metaweb studies, uncovering insights into spatiotemporal network dynamics, the impact of environmental variation and human activity on network properties, climate change effects, and species interaction turnover. Applications are also discussed in community assembly processes, conservation planning, keystone species identification, trait-based analyses, and the usefulness of existing metawebs to reconstruct metawebs from other regions. We highlight future directions, emphasising expanding geographical coverage, enhancing interaction data collection, integrating conservation, and improving trait-based approaches through latent trait analysis. This review sets a benchmark for future research, advancing our understanding of ecological interactions while supporting Sustainable Development Goals 13 (climate action), 14 (life below water), and 15 (life on land).

Keywords: Metanetwork; ecological network; interaction prediction; interaction diversity; interaction turnover; biodiversity

1. Introduction

Ecological interactions play a pivotal role in shaping the structure and functioning of ecosystems by determining species co-existence (Gravel et al., 2019; Ohlmann et al., 2023; Valladares et al., 2015), regulating population dynamics, energy flow and nutrient cycling (DeAngelis, 1992), and promoting biodiversity (McIntire and Fajardo, 2014; Wardle, 2006). Therefore, understanding these interactions is paramount, as it allows the identification of key species for targeted conservation (Harvey et al., 2017; Jordán, 2009; Martín González et al., 2010; Wu et al., 2020). Furthermore, studying these interactions provides valuable insights into the broader ecological implications of climate change, habitat loss, and other environmental stressors, aiding in formulating adaptive and resilient ecosystem management practices (Albouy et al., 2014; Chagaris et al., 2015; Harvey et al., 2017; Hattab et al., 2016; Jackson et al., 2020).

Ecological networks serve as simple yet powerful tools, enabling the integration and analysis of diverse arrays of interactions within a unified framework, collectively or individually (Kéfi et al., 2015). The study of ecological networks is greatly influenced by network science (Barabási, 2013; Newman, 2018), which provides many concepts, models, and tools for investigating ecological questions (Poisot et al., 2016). Graph theory (GT) aids in analysing the topological properties of ecological networks, providing insights into the eco-evolutionary mechanisms that shape their structure; different widely used GT-based indices and their ecological implications can be found in the literature (Dale, 2017; Delmas et al., 2019) and later in this review. Furthermore, adding weight to nodes (entities interacting with one another) and edges (interactions between nodes) helps to explore the functional aspects of ecological networks that provide deeper ecological understanding and a more realistic overview (Wulff et al., 1989).

The initial understanding of ecological networks was largely limited due to data unavailability (Delmas et al., 2019; Morales-Castilla et al., 2015), widely known as the Eltonian shortfall (Hortal et al., 2015). However, an increasing interest in understanding the dynamic patterns of interactions and the ecological mechanisms driving them has led to a gradual improvement in data availability (Pilosof et al., 2017; Strydom et al., 2021). Despite this progress, the static nature of networks remains a major obstacle to studying the dynamic patterns of ecological interactions (McCann and Rooney, 2009; Poisot et al., 2015). Therefore, to overcome this challenge, some multilevel hybrid modelling frameworks were developed which are capable of simulating static networks spatiotemporally, such as Ecopath with Ecosim and Ecospace (EwE) (Christensen and Walters, 2004; Colléter et al., 2015; Ren et al., 2023), AQUATOX (Park et al., 2008; Zhang et al., 2013; Zhang and Liu, 2014), and Atlantis (Audzijonyte et al., 2019; Nilsen et al., 2022; Tarnecki et al., 2016). However, applying these models is constrained by the need for extensive information, limiting their utility to data-rich contexts. For example, the EwE 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 (biomass of each node, production to biomass ratio, consumption to biomass ratio and ecotrophic efficiency). Meanwhile, spatiotemporal simulations with EwE additionally demand more essential inputs, such as a base map, habitat properties, dispersal rate, habitat preference, vulnerabilities, and migration of each species. Thus, despite focusing on realism and mechanistic understanding, extensive data requirements restrict its usage in data-poor situations (Walters, 1999).

A metaweb, also known as a meta-network (Suzuki et al., 2023; Tylianakis and Morris, 2017), offers a promising approach for analysing the dynamics of ecological networks with fewer data requirements compared to the aforementioned hybrid modelling frameworks. The term ‘metaweb’ (gr. μετά= comprehensive) first appeared in philosophy in 1982 (Briskman, 1982) and was later introduced in ecology in 2006 (Dunne, 2006). A metaweb was originally defined as a master web that includes all species in similar habitats and their interactions as if they co-occur in a single habitat (Dunne, 2006). However, in subsequent studies (Grünig et al., 2020; Maiorano et al., 2020; Strydom et al., 2022), the definition of the metaweb shifted to potential interactions within the regional species pool rather than a single habitat. Notably, the term ‘metacommunity’, although similar, carries a distinct meaning: referring to a set of local communities connected by species dispersal, akin to the concept of 'metapopulation' (Hanski and Gilpin, 1991).

Long-term evolutionary and biogeographical processes shape the species pool and interactions in a metaweb (HilleRisLambers et al., 2012; Saravia et al., 2022). However, local biodiversity is shaped by subsampling from the regional metaweb through metacommunity processes influenced by environmental conditions, dispersal ability, stochastic events, and biotic interactions (Saravia et al., 2022; Tylianakis and Morris, 2017). Therefore, not all potential interactions in the metaweb are realised in the local web due to variations in species abundances, phenological mismatch and habitat structure (Tylianakis and Morris, 2017). It is important to note here that the term ‘local web’ is used here to indicate component network (or subsampled network) at different spatial or temporal scales.

Despite metaweb being introduced as a concept in ecology in 2006 (Dunne, 2006), significant advances have only been witnessed within the last five years. This review begins by offering a comprehensive guide to developing a metaweb, encompassing various approaches. Subsequently, it explores diverse predictive methodologies to overcome Eltonian shortfalls, providing insights into their preferred applications across different scenarios. The following sections delve into the generation of local webs where understanding of local web is lacking with the metaweb approach. Then, the methods required for analysing metawebs and local webs to unravel distinct properties at various scales are elucidated. Next, the article briefly outlines various research endeavours conducted using metaweb approaches. Finally, we conclude with an overview of prospects for research in this field.

2. Development of a metaweb

Based on the reviewed literature, three distinct approaches have been identified for developing metawebs: observation-based, literature-based, and prediction-based metawebs. This section concisely overviews these three approaches, highlighting their utilities and applications. Regardless of the chosen method, the initial step in developing a metaweb involves defining its geographical, ecological, and taxonomic scopes. Following this, the metaweb can be constructed using one of the three distinct approaches discussed in the subsequent subsections and illustrated in Figure 1.

2.1 Observation-based metawebs

The first category is an observation-based metaweb (Fig. 1, Section A), which are metawebs directly constructed from observed local webs. In this case, the local networks can be documented from extensive field investigations; otherwise, already published networks from different spatial/temporal points can be considered local networks. Afterwards, the metaweb is developed by combining all the nodes and interactions observed during the study over various locations and periods. If the goal is to prepare a weighted metaweb, the weight of the nodes and edges from local webs should be normalised properly for metaweb development. This kind of metaweb is usually developed to understand gamma network properties, where local networks are well-documented (Pérez-Ortega et al., 2023; Rodríguez-Hernández et al., 2023), thus allowing an opportunity to study how potential interactions are realised at the local level (Cirtwill et al., 2023; Emer et al., 2018).

2.2 Literature-based metawebs

A literature-based metaweb is developed through an extensive literature survey (Fig. 1, Section B). Adhurya et al. (2024) provide a detailed guideline for this method. In this case, a list of focal taxa is first produced using regional knowledge, and data on potential interactions between these organisms are then collected from regional records or an extensive literature survey. As a directory of possible interactions between interacting organisms, interactions documented beyond the geographical and ecological boundaries of the metaweb can also be included, considering difficulties in collecting ecological interaction data. For this purpose, a list of databases is supplemented as an Electric supplementary material (Appendix 1). Thereafter, taxa can be categorised into taxonomic groups, functional groups, and age stages depending on the goal of the study and data availability. However, caution should be exercised when grouping to ensure that it does not lead to excessive structural alterations from the original network (Olivier and Planque, 2017). Afterwards, the metaweb should be tabulated as an adjacency matrix to check for inconsistencies. In this case, if a species has no interactions, it is either removed from the metaweb or merged with a similar species in terms of phylogenetic or functional relatedness (Albouy et al., 2019). Finally, the metaweb can be represented as a graph (Dunne, 2006). This method to develop metaweb is used when local scale interaction data are unavailable (Braga et al., 2019; Kortsch et al., 2019; Olivier et al., 2019).

2.3 Prediction-based metawebs

Collecting interaction data requires more effort and expertise than occurrence data, given the higher numbers and diverse types of interactions, with some interactions being particularly challenging to observe (Jordano, 2016). This absence of knowledge on interactions results in incomplete metawebs, with many species lacking interactions (Rohr et al., 2010). However, it is not possible for a species to not have any interactions except the ecosystem in the early successional stage. Many researchers use predictive tools to amend these knowledge gaps, with the resulting metaweb developed through predictions termed a prediction-based metaweb (Fig. 1, Section C).

Interactions between species develop through natural selection and co-evolution 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 et al., 2012). Meanwhile, life history traits influence species abundance and response to disturbances, thereby affecting the possibility of interactions (Laughlin et al., 2012; White et al., 2007;

Woodward et al., 2005). The combination of life-history traits, phenology, and environmental tolerance determines the likelihood of a species co-existing in the same spatiotemporal space. However, the morphological, physiological, and behavioural characteristics of a species ultimately determine potential interactions (Bartomeus et al., 2016). Species interactions and traits co-evolve, often showing phylogenetic relationships that can be used to predict missing interactions (Elmasri et al., 2020; Gray et al., 2015). Traits (or phylogenetic relationships) determine the probability of interactions, whereas neutral mechanisms linked to their local abundance influence the likelihood of interactions among potentially interacting species (Olito and Fox, 2015; Pichler et al., 2020; Pomeranz et al., 2019). Therefore, these relationships in species interactions can be used to infer unknown species interactions using predictive modelling approaches.

Indeed, many predictive models have been introduced since 1985 (Cohen and Newman, 1985) depending on the understanding of how species interact (Bartomeus et al., 2016). These models can be broadly classified according to their data requirements, which justifies their applicability in different situations: niche-based, interaction matrix-based, phylogeny-based, and supervised learning-based predictions (Table 1).

(a) Niche-based predictions

Niche-based prediction models, also known as the trait-matching model (Bartomeus et al., 2016; Brousseau et al., 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 and Newman, 1985) and **niche-**based models (Williams and Martinez, 2000) 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-based model does not allow for the cannibalism and predation of species with higher niche values. In contrast, the niche-based model considers cannibalism and predation for a more realistic output. Gravel *et al.* (2013) inferred a food web for Mediterranean fish using this approach. Bartomeus *et al.* (2016) modified the niche-based model to allow the incorporation of the abundance or interaction frequency effect. 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 et al., 2006; Petchey et al., 2008). Although the mechanistic approach is praised for the process-based formulation, it requires a lot of difficult information to gather (e.g., searching time and handling time) and does not perform well.

The ‘intervality problem models’ include four models developed to solve the issue of ‘intervality’ in the former models: nested hierarchy, generalised cascade, generalised 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 another 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 forming the desired network requires more links, random links are generated with any species, preferably with species of a lower niche value. The **generalised cascade model** (Stouffer et al., 2005) assumes 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 **generalised niche model** reduces the niche space to make it an interval and selects some prey randomly from the remaining unreduced niche space (Stouffer et al., 2006). Finally, the **minimum potential niche model** (Allesina et al., 2008) uses the inverse approach of the generalised 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 prey not consumed by the predators was counted to calculate the probability of forbidden links within the extended niche space. Therefore, interactions are predicted by removing random prey depending on the probability of forbidden links within the niche space (Allesina et al., 2008).

These niche-based models usually consider a single niche dimension (e.g., body size) to infer interactions. However, the multidimensional nature of the niche, in reality, leads to non-intervality in the observed data within a single niche dimension (Allesina et al., 2008; Allesina and Pascual, 2009; Cattin et al., 2004). Although modified cascade and niche models were developed to address this issue, their predictive performance is worse than that of the original niche model. Eklöf et al. (2013) suggest that considering ten niche dimensions is enough to predict most observed interactions, whereas good predictions can be obtained with five niche dimensions. However, limited data availability on the functional traits referred to as 'Raunkiæran shortfalls' (Hortal et al., 2015) often constrains the applicability of this approach.

(b) Interaction matrix-based predictions

In interaction-matrix-based models, only the pattern of the interaction matrix is analysed for the interaction prediction without any other inputs (e.g., traits, phylogeny, etc.). This kind of model is praised for its ability to handle large networks, good predictive performance (sometimes more than 90% correct prediction), non-reliance on intervality property and fewer data requirements (Table 1).

The **stochastic-block model** (SBM) also called the group-based model (Allesina and Pascual, 2009), utilises the modular properties of an ecological network. The model groups similarly interacting species in such a way that 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 and Sales-Pardo, 2009). Model performance was determined by the number of groups with the lowest value for the Akaike information criterion (AIC).

The **latent trait model** (Rohr et al., 2010) introduced the concept of a latent trait from social network research (Hoff et al., 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. Meanwhile, the latent trait 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, including the degree distribution concept. The model predicts the number of links each node can make by adding a 'centrality' property to each node. The matching part helps us understand which pairs can be linked according to the latent trait.

The **coverage deficit model** (Terry and Lewis, 2020) is based on the concept that ecologists often miss interactions between rare species. The model used the Chao1 (Chao and Jost, 2012) estimator to understand the sampling completeness of ecological interactions, which was further utilised to calculate the probability of interactions.

Finally, the **SOM model** (Adhurya and Park, 2024) uses the power of the Self-Organising Map (SOM) (Kohonen, 2001, 1982) algorithm to identify patterns in the observed network with unsupervised machine learning. The SOM groups similarly interacting nodes together and provides the prediction according to the position of the species on the map.

(c) Phylogeny-based predictions

Phylogenetic distances between nodes and the interaction matrix are required to predict interactions with phylogeny-based models. In this case, phylogeny is a proxy for multiple traits because traits and interactions are co-evolved during evolution (Agrawal, 2001; Thompson, 1999). Two purely phylogeny-based prediction models were proposed: a generalised linear model and a latent score network model. The **phylogeny-based generalised linear model** (Pearse and Altermatt, 2013) predicts interactions with a generalised linear model formulation using a node's documented interaction partners in the observed matrix and the phylogenetic distance as the dependent variable. In contrast, the latent score network (LS-net) model (Elmasri et al., 2020) combines phylogenetic distances and interaction affinity (similar to the centrality term in the matching-centrality model) between groups to predict the network using a Bayesian model. Phylogeny can improve network prediction since it represents 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 employing real traits and phylogeny with a generalised additive modelling approach and found better predictive performance when applying phylogeny as a predictor.

(d) Supervised machine learning-based predictions

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 might 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 the k-nearest neighbors (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 tree, 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 varying observation times. Another recent study (Barel et al., 2023) compared six machine learning algorithms (random forest, boosted regression tree, kNN, neural networks, generalised linear model, and Bayesian generalised linear model) to predict ecological interactions with trait and phylogeny data. Strydom *et al.* (2021) proposed a graph-embedding approach that involved reducing the dimensionality of the interaction matrix and applying 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).

(e) Comparison of performance of different models

Here, we provide a comparative overview of different models based on their performance, as highlighted across various studies. Performance metrics primarily include binary classification measures such as accuracy, sensitivity, specificity, precision, True Skill Statistics (TSS), and Area Under the Receiver Operating

Characteristic (AUROC) curve (Electronic supplementary material, Appendix B). Some earlier studies also employed metrics such as mean normalised error and link likelihood. However, direct comparison is challenging since each study used distinct methods and evaluation criteria. Therefore, our comparison relies on model performance indicators alongside key critiques from prior studies.

Williams & Martinez (2000) showed that the niche model (mean normalised error 0.22 ± 1.8) was superior to the cascade model (mean normalised error -3.0 ± 14.1) in predicting species interactions. Although the nested hierarchy model has the advantage of overcoming intervality, its predictive performance has not subsequently improved (Cattin et al., 2004). Indeed, Dunne (2009) criticised the nested hierarchy and generalised cascade models for their poor performance in representing several network structural properties compared with the niche model.

Allesina *et al.* (2008) compared different network models (niche, cascade, and nested hierarchy) based on their ability to predict observed links in empirical networks and 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 using a niche model based on TSS, which ranged between 0.13 and 0.76. Petchey *et al.* (2008) revealed that the mechanistic diet-breadth model correctly predicted observed links in 5–65% of 15 analysed food webs. However, the model performance was the worst for 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. These six food webs were notably 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, whereby Rohr *et al.* (2010) found that including latent traits alone could predict 29–87% of the links in the empirical food web, whereas including body size and latent traits could predict 44–93%. Additionally, the matching-centrality model displayed a 50–100% fit to the empirical data by considering two matching latent characteristics (Rohr et al., 2016).

Terry and Lewis (2020) showed that stochastic block (AUROC: 0.63–0.691), latent trait (AUROC: 0.631–0.66), and matching-centrality (AUROC: 0.671–0.718) models outperform the coverage-deficit model (AUROC: 0.589–0.6). However, the coverage deficit model can predict poorly sampled interactions. Therefore, combining the coverage deficit model with other models can improve the predictability of the model in some cases.

In phylogenetic models, a phylogeny-based generalised 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 and Altermatt, 2013). In another study, the predictive performance of LS-net was better than kNN based on the AUROC and the percentage of true interactions recovered in a host–parasite interaction network (Elmasri et al., 2020). However, the kNN method, which relies solely on the interaction matrix, also demonstrated good predictive power.

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 alone, with an accuracy of 74% and a TSS of 0.46, could better predict interactions than the best trait-matching combinations, which have an accuracy of 71.5% and a TSS of 0.37. Moreover, Brousseau *et al.* (2018) 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 kNN 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, the random forest, boosted regression tree, and deep neural network models are the most suitable for predicting ecological networks (Barel et al., 2023; Pichler et al., 2020). Strydom *et al.* (2022) used graph embedding followed by machine learning and reported that their model correctly predicted 92% of interactions.

The unsupervised machine learning method (SOM) shows an excellent predictive performance in terms of AUROC (0.88–0.99), F1 (0.84–0.98), TSS (0.77–0.95), accuracy (0.97–0.99), and proportion of observed links correctly predicted (77.63–95.2%). Additionally, this model predicts fewer interactions compared to other methods. However, predictive performance is better for large networks and networks with connectance > 0.1 (Adhurya and Park, 2024).

(f) Which predictive method should be used for metaweb development?

Metawebs often contain an overwhelming number of species. Thus, data on the functional traits and environmental tolerance of such a large number of species belonging to diverse taxonomic groups are usually challenging to gather. However, many emerging databases exist (see Electronic supplementary material, Appendix 1) to cover this gap. Therefore, our recommendation is based on the amount of data available. Firstly, interaction matrix-based predictive models, especially SOM, are the most accurate in predicting interactions with large metawebs. However, unsupervised methods, such as SOM, SBM, and kNN, do not provide any information on the ecological mechanisms alongside their prediction. Hence, a latent trait or matching centrality model can be a good alternative if the goal is to relate traits or phylogeny.

Our second choice was phylogeny-based models because of their superior predictive ability and ease of collecting phylogenetic data compared to trait data. Additionally, phylogenetic information reflects the effects of multiple traits (Brousseau et al., 2018). However, similar to SOM, phylogeny-based models do not provide an understanding of the mechanism behind the interactions.

Supervised learning can be used in data-rich conditions, where data about traits and/or phylogeny are available. Then, the random forest, boosted regression tree, and deep neural networks can be used due to their proven performance in predicting ecological interactions. Supervised learning also offers scope to understand the relative weight of different explanatory variables affecting the interaction prediction. Although the niche models are less suitable for large heterogeneous datasets for making robust predictions, they can still be utilised to gain a mechanistic understanding of the metaweb.

3. Inferring local webs using the metaweb approach

Utilising metaweb to generate 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 organisation. Two kinds of cases could arise during local web development with the metaweb approach: (i) when empirical data on local species are available and (ii) when local species data are absent (Fig. 2).

In the first case, locally observed species constitute the nodes of the local web, and interactions are assigned from the metaweb; nodes lacking interactions are excluded. This methodology has been consistently employed in various studies where local webs were derived from metawebs using local occurrence data (Albouy et al., 2019; Braga et al., 2019; Gaüzère et al., 2023; Ho et al., 2022; Kortsch et al., 2019; Olivier et al., 2019).

In scenarios where local-level data for different nodes are unavailable, the probability of species occurrence across space and time can be inferred using species distribution models (SDMs) with bioclimatic data. Simulated occurrence data are then utilised to construct local webs by subsampling interactions from the metaweb (Strydom et al., 2021). This methodology has been employed to assess changes in local networks under future climate scenarios in the Gulf of Gabès (Hattab et al., 2016) and Mediterranean Sea continental shelf (Albouy et al., 2014) metawebs, where species distribution models generated occurrence data for future climate scenarios. In the Canadian Rocky Mountains, species distribution modelling based on camera trap data is also deployed to improve understanding of species occurrence for local web development (Steenweg et al., 2023).

In these above approaches, interactions are inferred under two assumptions: (i) species are present in sufficient abundance and temporal synchrony to realise potential interactions, and (ii) species do not adjust their diet in response to biotic (e.g., competitors) or abiotic factors (Bauer et al., 2022; Tylianakis and Morris, 2017). However, co-occurrence does not necessarily imply interaction. Therefore, encounter probability based on local abundance data can be incorporated to address the potential overestimation of links in the local network. This approach assumes that more abundant species have a higher chance of interacting, while rare species have a lower chance, often referred to as a neutral process (Canard et al., 2012). In recent studies (Pomeranz et al., 2020; Vagnon et al., 2023), the interaction probability from a niche model was multiplied by encounter probability (scaled between 0.5 and 1), resulting in a final interaction probability matrix scaled between 0.01 and 0.99. These matrices were then used to infer multiple binary interaction matrices per location with Bernoulli’s trial. Note that this method may pose challenges when either the metaweb is binary, or there is no abundance of data at the local level. As an alternative, we propose converting the binary local web matrix developed from the metaweb into a probability matrix based on abundance-based encounter probability, followed by applying Bernoulli’s trial to generate binary local webs.

4.4 Analysis of metaweb and its local constituent webs

A thorough examination of the metaweb and its local constituent webs is essential for gaining ecological insights into network properties across different scales and understanding their temporal and spatial dynamics. The metaweb represents the gamma (γ) properties, encompassing all species and interactions within a region, while local webs reflect the alpha (α) properties, shaped by environmental and biotic filtering. The turnover between the metaweb and local webs, or differences among local networks, represents the beta (β) properties. Analysing node-level variations provides deeper insights into specific network components. Meanwhile, incorporating null models helps reveal how local networks and the metaweb deviate from random expectations.

We discuss these analytical approaches in the following subsections to provide a comprehensive framework for using the metaweb approach in various analyses. Metrics at the α, β, γ, and node levels from studies utilising metaweb analysis, along with their definitions and ecological significance, are summarised in Table 2.

4.1 Understanding network properties

The interaction matrix of the metaweb and inferred local webs is typically binary, leading to graph theory-based indices being used for network analyses. Common indices used to describe both α and γ properties of networks include interaction richness, linkage density, connectance, degree distribution, modularity, nestedness, clustering coefficient, and diameter. These indices are widely applicable and offer key ecological insights.

For example, connectance is considered a critical network descriptor due to its robustness (Dunne et al., 2002), invasiveness (Baiser et al., 2010; Smith-Ramesh et al., 2017), and correlation with most ecological properties (Dunne et al., 2002; Poisot and Gravel, 2014). Connectance decreases with increasing species richness in a network (Kay and Schemske, 2004). Degree distribution helps identify specialists and generalists in the network (Memmott et al., 2004), while increased modularity enhances network persistence by containing perturbations within modules (Stouffer and Bascompte, 2011, 2010). Nested networks support higher biodiversity, as specialists share interaction partners with generalists (Bastolla et al., 2009). Smaller network diameter indicates denser connections but higher vulnerability to perturbations (Minor et al., 2008), while network robustness measures its ability to resist disturbances (Dunne and Williams, 2009). Network specialisation (H_2) quantifies the balance between specialists and generalists, ranging from 0 (extreme specialisation) to 1 (extreme generalisation) (Blüthgen et al., 2006).

Ohlmann et al. (2019) introduced six Hill number-based (Hill, 1973) indices to assess node and link diversity at the α and γ levels. These include indices for node diversity (A_P and G_P), link diversity based on interaction probabilities (A_P and G_P), and link diversity based on link abundance (A_L and G_L). Link abundance indicates the likelihood of interaction between a pair of nodes, which multiplies the abundance of the interacting node. Additionally, they provide a clear guideline for using these indices in different species grouping levels from micro to macroscale.

Comparatively, due to their unique structure, trophic networks require specialised indices. For example, generality and vulnerability are alternatives to degree distribution, indicating the average number of resources per consumer and consumers per resource. Additional trophic-specific indices are outlined in Table 2, while further details can be found in related literature (Bersier et al., 2002; Delmas et al., 2019; Williams and Martinez, 2004).

Apart from an index-based understanding of network structure, the motif frequencies can also provide important ecological insights into different processes responsible for community assembly. Motifs are smaller subgraphs in a network (Milo et al., 2002), the smallest of which consists of three nodes (Holt, 1997). In total, 13 unique motifs are possible for directed networks with three nodes. The frequency of different motifs aids in understanding the prevalence of various processes in a network. Recent studies have explored the motif frequency variations in local networks (Bauer et al., 2022; Garrison et al., 2022) and how these differ from null expectations using the metaweb approach.

4.2 Understanding network turnover

Species composition and interactions vary spatially and temporally due to biotic and abiotic conditions (Gravel et al., 2019). Various diversity measures estimate species turnover, including formulations for presence–absence data (Koleff et al., 2003). However, interaction diversity often differs from species diversity and is not always correlated (Poisot et al., 2017, 2011). Many studies have used multivariate ordination analyses to explore how network properties change along environmental gradients (Baiser et al., 2012; Braga et al., 2019; Frelat et al., 2022; Kortsch et al., 2021, 2019; Vermaat et al., 2009). In contrast, many further studies employed other indices to focus on understanding the β-diversity of ecological interaction networks. Similar to ordination, where α-diversity measures are checked for their variation in environmental gradients, β-diversity measures can also be checked for their relationship to different distance measurements (i.e., environmental, geographical, functional traits, etc.) (Bauer et al., 2022; Dáttilo and Vasconcelos, 2019).

The three most widely used indices to understand β-diversity of ecological networks in metaweb studies are β_{WN}, β_{ST}, and β_{OS}. Here, β_{WN} measures total interaction turnover, which can be split into species turnover (β_{ST}) and rewiring of interactions between shared species (β_{OS} or β_{RW}) (Canard, 2011; Poisot et al., 2012). Additionally, dissimilarity indices such as Sorenson's and Simpson's have been applied to measure interaction network differences (Gaüzère et al., 2023), with Sorenson's index (Sorensen, 1948) capturing overall dissimilarity and Simpson's index (Simpson, 1943) capturing dissimilarity due to turnover.

However, neither of these indices relates a metaweb to the local web. β'_{OS} (Poisot et al., 2012) is the first index developed from the perspective of a metaweb and measures how the locally realised interactions differ from the potential interactions between the same species in a metaweb. However, the β'_{OS} index is not applicable if the local web is subsampled from the metaweb, 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).

Luna et al. (2020) argued that β'_{OS} is not a measure of β-diversity because instead, it compares the local network with the regional metaweb, i.e., comparing α-diversity with γ-diversity. They also argued that β'_{OS} does not highlight the presence of unique interactions in local networks because finding a locally unique interaction requires subtracting the focal network from the metaweb. Subsequently, they proposed two indices: Local Network Uniqueness (LNU) and Shared Interactions Frequency (SIF). LNU and SIF measure the proportion of unique and shared interactions in a focal web. 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 calculate 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.

Ohlmann et al. (2019) proposed three β-diversity indices by dividing their proposed Hill number-based γ-diversity indices with the α-diversity indices for node diversity (B_P), interaction probability (B_L), and link abundances (B_π). These diversity indices can be used at different grouping levels to obtain different macroecological insights, as mentioned in the previous section for α- and γ-diversity indices utilising this approach.

4.3 Understanding the node

Analysing networks at both the α- and γ-diversity levels is essential for understanding the characteristics of local and regional networks and their spatiotemporal dynamics. However, examining nodes provides insights into which species are regionally significant, their roles at the local level, and how these vary across time and space. Since nodes form the foundation of networks, understanding their interactions helps identify which parts are crucial for maintaining the network's structure and function, making this knowledge valuable for management and conservation.

Centrality remains the most widely used method for studying nodes, as it identifies the most influential species, aiding in discovering potential keystone species. Different centrality measures offer unique perspectives: degree centrality (Freeman, 1977) distinguishes between generalists and specialists; betweenness centrality (Freeman, 1977) identifies species that serve as connectors between modules; closeness centrality (Freeman, 1978; Freeman et al., 1979) measures a species' proximity to all other nodes, indicating how quickly disturbances may spread if that species is removed. A recent review (Delmas et al., 2019) discussed centrality measures in ecological network analyses, and Table 2 summarises those used in previous metaweb studies. Comparing similar species across different networks, such as multiple local webs, can be challenging due to variations in centrality values with network size and connectivity. In this case, centralisation, a normalised centrality metric, may prove useful for comparing nodes across local webs derived from metawebs, revealing their changing roles over time and space (Freeman et al., 1979).

Another area of interest is understanding how different nodes contribute to modularity and nestedness. Modularity is assessed using the within-module connectivity score (z) and the among-module connectivity score or participation coefficient (c) (Guimerà and Nunes Amaral, 2005). Species contributions to modularity are then understood through the z–c score pattern, as summarised in Table 2 (Olesen et al., 2007). For nestedness, a node's contribution is measured by nestedness contribution (Saavedra et al., 2011), comparing the observed nestedness of a network with a randomised network by altering the interaction of a focal node while maintaining the same degree. This concept can be extended to other metrics to assess how nodes contribute to other network properties (Delmas et al., 2019).

Another way to evaluate node importance is by examining their interaction specialisation. Degree centrality is a popular metric due to its simplicity and applicability across networks. Indeed, as previously mentioned, the degree extends to generality and vulnerability in trophic networks. However, incorporating interaction strength and species abundance provides a more realistic view of the roles of species, leading to weighted indices. For instance, species strength is a quantitative extension of the degree of mutualistic networks, indicating how much other species rely on a particular species based on interaction frequency (Bascompte et al., 2006). Similar indices, such as dependency and contribution coefficients, are used in trophic networks to assess the importance of resources and consumers (Wulff et al., 1989). Interaction specialisation (d') is another metric calculated using Kullback–Leibler distance, which measures how specialised a node is in terms of its interactions (Blüthgen et al., 2006). The advantage of d' is its normalisation between 0 and 1, making it easy to interpret, with higher values indicating greater specialisation.

4.4 Utilisation of null models

Null models are pattern-generating models used to test alternative hypotheses by comparing observed patterns against random expectations (Gotelli and Graves, 1996). Meanwhile, ecological networks help assess how network structure deviates from random patterns or changes along environmental gradients (Pellissier et al., 2018). At the node level, null models evaluate the significance of a node by generating random networks where the node maintains the same degree but interacts randomly. This produces a statistical distribution of a network property, allowing researchers to determine the node's role based on observed values, such as its contribution to nestedness. Comparatively, at the network level, null models explore the processes shaping network structure. By generating networks under specific constraints (e.g., fixed connectance or degree), researchers can compare them with observed networks to determine if patterns arise by chance. For instance, Fortuna and Bascompte (2006) used null models to study the impact of habitat loss on extinction, revealing that real communities decay faster but persist longer than random ones.

Null models are also used to study community assembly. Bauer et al. (2022) developed metawebs from local webs and generated random webs under different assumptions (e.g., no filtering, resource filtering, limiting similarity) to compare their properties with observed webs, shedding light on how local food webs form. Additionally, null models can help analyse network patterns across environmental gradients. For example, null models have been applied to study nestedness in Andean plant–pollinator networks along elevation gradients (Ramos-Jiliberto et al., 2010) and the variation of nestedness and modularity with latitude and climate factors in global seed dispersal networks (Sebastián-González et al., 2015).

5. Different metawebs and their applications

5.1 Overview

This section reviews published metawebs and their analyses up to 2023. We identified 42 research articles (including one doctoral thesis) that examined 33 metawebs. Of these, 17 metawebs represented terrestrial ecosystems, 12 focused on aquatic ecosystems, and four encompassed both. The metawebs include 19 unipartite networks, 12 bipartite networks, and two tripartite networks.

Recent metaweb developments have increasingly used observation-based approaches, with 11 metawebs relying on field observations, highlighting the growing importance of direct ecological data. However, most published metawebs (18) remain literature-based, with a smaller number (4) being prediction-based, underscoring the challenges and data gaps in documenting ecological interactions.

Most metaweb-related research has appeared in journals such as *Ecology* (six articles), *Global Ecology and Biogeography* (six articles), and *Ecography* (five articles). Notably, there has been a surge in metaweb publications over the past two years, with 17 metawebs published between 2022 and 2023 alone. Geographically, most metawebs have been developed in Europe and its surrounding seas (14 articles), followed by North America (eight articles) and South America (eight articles), pointing to a significant knowledge gap in regions such as Africa, Asia, and Australia.

The global marine fish metaweb (Albouy et al., 2019) is the largest, predicting 7,062,647 potential interactions among 11,367 fish species using a niche model. The Blue and Green metaweb of Switzerland (Ho et al., 2022) rank as the second largest, documenting 242,779 interactions among 2016 plant species, 191 butterfly species (larval stage), 109 grasshopper species, 155 bird species, 248 stream invertebrates, and 78 stream fish. Among terrestrial metawebs, the European Tetrapod metaweb (TetraEU) (Maiorano et al., 2020) is the largest, comprising 83,568 interactions among 288 mammal species, 509 bird species, 250 reptile species, and 104 amphibian species.

Metaweb studies generally fall into two categories. The first category consists of studies where metawebs were constructed for a specific region, with local webs inferred based on species occurrence. These inferred local webs are typically unweighted, although some studies have incorporated node weights based on local abundance (Kortsch et al., 2021, 2019; Olivier et al., 2019) and edge weights using allometric models (Kortsch et al., 2021). The second category involves the development of metawebs by combining observed local webs. This approach enables the study of interaction rewiring, which cannot be achieved with inferred local webs. The subsequent sections will explore various research domains where the metaweb concept has been applied.

5.2 Metawebs in understanding spatiotemporal dynamics of interaction

Metawebs have proven valuable in exploring the temporal and spatial dynamics of ecological interactions. The German Bight metaweb of the North Sea (Olivier et al., 2019) was used to assess food web properties from 1998 to 2015, finding temporal variations in these properties better captured by node-weighted metrics than by binary ones. Similarly, the Gulf of Riga metaweb (Kortsch et al., 2019) analysed food web dynamics from 1971 to 2016, introducing link-weighted metrics that emphasised the magnitude of energy flow through feeding preferences. This study (Kortsch et al., 2019) revealed contrasting patterns: while node- and link-weighted metrics reflected changes in species dominance and energy fluxes, unweighted metrics captured shifts in species richness and interaction diversity.

The North Sea metaweb (Frelat et al., 2022) used principal tensor decomposition to analyse spatial and temporal patterns across six regions from 1999 to 2014. The study found strong latitudinal patterning in food webs, though temporal changes were observed only locally. In the Baltic Sea (Garrison et al., 2022), four benthic trophic metawebs were developed for four regions (Bothnian Sea, Baltic Proper, Bornholm Basin, and Skagerrak) to compare network properties across two decades (1980–1989 and 2010–2019). The most saline site (Skagerrak) exhibited greater species richness and network complexity; however, a significant loss of species and interaction diversity occurred over time, while other regions showed no significant differences between the two decades. The mycobiont–photobiont metaweb of Antarctic lichens (Pérez-Ortega et al., 2023), based on data from 11 locations, was analysed to understand network properties and the roles of nodes. This study revealed networks with high modularity and specialisation but low connectance and nestedness (Pérez-Ortega et al., 2023). The lower interaction asymmetry indicated a strong reciprocal dependence between the interacting groups.

In the High Arctic, the plant–pollinator metaweb of Zackenberg, northeast Greenland, was used to generate random local webs for comparison with yearly and weekly empirical network structures (Cirtwill et al., 2023). However, while annual variations were observed, no directional change was detected. Phenology explained local network variations, and a few key species provided most pollination services, indicating a potential risk of network collapse if these species are affected by climate change.

In Japan, the temporal dynamics of Spider–Hexapod prey networks in warm temperate grasslands (Suzuki et al., 2023) were studied for nestedness, modularity, and species roles, including node specialisation and betweenness centrality. A metaweb was also constructed to understand the roles of species in modules. The study found the networks to be modular and largely anti-nested, with modules changing seasonally as central species shifted. A metaweb analysis identified core species across seasons, revealing their pivotal roles within the network.

5.3 Metawebs in exploring the impact of environment, human activity, and spatial variation on network structure

Metawebs have been instrumental in exploring how environmental factors, human activity, and spatial variations influence food web properties. For example, Braga et al. (2019) used the TetraEU to create local food webs across a 10 x 10 km² grid in Europe based on species occurrence data. They calculated various food web metrics, checked their significance against random expectations, and performed principal component analysis (PCA) for dimension reduction. The resulting composite metrics (first two PCA axes), primarily driven by species richness and connectance, were analysed using generalised additive models (GAMs) to assess relationships with climate, resource availability, habitat diversity, and human disturbance. The findings indicated that temperature and human footprint significantly influenced food web properties. Similarly, the Barents Sea metaweb (Planque et al., 2014) was used to infer local webs for 25 subregions, examining spatial variations in food web properties and their environmental drivers (Kortsch et al., 2019). Warmer, ice-free waters were associated with higher connectance, clustering coefficients, omnivory, and cannibalism, while colder, ice-covered areas exhibited greater modularity and variability in vulnerability.

The global marine fish metaweb (Albouy et al., 2019) was constructed using an allometric niche model and adjusted for herbivory, vertical distribution, and geographic co-occurrence factors. This metaweb was utilised to generate local webs at a 1° x 1° resolution, revealing that marine fish food webs are geographically interconnected, with low spatial modularity but high robustness. Furthermore, food web metrics strongly correlate with sea surface temperature, peaking in tropical regions (Albouy et al., 2019). Meanwhile, in China, a multitrophic metaweb for the Dongjiang River (Qin et al., 2023) was developed using an environmental DNA (eDNA)-based approach and literature review to study the effects of human land use and water pollution on species diversity and network structure. The study found that link density, connectance, and omnivory decreased with increased human land use and proximity to the estuary. Lastly, an ant–plant interaction metaweb for the Brazilian neotropical savanna (Dáttilo and Vasconcelos, 2019) explored how latitudinal gradients affect network properties. The study found that sites at higher latitudes were characterised by larger network sizes, greater interaction diversity, and higher dissimilarity, driven largely by net primary productivity (NPP) variations.

5.4 Metawebs to assess the impact of climate change

The Barents Sea metaweb (Planque et al., 2014) was utilised to understand the properties of boreal and Arctic food webs and how they are affected by climate change (Kortsch et al., 2015). Climate change was assessed by incorporating four boreal fish species into the Arctic food web, which are known to be shifting their ranges towards the Arctic. The Arctic food web was found to be more modular due to the presence of specialist species. However, with the poleward shift of generalist boreal species due to climate change, the Arctic network is expected to become less modular in the future, increasing the risk of disturbances spreading throughout the network.

Gaüzère et al. (2023) utilised the TetraEU to explore interaction and trophic group uniqueness. They calculated similarity using Sørensen’s dissimilarity and assessed the distance decay of similarity via a power law relationship, which was then used to compute uniqueness. The study evaluated the impact of climate change, human footprint, and site vulnerability (in terms of protected area coverage) on regions with unique networks or trophic groups. It was found that unique networks in the Arctic are particularly vulnerable to future climate change, while those in southern Europe are more exposed to human activities.

Additionally, changes in food web structure in response to climate change were studied in the Mediterranean Sea (Albouy et al., 2014) and the Gulf of Gabès (Hattab et al., 2016). These metawebs were refined using the allometric niche model, and species occurrence was predicted under current and future A2 climate scenarios (IPCC, 2000) using SDMs. Both studies revealed decreases in body size, number of links, generality, vulnerability, and mean trophic level, alongside increased average path length.

The European crop and forest pest metaweb was employed to predict how European ecological interactions might change under different climate scenarios (Grünig et al., 2020). Using SDMs to forecast species occurrences, the study revealed that climate change would likely increase linkage density in crop pest interaction networks in northern Europe; meanwhile, southern Europe exhibited a more saturated pattern. However, northern Europe is expected to become more suitable for growing a wider variety of crops, and this will also attract a greater diversity of pests. In contrast, southern Europe may face unfavourable conditions for some staple crops due to climate shifts.

5.5 Metaweb to understand species interaction patterns

The Jena Grassland metaweb in Germany (Hines et al., 2019), which focuses on invertebrates and their food sources, was developed to explore how plant diversity influences the prevalence of various interaction motifs (Giling et al., 2019). This metaweb was constructed using an intensive literature survey, knowledge of trophic levels, and a trait-based approach to estimate interaction probabilities. Subsequently, when developing local webs, this metaweb was filtered by species occurrence and their encounter probability, thereby considering their abundance (Poisot et al., 2015). The study found that motifs such as tri-trophic chains, apparent competition, and exploitative competition increased with plant species richness while omnivory motifs decreased. Additionally, plant diversity influenced local interaction patterns among arthropod consumers, even in cases where plants were not directly involved. Furthermore, combining this metaweb with the Cedar Creek metaweb from North America revealed that higher plant diversity promotes more energy flow into the food web, particularly to predators, strengthening top-down control. also led to lower food quality for herbivores, exerting bottom-up control by reducing their energy loss (Barnes et al., 2020).

In central Chile, a rocky shore metaweb was developed by compiling both trophic and non-trophic interactions using literature and expert knowledge (Kéfi et al., 2015). The analysis revealed more than double the number of non-trophic interactions compared with trophic ones, with non-trophic interactions more prevalent among basal taxa. These non-trophic interactions were predominantly negative and exhibited non-modular, non-nested patterns within the web.

The Mexican plant–Buprestid metaweb was analysed at the network, subnetwork, and node levels to examine structural and functional patterns (Pérez-Hernández et al., 2023). This metaweb was found to be modular and anti-nested, with different Buprestid tribes contributing uniquely to the observed modularity. Most species displayed specialised interaction patterns, leading to many peripheral species in the network, with taxonomically similar species showing contrasting host-use patterns. Lastly, the Mexican Haemosporidian–bird metaweb, developed using observational data from four vegetation types along elevational gradients (Rodríguez-Hernández et al., 2023), revealed high specialisation and modularity but low nestedness. Birds were shown to engage in more specialised interactions than their parasite counterparts.

5.6 Metaweb to reveal species and interaction turnover

The Eurasian rodent–flea metaweb, constructed from 57 community datasets (Hadfield et al., 2014), was utilised to investigate variability in potential species interactions, realised interactions, and species diversity across spatial scales (Poisot et al., 2017). The study found that realised interactions showed greater variability than potential interactions, with local webs developed from the metaweb underestimating this variation. It was also observed that climate affects hosts, parasites, and their interactions differently.

In Switzerland, a metaweb for the upper Thur catchment was developed to explore the spatiotemporal dynamics of biodiversity and food web properties (Blackman et al., 2022). Significant changes were noted in biodiversity and food web characteristics, although the shifts in biodiversity did not necessarily reflect changes in food web structure. In contrast, interaction turnover and species turnover were strongly correlated in the Barents Sea (Kortsch et al., 2019) and North Sea (Olivier et al., 2019), with interaction changes exceeding species composition shifts. However, in Brazilian anuran–arthropod metawebs (Ceron et al., 2022), species turnover increased more than interaction turnover with increasing geographical distance. A positive relationship between species and interaction turnover was observed in German Biodiversity Exploratories forest food webs and Adirondack Lakes food webs (Bauer et al., 2022). Both spatial and environmental distances were found to impact species turnover in both areas; however, food web dissimilarity was related to environmental distance only in the former networks. Meanwhile, species turnover was identified as a key driver of β-diversity in the Brazilian ant–trophobiont metaweb (Belchior et al., 2023) and the bird–Haemosporidian metaweb (Rodríguez-Hernández et al., 2023). In the former metaweb (Belchior et al., 2023), species turnover increased with geographical distance, while in the latter, turnover was driven by elevation (Rodríguez-Hernández et al., 2023). Moreover, the Mexican bird–Haemosporidian metaweb exhibited low β'os values, suggesting that potential interactions were realised locally; however, high LNU values indicated that metawebs were unique due to high species turnover. Similar low β'os values were observed in plant, lepidopteran herbivore, and insect parasitoid networks across tropical regions of North and South America (Sudta, 2023).

Interaction rewiring was found to play a significant role in interaction turnover in the Neotropical ant-plant networks of Brazil (Dáttilo and Vasconcelos, 2019), the Antarctic mycobiont–photobiont networks (Pérez-Ortega et al., 2023), and Brazilian anuran–arthropod metawebs (Ceron et al., 2022) In the Neotropical ant–plant metaweb, species and interaction diversity, as well as turnover, were observed to decrease with increasing latitude. However, no latitudinal effect was noted for the Antarctic mycobiont–photobiont networks.

5.7 Metaweb in conservation

In the Canadian Rocky Mountains, a metaweb comprising 16 mammal species was developed to identify suitable umbrella species for conservation (Steenweg et al., 2023). Umbrella species were evaluated based on their occupancy and the effect of their presence on food web properties, using generalised linear models that accounted for various biotic and abiotic factors. The grizzly bear (*Ursus horribilis*), a generalist carnivore, was identified as the best umbrella species for explaining species richness. Meanwhile, wolves (*Canis lupus*) and cougars (*Felis concolor*) were better umbrella species for maintaining ecosystem functions.

Another study used the Serengeti food web (Baskerville et al., 2011) to develop a metaweb from the African savanna (Higino et al., 2023). This metaweb produced local food webs at a 0.5-degree resolution, based on local species occurrence from IUCN range maps, to assess prey–predator mismatches in these maps. The study revealed that many predator ranges are over-represented in the IUCN range maps, with an absence of prey in large portions of their range.

5.8 Metaweb to understand the effect of spatial extent of sampling on network properties

Wood et al. (2015) explored how the spatial extent of sampling influences food web properties by constructing food webs at various spatial scales using occurrence data and the metaweb of the marine intertidal ecosystem in the Sanak Archipelago, Eastern Aleutian Islands, Alaska. The study found that fundamental network properties, such as the number of nodes, links, and links per node, increased with the sampled area, while connectance exhibited an inverse trend. Further analysis of 14 additional food web indicators (Table 2) showed that variations in most of these indicators could be attributed to changes in the number of nodes and connectance, as supported by niche model analysis (Williams and Martinez, 2000) and power-law scaling relationships (Riede et al., 2010). However, the study revealed that the number of species involved in loops and cannibalism increased more than expected as the spatial scale expanded.

5.9 Metaweb to understand food web properties in different ecosystems

The blue and green metawebs of Switzerland, representing aquatic and terrestrial ecosystems, respectively, were utilised to infer local webs and examine both the structural and ecological (niche overlap) properties of food webs and their response to environmental patterns (Ho et al., 2022). The study found that aquatic food webs are generally smaller, less modular, and more connected than terrestrial ones. Further, elevation was observed to influence structural and ecological properties, positively impacting modularity and negatively affecting niche overlap in terrestrial food webs. In contrast, the opposite pattern was seen in aquatic food webs, where elevation decreased modularity and increased niche overlap.

A global investigation of marine fish food webs revealed that coastal ecosystems, with higher interaction redundancy, are more robust to species extinctions than open sea food webs (Albouy et al., 2019).

5.10 Metaweb to understand the community assembly process

Bauer et al. (2022) examined how spatial and environmental gradients affect species composition and food web structures by utilising two metaweb datasets: the German Biodiversity Exploratories forest and the Adirondack Lakes. Additionally, to explore how local webs are derived from the regional species pool, they used these metawebs to generate random local webs via three approaches: (i) no filtering, where species were randomly selected from the metaweb; (ii) resource filtering, where after (i), species without interactions were replaced by others from the metaweb until each species had a resource; (iii) limiting similarity, where after (i), species with similar trophic positions were replaced by others. The study found that biotic filtering plays a key role in shaping local community assembly by comparing the statistical distributions of food web properties from these models with observed values (Bauer et al., 2022).

The metaweb of willows, willow-galling sawflies, and their natural enemies in Europe (Kopelke et al., 2017) was used to understand how environmental factors and species co-occurrence affect interactions, applying a probabilistic generalised linear model (Gravel et al., 2019). The study found that species co-occurrence is environmentally dependent; however, the likelihood of interaction between co-occurring species is largely stochastic, with environmental factors having little influence on the probability of interaction.

Another study Galiana et al. (2023) focused on interactions between willow-galling sawflies and parasitoids to investigate the relationship between climatic and dietary niches. They found that widely distributed species tend to be generalists at both local and regional levels, possessing broader climatic and dietary niches while showing significant interaction rewiring. Null model analysis revealed that species typically have broader dietary niches and narrower climatic niches than expected by chance, suggesting dietary niche constraints on species distribution. The study also highlighted that consumers with narrow ranges tend to interact with widely distributed resources and vice versa, indicating a pattern of complementary interactions between species with contrasting ranges.

5.11 Metaweb to understand the role of functional traits in structuring communities

The Brazilian–Atlantic forest bird–seed dispersal metaweb, constructed using observational data from 16 studies (Emer et al., 2018), was analysed to assess connectance, modularity, and node centrality. This analysis revealed that interactions within different forest patches were concentrated in certain modules, with only a few species serving as key connectors to these modules. The study examined the body size of the birds and seed size to identify the functional traits driving these connections. Small-sized birds feeding on small-seeded plants acted as connectors in fragmented areas. In contrast, large-sized birds had disappeared from these fragments, leading to sparse interactions between species of contrasting sizes.

The Brazilian–Atlantic frugivory metaweb (Bello et al., 2017) was used to examine the role of native and invasive species (Dáttilo et al., 2023). The study found that both native and invasive species played similar roles in the metaweb regarding centrality, contributing equally to nestedness and modularity. However, plants producing smaller, lipid-rich fruits were more frequently involved in interactions, regardless of their native or invasive status.

The relationship between trophic and non-trophic interactions was analysed in the central Chile rocky shore metaweb (Kéfi et al., 2015). Sessile species were found to establish more non-trophic interactions, while mobile species formed more trophic interactions. Comparatively, predators tended to have larger body masses than prey in the trophic network. Smaller, lower-trophic-level species with low generality and high vulnerability primarily initiated positive non-trophic interactions. Meanwhile, negative non-trophic interactions were driven by small species with low trophic levels on target species with similar characteristics.

5.12 Metaweb used to reconstruct another metaweb via machine learning

The Canadian mammal metaweb was constructed by transferring knowledge about phylogeny and latent traits from TetraEU (Strydom et al., 2022). Latent traits related to generality and vulnerability were extracted from the TetraEU dataset and then applied to Canadian mammals based on their phylogenetic relatedness to European species. Subsequently, this information was used to reconstruct the Canadian metaweb. Although only 4% of species overlapped between the Canadian and European metawebs, the method accurately predicted 91% of known interactions, demonstrating the effectiveness of using machine learning and phylogenetic relatedness in metaweb construction (Strydom et al., 2022).

6. Perspectives and future directions in metaweb approaches

The preceding sections indicate that applying metawebs in ecology is a rapidly expanding field, creating numerous avenues for research due to their ability to model complex interactions and enhance our understanding of biodiversity, community structure, and ecosystem functioning. Below, we discuss some promising research scopes for metawebs.

6.1 Expanding geographical coverage

Most metawebs have been developed in Europe and the Americas, with limited representation from Asia and Africa and an almost complete absence in Oceania. While metawebs have been created for temperate and polar regions, the biodiverse tropics—particularly South Asia and Africa—have received little attention. Therefore, addressing this gap would improve understanding of ecological interactions in these regions, and developing metawebs from these understudied areas could reveal new interaction dynamics unique to highly biodiverse tropical ecosystems. Boosting data collection in these regions may eventually lead to global metawebs integrating data from diverse ecosystems, offering unprecedented insights into biodiversity patterns, global species extinction risks, and ecosystem connectivity. Furthermore, studying food web structures across different biomes could help uncover universal principles of ecological networks alongside region-specific dynamics.

6.1 Enhancing data collection efforts

The creation of large regional ecological networks is often hindered by limited data availability, especially in developing or underdeveloped regions where funding is scarce despite high biodiversity. Habitat destruction in these regions also threatens biodiversity at alarming rates, making data collection even more urgent. Although citizen science initiatives have increased biodiversity data collection, generating billions of records annually, most platforms focus on species occurrences rather than interactions. Hence, while a few portals encourage abundance data (e.g., eBird), few support data collection on ecological interactions (e.g., iNaturalist), which are often under-promoted.

Recent studies have employed eDNA and metabarcoding to collect ecological interaction data, ranging from mutualistic to trophic networks (Banerjee et al., 2022; Blackman et al., 2022; Qin et al., 2023). Thus, resources for integrating eDNA and metabarcoding in ecological interaction studies already exist (Evans et al., 2016; Pereira et al., 2023), and citizen science-based eDNA monitoring programs are beginning to support biodiversity monitoring, including identifying prey bases of migratory species (Clarke et al., 2023; Kvalheim et al., 2024; Padró, 2024; Zhang et al., 2023). Increased citizen involvement in eDNA–metabarcoding approaches could significantly bridge knowledge gaps in ecological interactions, particularly in data-poor regions. Additionally, collecting quantitative rather than qualitative data would allow for more realistic analyses, as weighted networks capture strong versus weak interactions, thereby enhancing understanding of the roles of species in local ecosystems and revealing possible shifts in interaction networks. Moreover, a quantitative local network will help to develop a quantitative metaweb where the interacting partner preference of each node can be demonstrated.

6.2 Assessing environmental change

Metawebs have proven effective in predicting climate change impacts on species interactions and network resilience, and further research could extend these applications to habitat fragmentation, pollution, and vulnerability assessments related to development projects. Studies could also explore which networks are resilient or vulnerable to change. Furthermore, obtaining node-level information on the roles of species within networks and how these roles change spatially or temporally under different environmental conditions represents another promising research area. Additionally, metawebs may help predict how restored ecosystems will function post-intervention, guiding which species and interactions should be prioritised for ecosystem recovery.

6.3 Conservation planning

Most conservation efforts focus on protecting specific species or habitats without fully understanding which species or interactions are key to ecosystem function. Meanwhile, metawebs can help identify keystone species, interactions, and ecosystems that maintain critical services, such as pollination, seed dispersal, or nutrient cycling, informing efforts to protect species that disproportionately contribute to ecological networks. Metawebs could also be instrumental in predicting and managing the impacts of biological invasions, allowing conservationists to assess the consequences and prioritise intervention efforts.

6.4 Integration of metawebs with the species distribution model

SDMs usually consider the habitat and climatic suitability of a species, i.e., they predict the fundamental niche. However, the fundamental niche of a species is further shaped by biotic factors, resulting in the realised niche. Joint species distribution models (JSDMs), which simultaneously predict the occurrence of many species from the environmental data to understand the relationship between two species, sometimes also provide misleading information about species interaction patterns (Zurell et al., 2018). In this scenario, it should be useful to integrate species interaction data directly into the species distribution model. The concept of including species interaction in the SDM is not novel (Wisz et al., 2013); however, the application of this concept is very scarce (Staniczenko et al., 2017; Zhang et al., 2022). Overall, the metaweb can be an important asset for improving existing species distribution models to obtain a more realistic prediction. This can be further used to assess the range maps and responses of species to climate change and habitat modification.

6.5 Hybrid metawebs

A hybrid metaweb, consisting of both trophic and non-trophic interactions, can provide a more realistic picture of the ecological network; however, data for such diverse kinds of interaction between lots of species is sometimes difficult to collect, only a few researchers can explore this avenue (Kéfi et al., 2015; Morrison et al., 2020). Another approach to understanding species interactions is incorporating multi- or hypergraphs, where an interaction between two species may affect another interaction, representing ecosystem complexity more accurately (Delmas et al., 2019). Future developments in hypergraphs and hybrid metawebs are expected to provide a deeper understanding of how different interaction types contribute to ecosystem health.

6.6 Improvement in the niche model from latent trait and supervised learning informed trait selection

The basis for the niche-based prediction is that two species interact based on their functional traits. However, using niche-based models, it is difficult to understand how two species interact based on exactly which functional traits resulted in poor model performance. Comparatively, predictive performance was greatly improved using latent traits, which learn from the patterns of networks. The application of latent traits has also been observed for machine learning-based predictions (Strydom et al., 2022). Moreover, latent traits can be compared with real traits to understand the relative importance of different traits in shaping interactions.

Here, we propose an inverse approach to improve our mechanistic understanding of the role of traits in shaping ecological networks. First, we should analyse the network to obtain latent traits and then compare the latent traits with the real traits to identify several actual traits shaping the network structure. We can build a niche model and evaluate its performance using these identified traits. Testing this approach across various ecosystems will enhance our knowledge of trait–trait interactions in different scenarios while paving the way for more process-based ecological network modelling. Notably, supervised learning also allows the identification of functional traits impacting its prediction.

6.7 Evolutionary dynamics

Metawebs can be used to explore co-evolutionary dynamics within ecosystems, helping to understand how mutual adaptations among species shape ecological networks over evolutionary timescales. Future research could also investigate how evolutionary history and phylogenetic relatedness constrain or influence species interactions within metawebs, particularly in understanding the persistence or extinction of species.

7. Conclusions

In conclusion, metaweb research has become pivotal for understanding ecological interactions across spatial and temporal scales, providing a structured framework to explore the complex networks of species interactions in diverse ecosystems. This review serves as a foundational reference for researchers aiming to harness the full potential of metawebs in addressing complex ecological questions. It highlights methodological advances in constructing, analysing, and applying metawebs, demonstrating their effectiveness in bridging data gaps, capturing interaction diversity, and predicting network dynamics under various environmental pressures. Meanwhile, challenges remain in developing regionally representative metawebs, improving data accuracy, and expanding geographical coverage, especially in biodiverse but under-represented areas. Therefore, future research should prioritise refining predictive models, incorporating diverse data sources such as eDNA, advancing hybrid metawebs that include both trophic and non-trophic interactions, and exploring co-evolutionary dynamics. Metawebs hold significant potential to deepen ecological understanding and inform conservation efforts, supporting global initiatives such as the UN Sustainable Development Goals, especially those related to climate action (13) and biodiversity (14-15). Overall, metaweb-based approaches offer a promising avenue for anticipating the responses of ecosystems to environmental change and fostering a more holistic approach to ecosystem management.

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Tables

Table 1. Summary of the different predictive models.

Category		Model	Characteristics	Advantage	Disadvantage
Niche-based	Intervality property model	Cascade model (Cohen and 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 and Martinez, 2000)	Species interact within a beta-distributed niche range, centered at or below their niche value	Allows cannibalism and feeding on species with higher niche values.	Accurate 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.	It requires more parameters and has low predictive performance.
	Intervality problem model	Nested-hierarchy model (Cattin et al., 2004)	The model, based on the niche model, links predators with shared prey and adds random links to achieve desired connectance.	This is the 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.
		Generalised cascade model (Stouffer et al., 2005)	It follows the rule of the cascade model. Niche distribution follows either exponential or beta distribution. Predator selects prey randomly from niche space.	The model addresses intervality issues through random link formation within the niche space.	Model performance is not as good as the niche model.
		Generalised niche model (Stouffer et al., 2006)	It modifies the niche model by reducing the niche space to make it interval, then selecting some prey 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 than the niche model, with similar predictive performance.
Interaction matrix-based		Stochastic block model (Allesina and Pascual, 2009)	The model uses network modularity properties to group similarly interacting nodes by organising the interaction matrix.	The model is capable of predicting large networks accurately.	Performance to predict small-sized networks 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 and 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 generalised linear model (Pearse and Altermatt, 2013)	This model predicts interactions using a generalized linear model based on a node's interaction partners 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 the 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.	It requires large data and information on 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.	It requires large amounts of data and information about explanatory variables.

Table 2. Different network indices applied in previous research based on metaweb. Their reference, ecological implication and applications are available in Electronic supplementary material (Appendix 1).

Index	**Definition**
1. Indices to describe a network (α-diversity and γ-diversity)	
Interaction richness	Number of interactions in a community
Linkage density	Average number of links per node
LinkSD	The standard deviation of links per species
Connectance	The proportion of links realised out of the maximum possible links.
Clustering coefficient	The probability that two linked species are also linked with a third species.
Modularity	Measures how much the network is distributed to subsystems of densely connected nodes.
Nestedness	Measures how much the specialist edges are a subset of generalist edges in the network.
Path length	Longest of the shortest distances between every pair of nodes
Characteristic path length	Average distance between all pairs of nodes
Robustness	Ability of a network to withstand perturbation is usually measured by how well the network can withstand the loss of species or interactions
Flow diversity	Shannon index-based measures which increases with the richness and evenness of flows in a network
Flow specialisation	Indicates average niche breadth of all nodes in the network.
A_L	Diversity of link abundances of local networks.
G_L	Diversity of link abundances in metaweb
A_π	Diversity of link probabilities of local networks
G_π	Diversity of link probabilities of local networks
Average chain length	Average of the maximal food chain
Vulnerability	Mean number of consumers per resource
Generality	Mean number of resources per consumer
VulSD	The standard deviation of vulnerability
GenSD	The standard deviation of generality
Mean trophic level	Mean of the prey-averaged trophic level
Maximum trophic level	Maximum of the prey averaged trophic level
Standard deviation of trophic level	The standard deviation of the trophic level of all nodes
Mean Short-weighted trophic level	Mean of the short-weighted trophic level
Level of omnivory	The standard deviation of the trophic level of its resources.
Proportion of basal species	Proportion of nodes with no prey
Proportion of intermediate species	Proportion of nodes with both prey and predator
Proportion of top species	Proportion of nodes with no predator
Proportion of the herbivores	The proportion of nodes consuming the autotrophs
Proportion of omnivores	The proportion of nodes that consume other nodes belongs to more than one trophic level
Proportion of cannibals	Proportion of nodes having self-edge
Proportion of nodes in loop	The proportion of nodes that are in the loop.
Trophic coherence	Measures the tendency of nodes to form distinct trophic levels by resources and consumers
2. Indices to understand interaction turnover (β-diversity)	
Simpson's dissimilarity index	Dissimilarity between two samples based on shared species and minimum of the unshared species between two sites.
Sorenson's dissimilarity index	Dissimilarity between two samples by considering the number of shared and unshared species.
β_{WN}	Dissimilarity of interactions
β_{ST}	Variation of interaction between two networks due to variation in their species composition
β_{OS}	Variation of interaction between shared species of two networks
β'_{OS}	Difference between the interaction of two species in local networks and metaweb
LNU	The proportion of unique interaction in a local network with its quasimetaweb
B_L	Turnover of link abundance between local networks.
Bπ	Turnover of interaction probability between local networks.
3. Indices to understand node properties	
Degree centrality	Sum of number of links of a node
Closeness centrality	Reciprocal of the sum of the shortest path distances from a node to all other nodes in the network
Betweenness centrality	Extent to which a node lies on the shortest paths between other pairs of nodes in a network.
Katz centrality	Number of directs and indirect connections of a node penalised by distances factor.
Interaction specialisation	Node level interaction specialisation by comparing observed distribution pattern and null expectation with Kullback-Leibler distance
Species strength	Sum of dependencies of each species in a network, a weighted extension of degree centrality concept.
Interaction asymmetry	Dependence of a species on another guild's species in a bipartite network
Nestedness contribution	Contribution of each node towards the nested structure of the network
Within module connectivity	Standardised within module degree
Among-module connectivity	Standardised among module degree

Table 3: List of metawebs included in this review.

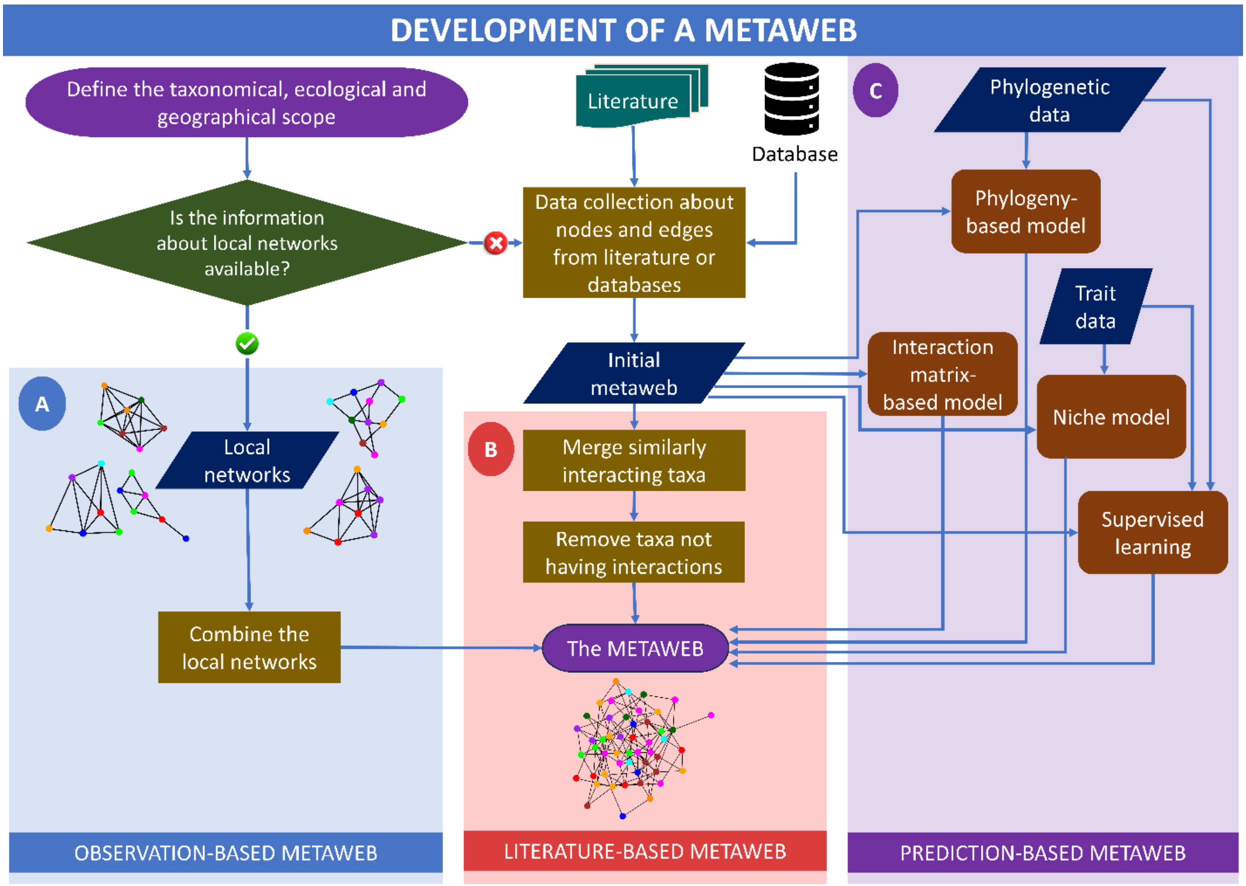
Metaweb name	Nature	Ecosystem	Type	Taxa
Eurasian rodent-flea metaweb (Hadfield et al., 2014)	Bipartite	Terrestrial	Observed	Interaction between 121 rodents and 206 flea species from 51 different regions
Barent sea metaweb (Planque et al., 2014)	Unipartite	Aquatic	Literature-based	1589 trophic links between 244 taxa from plankton to marine mammals
Mediterranean Sea continental shelf metaweb (Albouy et al., 2014)	Unipartite	Aquatic	Predicted	11055 interactions between 256 species
Central Chile Rocky shore metaweb (Kéfi et al., 2015)	Unipartite	Aquatic	Literature-based	3296 non-trophic and 1458 trophic interactions between 104 species
Metaweb of Sanak, Alaska (Wood et al., 2015)	Unipartite	Aquatic	Literature-based	912 links between 131 taxa
Gulf of Gabes metaweb (Hattab et al., 2016)	Unipartite	Aquatic	Predicted	929 links between 62 species
Metaweb of Willow-willow-galling sawflies and their natural enemies in Europe (Kopelke et al., 2017)	Tripartite	Terrestrial	Observed	1173 links between 52 plants, 96 herbivores and 126 parasitoids
Brazilian Atlantic Frugivory metaweb (Bello et al., 2017)	Bipartite	Terrestrial	Observed	787 plants and 344 frugivore
Brazilian Atlantic Forest Bird Seed dispersal metaweb (Emer et al., 2018)	Bipartite	Terrestrial	Literature-based	2587 interactions between 335 plant species and 170 bird species
Brazilian ant-tree metaweb (Dáttilo and Vasconcelos, 2019)	Bipartite	Terrestrial	Observed	3900 interactions between 100 ant and 177 tree species
German Blight Metaweb (Olivier et al., 2019)	Unipartite	Aquatic	Literature-based	588 links between 21 epifaunal invertebrate and 27 fish species
Global Marine fish metaweb (Albouy et al., 2019)	Unipartite	Aquatic	Predicted	7062647 interactions between 11367 fish species
Jena grassland meta food web (Hines et al., 2019)	Unipartite	Terrestrial	Literature-based	51496 links between 63 plants, 647 invertebrates, carrion, fungi, microbes and dung
European crop-forest pest metaweb (Grünig et al., 2020)	Bipartite	Terrestrial	Literature-based	937 interactions between 126 host plants (crop and forest tree) and 89 insect pest species
European Tetrapod metaweb (Maiorano et al., 2020)	Unipartite	Terrestrial	Literature-based	83,568 interactions between 288 mammals, 509 birds, 250 reptiles and 104 amphibians
Gulf of Riga metaweb (Kortsch et al., 2021)	Unipartite	Aquatic	Literature-based	207 interactions between 34 species
Metaweb of Baltic sea benthic macroinvertebrates (Garrison et al., 2022)	Unipartite	Aquatic	Literature-based	Bothnian Sea 57 links between 19 species, 82 links between 27 species in Baltic proper, 102 links between 31 species in Bornholm basin, 10647 links between 381 species in Skagerrak
Anuran-arthropod metawebs of Brazil (Ceron et al., 2022)	Bipartite	Semi-aquatic	Observed	43 anuran species and 42 kinds of prey items
Canadian mammals metaweb (Strydom et al., 2022)	Unipartite	Aquatic and terrestrial	Predicted	260 mammals
Metaweb of Adirondack Lake and German Biodiversity Exploratories forest datasets (Bauer et al., 2022)	Unipartite	Aquatic and terrestrial	Observed	-
North sea metaweb (Frelat et al., 2022)	Unipartite	Aquatic	Literature-based	114 fish and epifauna, phytoplankton, benthic microalgae, macroalgae, detritus and zooplankton

Swiss Blue and Green metaweb (Ho et al., 2022)	Unipartite	Terrestrial and aquatic	Literature-based	242779 interaction between 2016 plant, 191 butterflies, 109 grasshoppers, 155 birds, 248 stream invertebrates, and 78 stream fish taxa
Upper Thur catchment metaweb of Switzerland (Blackman et al., 2022)	Unipartite	Aquatic	Literature-based	12 fish genera, 80 invertebrate genera and 282 bacteria genera
Mexican plant-buprestid metaweb (Pérez-Hernández et al., 2023)	Bipartite	Terrestrial	Literature-based	1061 interactions between 365 buprestids and 376 plants
Ant-trophobiont metaweb of Minas-Gerais, Brazil (Belchior et al., 2023)	Bipartite	Terrestrial	Observed	189 interactions between 22 ant and 11 trophobiont species
African Savannah mammalian herbivore-predator metaweb (Higino et al., 2023)	Unipartite	Terrestrial	Literature-based	32 mammals
Canadian Rocky Mountain Large Carnivore Metaweb (Steenweg et al., 2023)	Unipartite	Terrestrial	Literature-based	16 large mammals
Dongjiang river metaweb (Qin et al., 2023)	Unipartite	Aquatic	Literature-based	526 fish OTU, 411 aquatic insect OTU, 482 protozoa OTU and 4010 bacteria OTU.
American Plant-lepidopteran herbivore-insect parasitoid metaweb (Sudta, 2023)	Tripartite	Terrestrial	Observed	-
Antarctic Mycobiont-photobiont (lichens) metaweb (Pérez-Ortega et al., 2023)	Bipartite	Terrestrial	Observed	248 interactions between 77 mycobionts and 45 photobionts
High arctic plant-pollinator metaweb of Zackenberg, Northeast Greenland (Cirtwill et al., 2023)	Bipartite	Terrestrial	Observed	122 insects and 45 plants
Mexican Birds-Haemosporidian parasite metaweb (Rodríguez-Hernández et al., 2023)	Bipartite	Terrestrial	Observed	78 haemosporidians and 38 birds
Spider-Hexapoda prey metaweb of temperate grassland, Japan (Suzuki et al., 2023)	Bipartite	Terrestrial	Observed	50 species of spider and 974 prey operational taxonomic unit

Figure legends

Fig. 1. Flowchart of the development of a metaweb through different pathways. First, the taxonomical, geographical and ecological scopes of the metaweb should be defined. Suppose data on local webs across spatial and temporal points are available. In that case, a metaweb can be created through the aggregation of these local webs into what is termed an observation-based metaweb. If local interaction data are unavailable, information on nodes and potential interactions can be compiled from literature and databases to build an initial metaweb. Here, nodes with similar interactions may be merged and unconnected nodes removed, producing a literature-based metaweb. To further improve the initial metaweb, predictive methods can be applied to estimate potential interactions, resulting in a prediction-based metaweb. Predictive approaches include several methodologies: the interaction matrix-based predictive model, which relies solely on analysing the interaction matrix; the phylogeny-based predictive model, which incorporates the phylogenetic relationships among nodes; the niche model, which uses species traits. Additionally, supervised learning-based models integrate interaction data, traits, and/or phylogeny to infer potential interactions using machine learning techniques.

Fig. 2. Flowchart of the process of inferring local webs using the metaweb approach. If information about locally available species is accessible, interactions from the metaweb can be subsampled to infer local networks. When such information is unavailable, species distribution modelling can first be used to estimate local species assemblages, which can then be applied to generate local webs. However, mere co-occurrence of potentially interacting species does not guarantee interactions. To address this, local abundance data can be incorporated to estimate interaction probabilities, where more abundant species are assigned higher interaction likelihoods. Subsequently, Bernoulli trials can generate local webs based on these interaction probabilities.



1369 **Figure 1.**

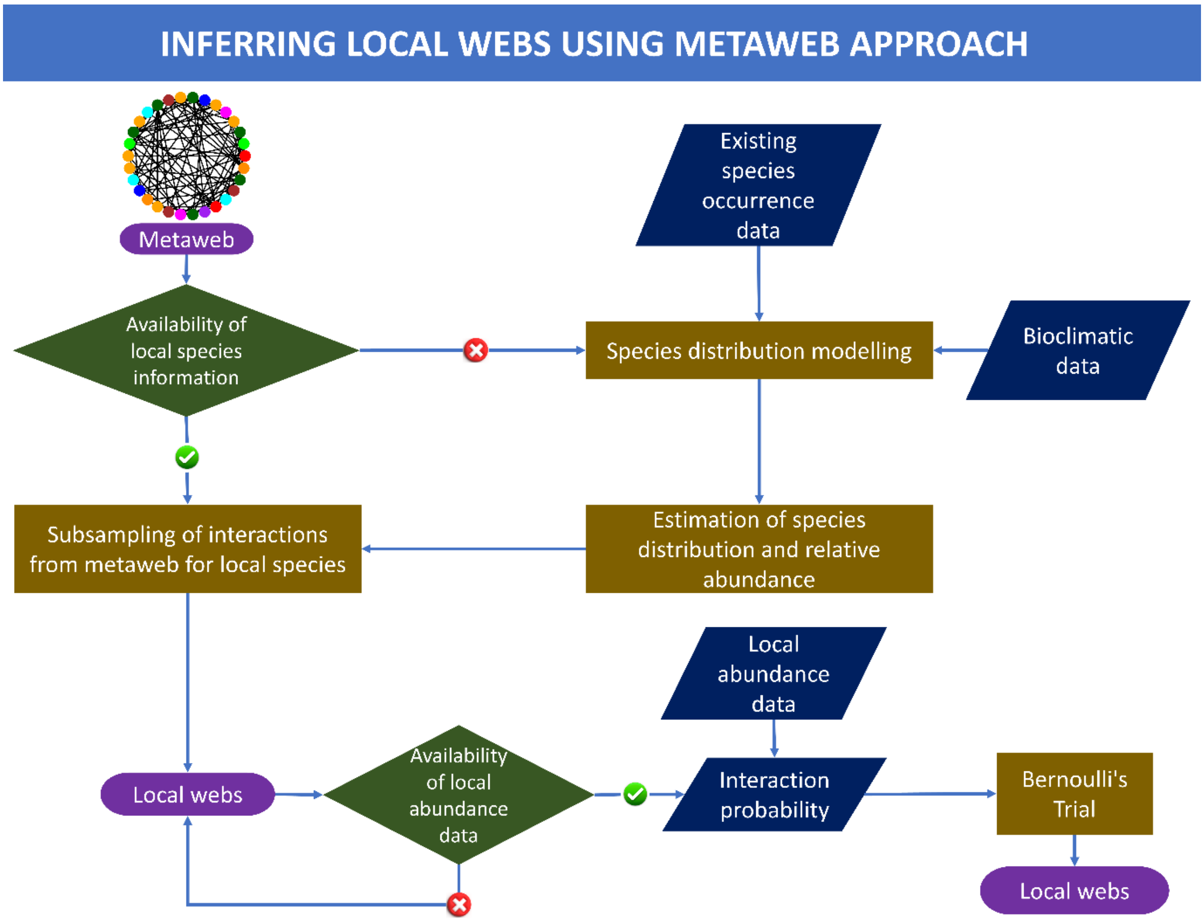

INFERRING LOCAL WEBS USING METAWEB APPROACH
Metaweb
Existing species occurrence data
Availability of local species information
Species distribution modelling
Bioclimatic data
Subsampling of interactions from metaweb for local species
Estimation of species distribution and relative abundance
Local abundance data
Local webs
Availability of local abundance data
Interaction probability
Bernoulli's Trial
Local webs

Figure 2.