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PERSPECTIVE

A new perspective for revealing 'hidden' interactions in ecological networks

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Abstract

- 1. Ecological network models are essential for developing and quantifying ecosystem-based management strategies. Unobserved species interactions alter the interpretation of structural and functional characteristics of the ecosystem being studied. Link prediction algorithms can help to identify such unobserved, 'hidden' interactions. However, due to general unfamiliarity and insufficient ecological interpretations, the use of link prediction algorithms in ecology remains limited.
- 2. In this study, we enhance the link prediction applicability in ecological networks by considering and quantifying the algorithm results from the link as well as the node perspective using a coastal food web model from the northern Wadden Sea as a case study. For this purpose, we have defined the Weighted Unobserved Node Connectivity (WUNC) representing a new node property.
- 3. The WUNC facilitates the estimation of the missing connectivity of a species in relation to a considered original source network. Such a new combination of both link and node perspectives helps to uncover unobserved interactions as well as the resulting lack of species connectivity in poorly understood environments without active sampling.
- 4. The bi-dimensional perspective presented in this study provides a more effective use of link prediction algorithms to identify and prioritize under-connected species and their unobserved interactions. This enables the design of more targeted, species-specific measurement campaigns to validate predicted interactions, thereby supporting refinements of existing ecological network models. A more comprehensive representation of interactions in ecological network models contributes to more accurate modelling results and improves their interpretation to support better management strategies in times of environmental changes.

KEYWORDS

biomonitoring, ecological networks, food webs, link prediction, missing interactions

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1 | INTRODUCTION

Species interact both directly and indirectly with themselves (intraspecific), with other species (interspecific), and with their environment. This plays a large role in defining their ecological success. These diverse and numerous interactions among and between species and their environment can be seen as complex networks. The shift in perspective from a simple, species-centred viewpoint to a complex structure of interactions is known as the 'network perspective'. Such a 'network perspective' is necessary for understanding, investigating and assessing the structure and function of ecological interactions and food webs and ever more so in the context of environmental changes (as also emphasized by the Marine Strategy Framework Directive [MSFD] of the European Union, European Commission, 2020).

The validity and thus the applicability of ecological network models and their analyses is dependent upon their accuracy and on the comprehensiveness of included species (nodes of the network) and their interactions (links in the network). The validity of already known network models is primarily limited by two factors: (1) the inclusion of non-existing ('incorrect') species and interactions in the network model, or (2) the omission of existing ('correct') but unrepresented species and interactions. While this problem is well recognized at the species level, the importance of accurately representing interactions is often neglected (Jordano, 2016). Hortal et al. (2015) described this deficiency in knowledge of species interactions as the 'Eltonian shortfall'. These unobserved. 'hidden' interactions could affect network stability and its susceptibility to external stressors (Gray et al., 2014), as well as the richness and diversity of ecosystem functions (Jordano, 2016). Consequently, from the outset of ecological studies, sampling design and effort have direct effects on the quality of network models and the analysed results, which in turn affect management decisions based on them.

Indeed, the Eltonian shortfall can be mitigated by optimizing sampling design and effort. This would enhance the validity of the ecological networks and their reliability. However, there is a tradeoff between the enhanced validity and the corresponding personnel and financial costs, for example, of data collection. Improving existing ecological network models with contemporary methods such as experiments and extensive sampling involves considerable effort in prioritizing specific interactions for measurement.

Link prediction algorithms can help to optimize the trade-off between increased sampling effort and associated costs, by enabling a targeted, network-specific data collection (Clauset et al., 2008). These algorithms estimate unseen and thus non-represented links between nodes in a given source network, utilizing the network's topology or incorporating additional properties depending on the prediction technique used. It is important to distinguish this class of link prediction algorithms—based on existing network structures—from algorithms that generate networks de novo without prior knowledge of interactions (Caron et al., 2022; Strydom et al., 2022). Applications of link prediction algorithms use already established base networks, currently primarily in social sciences, include finding new contacts via social media (Aiello et al., 2012), generating customized product recommendations in e-commerce (Huang et al., 2005) or identifying possible collaborations in academia (Chuan et al., 2018). In a biological context, these algorithms have been applied in bioinformatics (Himmelstein & Baranzini, 2015; Lei & Ruan, 2013) to investigate gene interactions, for example, as well as in initial ecological applications, like host-virus networks (Dallas et al., 2017; Poisot et al., 2023) or food web models (Catchen et al., 2023; Strydom et al., 2021; Terry & Lewis, 2020). In ecological networks such as food webs, the existence of interactions between species has been estimated using structural properties of the food web (Clauset et al., 2008; Lü et al., 2015; Stock et al., 2017), ecologically relevant trait data (Bartomeus et al., 2016; Gravel et al., 2013) or by acknowledging spatiotemporal variation in species interactions (Cirtwill et al., 2019; Gravel et al., 2019).

The potential of link prediction algorithms remains, nevertheless, underestimated and therefore also underutilized, especially in the context of ecological interaction networks (Terry & Lewis, 2020). This is due to the general unfamiliarity of these algorithms in ecological contexts and due to the lack of basic evidence for ecological interpretation. Typically, in ecology, results are viewed solely from a binary link perspective, focusing on whether an unrepresented interaction (link) exists between two species (nodes) of the source network. Other perspectives, such as considering predicted links from the node perspective or interpreting the ecological implications of the network topology changes due to the addition of predicted links, are not considered.

In this study, we extend the ecological application of link prediction algorithms by incorporating the node perspective. For this purpose, we introduce a novel node property derived from the link prediction process. Utilizing both the link and node perspectives together enable a clearer and more comprehensive interpretation of link prediction results within an ecological context. Our aim is to improve the practical applicability of link prediction algorithms for ecologists by identifying under-connected species and their unobserved 'hidden' interactions in order to develop, expand and optimize ecological network models. The proposed bi-dimensional perspective promotes a more effective application of link prediction techniques by guiding the prioritization and resource-efficient design of field measurement campaigns for validating predicted interactions.

2 | ONE PREDICTION-TWO PERSPECTIVES

Numerous algorithms from various disciplines of science exist for predicting links in networks (Kumar et al., 2020; Lü et al., 2015; Martínez et al., 2017). These algorithms are based on different methods but lead to similar results. They allow the presumption that a hidden link exists between two network nodes that has not yet been observed. Ecologically, these algorithms predict an unobserved or unrepresented interaction between two species within an interaction network (such as food webs, pollination networks or

socio-ecological networks). Instead of focusing on a single specific interaction, these algorithms evaluate all potential or previously specified unobserved interactions in relation to the research question. The result is a list of potential unobserved (hidden) interactions with an associated estimation of occurrence.

The interpretation of predicted interactions between species is referred to as the 'link perspective'. This perspective represents the standard evaluation level of predicted interactions, regardless of the algorithm employed. By categorizing the likelihood of unobserved interactions, the link perspective reduces the need for untargeted estimations of unobserved links that rely on brute-force approaches to enable a resource-efficient estimation of interactions.

Examining link prediction algorithms solely from the link perspective fails to capture their full potential in addressing ecological questions. Particularly within interaction networks, it is necessary to consider the connectivity of individual species in relation to the entire network. Here, connectivity refers to the extent to which a species is integrated into the interaction network via its interactions with other species. The 'node perspective', when applied to link prediction results, enables the estimation of missing connectivity due to unobserved links of individual species. Underestimating the connectivity of individual species results in significant inaccuracies in the structural and functional assessment of ecological interaction networks.

Interpreting the results of the link prediction algorithm in ecological networks requires both the link and node perspectives. Together, these perspectives provide a comprehensive understanding of the influences of unobserved links on the structure and function of network models in order to mitigate the Eltonian shortfall.

3 | QUANTIFICATION OF THE NODE PERSPECTIVE

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The node perspective can be used to describe the missing connectivity of species within interaction networks due to unobserved interactions between them. To quantify this perspective, we introduce a new measure designed to characterize the lack of connectivity, the Weighted Unobserved Node Connectivity (WUNC). The considerations presented here relate to any link prediction algorithms that are capable of estimating the likelihood of unobserved interactions by specifying a probability of existence. As such, the quantification of the node perspective is not tied to a specific algorithm but allows for the integration of different prediction techniques, depending on the user's data availability, research objectives or available resources.

The node perspective is directly dependent on the link perspective. In this study, the link probability represents the predicted likelihood that an interaction should exists within the network, despite not being currently represented. Therefore, as shown in Figure 1b, the link prediction algorithm estimate the probability p_{ij} if an unobserved interaction exists between two species *i* and *j* of the source network. Since most link prediction algorithms are based on undirected networks (cf. Kumar et al., 2020), $p_{ij} = p_{ji}$ holds true for all unobserved interactions. We thus obtain a list of unobserved interactions of the basic network with an associated probability of occurrence.

From the species perspective, the result of link prediction algorithms can be quantified at the node level using two simple



FIGURE 1 Schematic representation of the results of a probabilistic link prediction algorithm applied to a base network model (a), presented from both (b) link and (c) node perspective. Known species interactions are shown in green, while predicted interactions are shown in orange, along with their associated probabilities (as detailed also in panel b). The algorithm estimates the likelihood of unobserved interactions (link perspective), which can subsequently be used to identify under-connected species within the interaction network (node perspective).

Basic interaction network

Link prediction

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properties: The first is the sum of predicted link probabilities $\sum_{j} p_{ij}$ with $i, j \in B$, where p_{ij} represents the probability that an unobserved interaction exists between species i and j and where B denotes the set of unobserved interactions predicted by the selected algorithm. The set B can either contain all previously predicted unobserved interactions or a subset defined by a certain threshold. Therefore, the sum of predicted link probabilities describes an overall estimator of unobserved interactions per species. The second node property is the cardinality of the predicted unobserved interactions per species, denoted as #i with $i \in B$. It describes the number of unobserved interactions per species over the set of predicted interactions B, as determined by the algorithm, along with possible additional assumptions like probability thresholds above which a link is assumed to be missing. For an example of both node properties, see Figure 1c.

From the two introduced node properties, we can define a comprehensive metric that quantifies the node perspective. This metric needs to satisfy the following conditions: (1) it should combine the sum of predicted link probabilities and the cardinality of predicted unobserved interactions, (2) it should incorporate these two properties on a weighted scale and (3) it should be restricted to the interval [0,1]. In accordance with these a priori requirements, the WUNC is constructed by combining species-level information derived from the predicted unobserved interactions. The relative metric WUNC at species *i* is defined as

$$WUNC_{i} = \alpha \left(\frac{\sum_{j} p_{ij}}{\# i \cdot \max_{k, \ell \in B} (p_{k\ell})} \right) + (1 - \alpha) \left(\frac{\# i}{\max_{k \in B} (\# k)} \right) \text{ with } i, j \in B,$$
(1)

where $\sum_{i} p_{ij}$ refers to the sum of predicted link probabilities and *#i* to the cardinality of the unobserved interactions of species *i*. The term max $_{k,\ell\in B}(p_{k\ell})$ denotes the unobserved link with the highest probability of existing over the set *B* of the predicted interactions considered. Similarly, max $_{k\in B}(\#k)$ denotes the maximum cardinality of unobserved interactions over the set *B*. The variable α , constrained by $0 < \alpha < 1$, restricts the WUNC to the interval [0,1] and allows a user-defined weighting between the two terms of Equation (1).

The WUNC quantitatively characterizes the node perspective with regard to predicted unobserved interactions in ecological networks. It serves as a metric to determine the missing connectivity of nodes to the base network due to unobserved links. More specifically, from an ecological standpoint, the WUNC quantifies the lack of connectivity of a species caused by previously unobserved interactions within the source network.

4 | CASE STUDY

A case study is presented here to demonstrate the extended interpretative capabilities of predicted interactions by incorporating the node perspective. For this, we used a food web model of the Sylt-Rømø Bight (SRB) (de la Vega et al., 2018), located at the Danish-German border, as our base model. The network consists of 66 compartments, including 63 living and three non-living compartments, and covered sedimentary, benthic as well as pelagic interactions.

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We utilized the Hierarchical Random Graph (HRG) approach after Clauset et al. (2008) as the link prediction algorithm, applied to the SRB model. The HRG algorithm provides a good prediction performance compared among topology-based methods (Clauset et al., 2008; Kumar et al., 2020) with minimal requirements on the base network (i.e. undirected and unweighted). The approach assumes that the likelihood of interaction between two nodes depends on the degree of their relationship. Thus, hierarchy refers to the property where nodes form groups through their interactions, which in turn are part of larger groups, and so on across scales (Clauset et al., 2007). This method accounts for hierarchical organization at all network levels and, compared to other link prediction approaches, also incorporates disassortative mixing (defined after Newman, 2002 as: preference for '[...] high-degree vertices [to] attach to low degree ones'). Both these properties are important characteristics for biological networks (Clauset et al., 2008; Newman, 2002, 2003).

The SRB model was imported and analysed using the R package enaR (version 3.0.0; Lau et al., 2017) and preprocessed as our source model. All subsequent calculations were conducted in R (version 4.2.2; R Core Team, 2023). Prior to predicting unobserved interactions, the predictive performance of the HRG algorithm was validated against the known SRB network following the guidelines described by Poisot (2023) (see Supporting Information for details). Afterwards, the HRG algorithm of function predicted_edges() (package igraph; Csardi & Nepusz, 2006; version 2.0.3) was applied to predict the unobserved interactions between all species of the network. The node perspective was subsequently quantified from the link prediction result via the WUNC, as described in Equation (1), with a weighting factor α of 0.5. Only predicted links up to a cumulative probability threshold (ordered from highest to lowest predicted probability) were considered to select the most likely interactions. To minimize bias introduced by threshold selection, the WUNC was averaged across a threshold range from 1% to 50% of the cumulative probability of all predicted interactions, as the algorithm demonstrates a good predictive performance within this range (see Supporting Information for details). To account for the uncertainty of the HRG algorithm, the steps of (1) executing the link prediction algorithm, (2) threshold selection and (3) WUNC calculation were repeated 1000 times with a subsequent averaging. Further details can be found in the attached R scripts (Habedank, 2025).

Figure 2 illustrates the predictions of the HRG algorithm applied to the SRB food web model, from both the link (Figure 2a) and the node perspective (Figure 2b). These perspectives were further mapped to the effective trophic levels (ETLs) of the food web (Figure 2c), providing an additional interpretative dimension. This mapping enables the incorporation of cross-species considerations into the assessment of how missing interactions influence the structure and function of the overall food web. Uncertainties arising from unobserved interactions, when aggregated across ETLs, can influence the accuracy of modelled energy flows within the network.

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FIGURE 2 Link prediction results of the Hierarchical Random Graph algorithm (after Clauset et al., 2008) described from the link (a) and node perspective (b) of the Sylt-Rømø Bight network model. The node perspective was averaged over a threshold range of 1%–50% of the cumulative probability of all unobserved, predicted interactions (cf. Section 4). Part (c) presents the two perspectives in relation to the corresponding effective trophic level (ETL). The relative Weighted Unobserved Node Connectivity (rel. WUNC) of each ETL is calculated by normalizing the WUNC to the number of species per ETL; p_{ETL} describes the sum of predicted link probabilities between the corresponding ETL's, normalized to their number. The complete results with all abbreviations can be found in Supporting Information.

From the link perspective, the top seven predicted unobserved interactions exhibit similarly high probabilities, averaging around 0.80 (Figure 2a). However, the probability of subsequent interactions decreases considerably (Table S1). Based on this, the quantification of the node perspective using WUNC revealed differences between the species. The WUNC indicated that the green shore crab (Carcinus maenas) had the highest value of unobserved connectivity with the source network (0.76) followed by the marine catworm (Nephtys spp.) with 0.72 and the brown shrimp (Crangon crangon) with 0.65. High values of unobserved connectivity were especially found for species belonging to the third trophic level as shown in analyses using ETL (Figure 2c). Correspondingly, the predicted interactions associated with an ETL of three (ETL two and four) also exhibited the highest sum predicted link probabilities p_{FTI} (Figure 2c). The combination of both perspectives shows us that species and their associated interactions at the third trophic level are as yet not sufficiently connected in the SRB food web model.

5 | DISCUSSION

Link prediction algorithms have rarely been applied to ecological network models (Terry & Lewis, 2020). This is due to a lack of familiarity with the method in ecological questions and a lack of interpretation of the algorithm results. Approaches to address this unfamiliarity can already be found in the literature through reviews (cf. Kumar et al., 2020; Martínez et al., 2017) and initial ecological application examples (cf. Clauset et al., 2008; Lü et al., 2015; Pichler et al., 2020). In this study, we focused on the second issue—the lack of ecological interpretation. For this purpose, we looked at the predicted interactions from two different perspectives.

Both perspectives—the link and node perspective—cannot be considered independently from one another; they are mutually dependent. The link perspective, directly inferred from the result, estimates how likely unobserved interactions between two species actually are. Based on this, the node perspective is quantified using the WUNC, providing insights into the unobserved connectivity of the respective species. In combination, both perspectives provide an effective tool for mitigating the Eltonian shortfall, as discussed above. It enables the identification of under-connected species due to unobserved interactions without the need for active sampling and supports more effective validation through resource-efficient field campaigns by using its prioritizing bi-dimensional perspective. Incorporating these unobserved interactions into the source models leads to a more accurate representation of the natural system and improves the accuracy of subsequent analyses.

The spatiotemporal scale of the source network must be considered when interpreting and validating the predicted interactions. The resolution of the network model, or more precisely, its research question, defines the resolution of the predicted interactions. Especially when validating predicted interactions through measurements in the field, it is crucial that their spatial and temporal scales match those of the source model. This constraint is well illustrated by our case study of the SRB in Section 4 above. This model represents a food web averaged across the entire year and bight, where species interactions are defined by biomass flows (de la Vega et al., 2018). A validation of the unobserved interactions, as presented in Figure 2, cannot rely solely on point measurements from specific habitats of the bight or times within a season. Instead, the predicted links must be interpreted and measured as biomass fluxes averaged over the year and across the entire bight.

The application of both perspectives to predicted interactions in ecological networks is a generalized interpretative concept. It is not tied to a specific link prediction algorithm and only requires topological information (undirected, unweighted networks are sufficient) of the source network to quantify the node level using WUNC. These low network requirements are promising as they address a wide range of potential applications for ecological networks. This could not only simplify the validation of existing network models but also the development of new models.

Given that these algorithms are based on stochastic principles, each prediction is accompanied by several uncertainties, which may lead to incorrect predictions (cf. unlikely but predicted interactions between the first and fourth ETL in the SRB model in Figure 2c). These predicted interactions may be incorrect for several reasons. For example, due to morphological mismatches (Jordano et al., 2003), phenological uncoupling (Olesen et al., 2011) or external abiotic (habitat specific) limitations to establish the interaction. Jordano (2016) refers to these unobserved but ecologically incorrect interactions as 'forbidden links'. The algorithm does not filter out these forbidden links, necessitating the need for the ecologist's expertise as a subsequent control instance.

A possible further development of the approach presented in this study is to remove forbidden links from the prediction results. This could be achieved, for example, by matching species traits (such as size, diet or habitat preference) using databases and other relevant literature (Caron et al., 2022; Gravel et al., 2013; Strydom et al., 2021). Another possible extension is to estimate the weights of the predicted interactions. Depending on the modelled flow currency of the source network, such weighting could provide insights into the magnitude of carbon or nutrient fluxes leading to more reliable networks, also at a functional level.

Link prediction algorithms should be considered more often in ecological applications and as a valuable extension of the ecological toolbox for improving ecological network models. Nonetheless, the ecologist's expertise, real data as well as experiments in using and evaluating networks and their modelled processes still remain indispensable.

6 | CONCLUSION

In our study, we broadened the scope of link prediction by introducing a new perspective designed to enhance the practical applicability of the prediction approach for ecologists. Considering results from link prediction algorithms from both the link and node perspective allows us to identify under-connected species due to unobserved 'hidden' interactions without the need for active sampling. At the same time, our bi-dimensional perspective supports the targeted and resource-efficient planning of measurement campaigns by prioritizing predicted interactions for validation and thereby contributing to the refinement of ecological network models. Under ongoing environmental changes, the development of more comprehensive network models will improve the ability to quantify management strategies and provide more accurate assessments of their effectiveness.

AUTHOR CONTRIBUTIONS

Joel Habedank conceived the conceptual ideas and designed the methodology with the support of Sabine Horn, Peter Lemke and Karen H. Wiltshire. Joel Habedank carried out the numerical simulations. Sabine Horn and Karen H. Wiltshire collected and facilitated access to the data for the case study. Joel Habedank led the writing of the manuscript, with further edits and comments by Sabine Horn, Peter Lemke, Vera Sidorenko and Karen H. Wiltshire. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no competing financial interests or personal relationships that are relevant to the content of this article.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

The applied food web model of the Sylt-Rømø Bight was compiled and published by de la Vega et al. (2018). All R-scripts of this study are deposited via the Zenodo repository: https://doi.org/ 10.5281/zenodo.15544038 (Habedank, 2025). All data and code used in this manuscript have been uploaded as a file along with this manuscript.

STATEMENT ON INCLUSION

This study was collaboratively compiled and written by authors from diverse disciplines. The local food web model utilized in this research has been developed and refined over decades at the Wadden Sea Station of the Alfred-Wegener-Institute on the island of Sylt. The methodology presented in this 'Perspective' article offers valuable insights for creating and expanding existing food web models, with significant relevance for stakeholders across various fields and regions.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Supplemetary. Validation of the HRG Algorithm to our case study.

Table S1. Probabilities of unobserved interactions in the Sylt-RømøBight model predicted by the HRG algorithm.

Table S2. Summed probability of predicted interactions among the individual ETL's.

Table S3. Node perspective quantified via WUNC of the Sylt-RømøBight model species.

Table S4. Relative WUNC per ETL of the Sylt-Rømø Bight model.

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