A Primer on Predicting Species Interaction Networks (Across Space and Time)

Tanya Strydom [1,2,‡], Michael D. Catchen [3,2,‡], Francis Banville [1,4,2], Dominique Caron [3,2],
Gabriel Dansereau [1,2], Philippe Desjardins-Proulx [1,2], Norma Forero [1,2], Gracielle Higino [5],
Benjamin Mercier [4,2], Andrew Gonzalez [3,2], Dominique Gravel [4,2], Laura Pollock [3,2], Timothée Poisot [1,2]

[1] Université de Montréal; [2] Québec Centre for Biodiversity Sciences; [3] McGill University; [4] Université de Sherbrooke; [5] Universidade Federal de Goiás
[‡] These authors contributed equally to the work

Correspondance to:
Timothée Poisot — `timothee.poisot@umontreal.ca`

Abstract: Networks of species interactions can capture meaningful information on the structure and functioning of ecosystems. Yet the scarcity of existing data, and the difficulty associated with comprehensively sampling interactions between species, means that to describe the structure, variation, and change of ecological networks over time and space, we need to rely on modeling tools with the capacity to make accurate predictions about how species interact. Here we provide a proof-of-concept, where we show a simple neural-network model makes accurate predictions about species interactions, and use this model to reconstruct a metaweb of host-parasite interactions across space, and assess the challenges and opportunities associated with improving interaction predictions. We then provide a primer on the relevant method and tools that will guide the development and integration of these tools, and provide a road map forward toward integration of multiple sources of data and methodlogical approaches (including statistical, dynamical, and inferential models) to sketch the path forward for this research program.

Keywords:
ecological networks
ecological forecasting
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Introduction

Ecosystems *are* interactions – organisms interact with one-another and with their environment, either directly or indirectly. Between organisms, these interactions form networks of varying complexity, drive ecological and evolutionary dynamics, and maintain ecosystem diversity and functioning (Delmas et al. 2018; Landi et al. 2018; Albrecht et al. 2018). Networks of species interactions underpin our understanding of key ecological processes (Pascual and Dunne 2006; Heleno et al. 2014). Yet, even basic knowledge of species interactions (like being able to list them, or guess which ones may exist) is one of the most severe shortfalls in biodiversity science (Hortal et al. 2015). This is due in large part to the tedious, time-consuming, and expensive data collection process. As with many ecological systems, networks of species interactions have entered their "long now" (Carpenter 2002), where contemporary actions have long-term, low-predictability consequences (Burkle, Marlin, and Knight 2013). Therefore, our field needs a conceptual path forward toward models that enable prediction (for the present) and forecasting (for the future) of species interactions and the networks they form (McCann 2007; Seibold et al. 2018).

Methods for predicting interactions between species exist, but can be limited in that they are often built around mechanisms represented at a single organisational scale: position in the trophic niche (Gravel et al. 2013; Petchey et al. 2008), phylogenetic matching (Pomeranz et al. 2018; Elmasri et al. 2020), functional traits (Bartomeus et al. 2016), and so on. Species interaction networks are the product of ecological and evolutionary mechanisms interacting across spatial and temporal scales. The interwoven nature of these processes imposes structure on biodiversity data which is invisible when examined only through a single mechanism or at a single scale. In addition to the recent application ensemble models (Becker et al. 2020), machine learning methods show promise to take the field in a radically different direction, by finding structure in data, and synthesizing mechanistic models from different learning frameworks (Desjardins-Proulx, Poisot, and Gravel 2019). Here we provide a proof-of-concept to show how machine-learning models can enable unreasonably effective prediction of species interactions, whereby we construct a metaweb of host-parasite interactions across space. We then provide a primer on the relevant tools and methods that could be incorporated these models in the future, in order to account for the spatial, temporal, and climatic dimensions of network prediction (Burkle and Alarcon 2011), and propose a roadmap forward for how to improve predictions using this approach.

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Proof-of-Concept

2.1. Can we predict ecological networks? The core premise of this manuscript is that ecological networks can be predicted. In this section we provide a proof-of-concept, in which we use data from Hadfield et al. (2014) describing 51 host-parasite networks, where not all species pairs co-occur across sites. This implies that there may be "negative associations" — interactions between species that might be biologically feasible but not observed because the two species have not been observed co-occurring. To do this we (i) aggregate a series of host-parasite interaction networks collected across space into a metaweb, (ii) extract species features based on species co-occurrence, (iii) use these features to train a neural network to predict interactions, and (iv) apply this classifier to the original features to predict possibly missing interactions across the entire species pool. The entire analysis is presented in fig. 1, and the code to reproduce it is available at `https://osf.io/6jp4b/`; the entire example was carried out in *Julia 1.5.3* (Bezanson et al. 2017), using the *Flux* machine learning framework (Innes 2018). Note that this analysis is meant to serve as an *example only*, and the models should in practice be fine-tuned according to the state of the art (*e.g.* Goodfellow, Bengio, and Courville 2016). As these data have no features (like species traits) on which to base a predictive model, we have aggregated all interactions into a binary metaweb (J. Dunne 2006) to represent co-occurrence among species, and then we transform this co-occurrence matrix via probabilistic PCA (Tipping and Bishop 1999), so as to create a number of latent features for the species in a context where the dataset is both unbalanced and likely to have many missing values. The goal is then to predict whether an interaction between two species i and species j occurs based on a features vector $v_{ij} = [v_i, v_j]$ where v_i is the values of the selected features for the parasite and v_j is the features of the host. Here, v_i is the first 15 components of the co-occurrence PCA. This features vector is then fed into the input layer of a neural network, which uses three hidden layers with appropriate dropout rates (0.5), and finally an output layer whose result is softmaxed to pick the most likely outcome — the interaction bit describing an interaction when equal to 1, and no interaction when equal to 0.

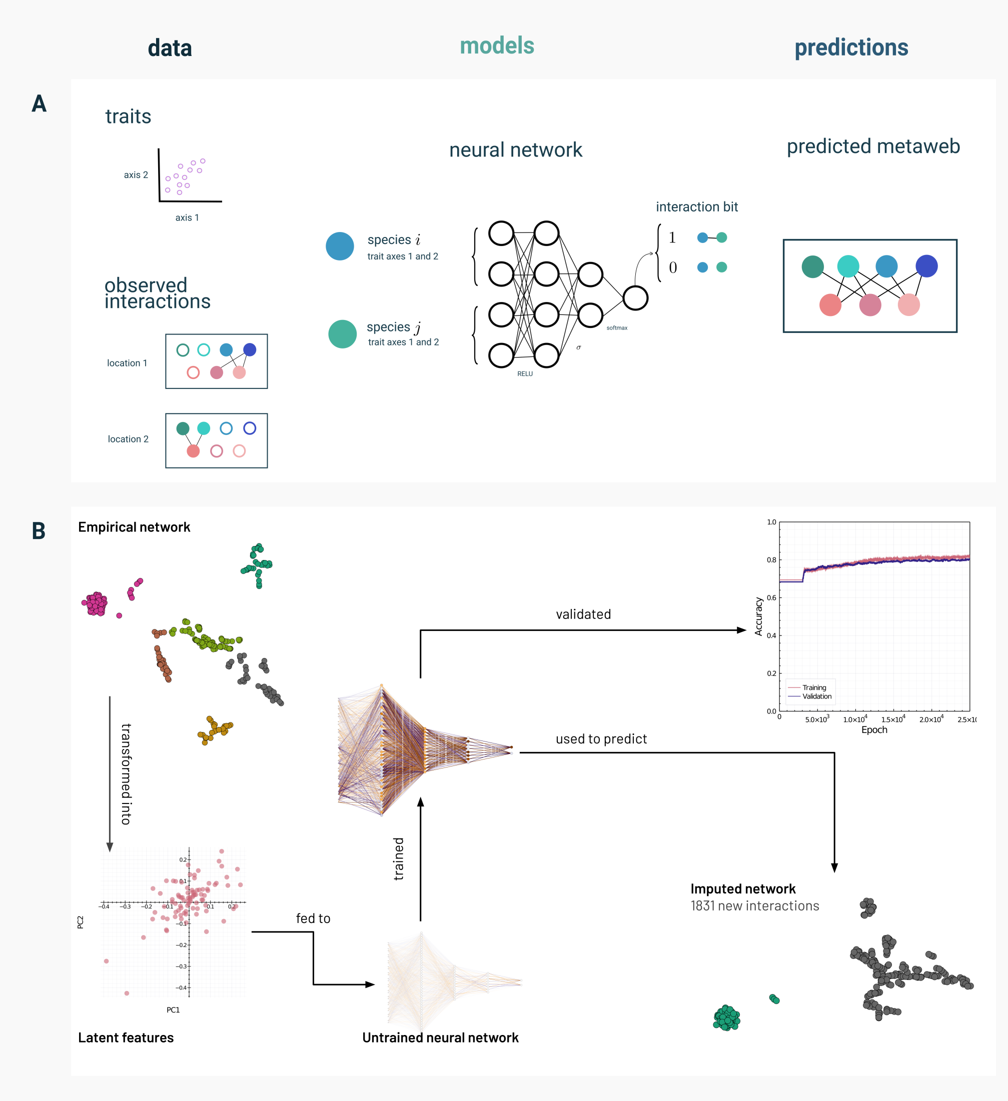

Figure 1 (A) A conceptual overview of the process of network prediction. Beginning with data of observed interaction between species, we aim to predict the metaweb of interaction across the entire species pool, even those that have not been observed together. (B) Proof-of-Concept: An empirical network (from Hadfield et al. 2014) is converted intro latent features using probabilistic PCA, then used to train a deep neural network to predict species interactions. The initial and imputed networks are represented as their tSNE embedding, and the colors of nodes are the cluster to which they are assigned based on a *k*-means clustering of the tSNE output.

During the training of this neural network, we exploited ecological constraints in two ways: First by selecting features so absent interactions for a species pair that was not observed to co-occur were removed from the data. This ensures that the network is trained only on the subset of the data for which we have actual information about the interaction. Second, the batches of 16 items used for training were constrained to have at least 10 positive interactions. The reasoning for this choice was made based on three observations: the network is sparse, meaning negative interactions have a chance of being false negatives due to lack of reporting in the field, and there is no way to ensure an interaction not observed to occur is a true negative. Slightly inflating the dataset with positive interactions enables us to counterbalance these biases (Chawla 2010).

After the training (2.5×10^4 epochs in fig. 1), our model reached an accuracy of ≈ 0.8, with no marked deviation between the training and testing sets (respectively 80% and 20% of the data), suggesting no to minimal overfitting, which is replicable across random partitions of test and training sets. Applying this model to the entire dataset (including species pairs never observed co-occuring in the dataset) identified 1831 new possible interactions – 382 of which were in pairs of species never considered prior. This suggests that meaningful information about ecological interactions is structured within network data. Now, the question becomes: home do we make our prediction of interaction networks *better*?

2.2. Challenges: the many constraints on prediction

2.2.1 Ecological network data are scarce and hard to obtain At the moment, we are primarily limited by the availability of data. Although we have seen a growth in species occurrence data, this growth is much slower for ecological interactions because species interactions are challenging to sample comprehensively (Bennett, Evans, and Powell 2019; Jordano 2016b) and sampling methodology has strong effects on the resulting data (de Aguiar et al. 2019). In turn, the difficulty of sampling interactions can lead to biases in our understanding of network structure (de Aguiar et al. 2019). This knowledge gap has motivated a variety of approaches to deal with interactions in ecological research based on assumptions that do not always hold, such as the assumption that co-occurrence is equivalent to meaningful interaction strength, when it is known that co-occurrence is not the only prerequisite for an interaction to occur (Blanchet, Cazelles, and Gravel 2020). Spatial biases in data coverage are prevalent at the global scale (with South America, Africa and Asia being under-represented) and different interaction types show biases towards different biomes (Poisot et al. 2020). These “spatial gaps” serve as a limitation to our ability to confidently make predictions when accounting for real-world environmental conditions, especially in environments for which there are no analogous data.

Further, empirical estimation of interaction *strength* is highly prone to bias as existing data is usually lumped together, making it difficult to differentiate the strength in per-individual interactions from the strength of a whole species interaction (Wells and O’Hara 2013). Empirical estimations of interaction strength are still crucial (Novak and Wootton 2008), but are a hard task to quantify in natural communities (Wootton 1997; Sala and Graham 2002; Wootton and Emmerson 2005), especially as the number of species composing communities increases, compounded by the possibility of higher-order interactions or non-linear responses in interactions (Wootton and Emmerson 2005). Further, interaction strength is often variable and context dependent and can be influenced by density-dependence and spatiotemporal variation in community composition (Wootton and Emmerson 2005).

2.2.2 Powerful predictive tools work better on large data volumes This scarcity of data limits the range of computational tools than can be used by network ecologists. Most deep learning methods, for instance, are very data expensive. The paucity of data is compounded by a collection of biases in existing datasets. Species interaction data are typically dominated by food webs, pollination, and host-parasite networks (Ings et al. 2009; Poisot et al. 2020). This could prove to be a limiting factor when trying to understand or predict networks of underrepresented interaction types or when trying to integrate networks of different types (Fontaine et al. 2011), especially given their inherent structural variation (Michalska-Smith and Allesina 2019). This stresses the need for an integrated, flexible, and data-efficient set of computational tools which will allow us to predict ecological networks accurately from existing and imperfect datasets, but also enable us to perform model validation and comparison with more flexibility than existing tools. We argue that fig. 1 is an example of the promise of these tools *even* when facing datasets of small size. When carefully controlling for overfitting machine learning systems are at least adequate at generalizing. The ability to extract and engineer features also serves to bolster our predictive power. In short, the current lack of massive datasets must not be an obstacle to prediction; it is an ideal testing ground to understand how little data is sufficient to obtain actionable predictions.

2.2.3 Scaling-up predictions requires scaled-up data We are also currently limited by the the level of biological organisation at which we can describe ecological networks. For instance, our understanding of individual based networks (*e.g.* M. S. Araújo et al. 2008; Tinker et al. 2012) is still in its infancy (Guimarães 2020) and acts as a resolution-limit. Similarly, the resolution of environmental (or landscape) data also limits our ability to predict networks at small scales, although current trends in remote sensing would suggest that this will become less of a hindrance with time (Makiola et al. 2020). Ecosystems are a quintessential complex-adaptive-system (Levin 1998) with a myriad of ways in which processes at different spatial, temporal, and organizational scales can influence and respond to one another. Understanding how the product of these different processes drive the properties of ecosystem across different scales remains a central challenge of ecological research, and we should strive to work on methods that will integrate different empirical "snapshots" of this larger system.

2.3. Opportunities: the emerging ecosystem of open tools and data The acquisition of biodiversity and environmental data has tremendously increased over the past decades thanks to the rise of citizen science (Dickinson, Zuckerberg, and Bonter 2010) and of novel technology (Stephenson 2020), including wireless sensors (Porter et al. 2005), next-generation DNA sequencing (Creer et al. 2016), and remote sensing (Skidmore and Pettorelli 2015; Lausch et al. 2016). Open access databases, such as GBIF (for biodiversity data), NCBI (for taxonomic and genomics data), TreeBASE (for phylogenetics data), CESTE (Jeliazkov et al. 2020) (for metacommunity ecology and species traits data), and WorldClim (for bioclimatic data) contain millions of data points that can be integrated to monitor and model biodiversity at the global scale. For species interactions data, at the moment Mangal is the most comprehensive open database of published ecological networks (Poisot et al. 2016), and GloBI is an extensive database of realized and potential species interactions (Poelen, Simons, and Mungall 2014). Developing standard practices in data integration and quality control (Kissling et al. 2018) and in next-generation biomonitoring (NGB; Makiola et al. 2020) would improve our ability to make reliable predictions of ecosystem properties on increasing spatial and temporal scales. The advancement of prediction techniques coupled with a movement towards standardising data collection protocols (e.g. Pérez-Harguindeguy et al. (2013) for plant functional traits) and metadata (e.g. DarwinCore)—which facilitates interoperability and integration of datasets—as well as a growing interest at the government level (Scholes et al. 2012) paints a positive picture for data access and usability in the coming years.

In turn, this effort is supported by a thriving ecosystem of data sources and novel tools. Machine learning encompasses a broad variety of techniques applied with or without human supervision. These techniques can often be more flexible and perform better than classical statistical methods, and can achieve a very high level of accuracy in many predictive and classification tasks

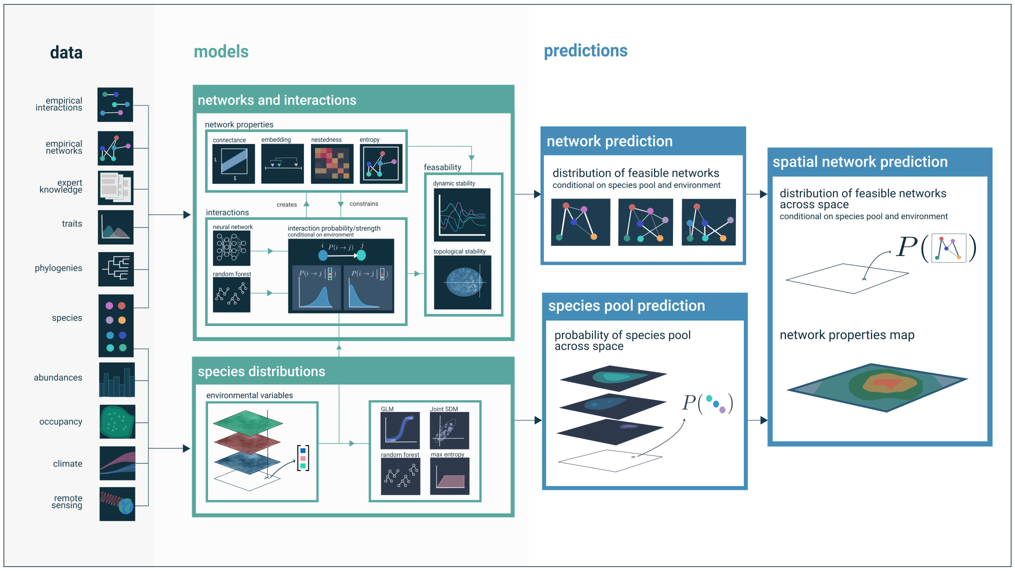

Figure 2 A conceptual roadmap highlighting key areas for the prediction of ecological networks. Starting with the input of data from multiple sources, followed by a modelling framework for ecological networks and the landscape, which are then ultimately combined to allow for the prediction of spatially explicit networks.

in a relatively short amount of time (e.g. Cutler et al. 2007; Krizhevsky, Sutskever, and Hinton 2017). Increasing computing power combined with recent advances in machine learning techniques and applications shows promise in ecology and environmental science (see Christin, Hervet, and Lecomte (2019) for an overview). Moreover, ongoing developments in deep learning are aimed at improvement in low-data regimes and with unbalanced datasets (Antoniou, Storkey, and Edwards 2018; Chawla 2010). Considering the current biases in network ecology (Poisot et al. 2020) and the scarcity of data of species interactions, the prediction of ecological networks will undoubtedly benefit from these improvements. Machine learning methods are emerging as the new standard in computational ecology in general (Olden, Lawler, and Poff 2008; Christin, Hervet, and Lecomte 2019), and in network ecology in-particular (Bohan et al. 2017), as long as sufficient, relevant data are available. As many ecological and evolutionary processes underlie species interactions and the structure of their ecological networks (e.g. Vazquez et al. 2009; Segar et al. 2020), it can be difficult to choose relevant variables and model species interactions networks explicitly. A promising application of machine learning in natural sciences is Scientific-Machine Learning (SciML), a framework that combines machine learning with mechanistic models (Chuang and Keiser 2018; Rackauckas et al. 2020). Many studies have used machine learning models specifically with ecological interactions. Relevant examples include species traits used to predict interactions and infer trait-matching rules (Desjardins-Proulx et al. 2017; Pichler et al. 2020), automated discovery of food webs (Bohan et al. 2011), reconstruction of ecological networks using next-generation sequencing data (Bohan et al. 2017), and network inference from presence-absence data (Sander, Wootton, and Allesina 2017).

3

A Primer on Predicting Ecological Networks

Below we provide a primer on the background concepts necessary to build models to predict species interaction networks, with a focus on using machine learning approaches in the modelling process. We also present a conceptual roadmap (fig. 2) which we envisage to be the path toward improving our prediction of species interaction networks, and developing spatially explicit models of network structure.

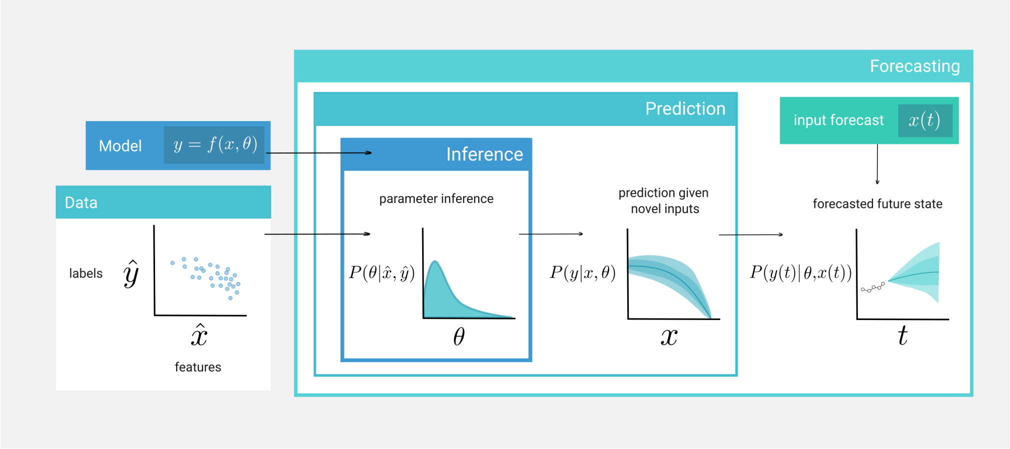

Figure 3 The nested nature of developing predictive and forecasting models, showcases the *forward problem* and how this relies on a hierarchical structure of the modelling process.

3.1. Models

3.1.1 What is a predictive model? Models are used for many purposes, and the term "model" embodies a wide variety of meanings in scientific discourse. All models can be thought of as a function, f, that takes a set of inputs x (also called features, descriptors, or independent variables) and parameters θ, and maps them to predicted output states y (also called label, response, or dependent variable) based on the input to the model: $y = f(x, \theta)$. However, a given model f can be used for either descriptive or predictive purposes. Many forms of scientific inquiry are based around using models *descriptively* (also called inference, the inverse problem, fitting a model, or training a model) (Stouffer 2019). In this context, the goal of using a model is to estimate the parameters, θ, that best explain a set of empirical observations, $\{\hat{x}, \hat{y}\}$. In some cases, these parameter values are themselves of interest (e.g the strength of selection, intrinsic growth rate, dispersal distance), but in others cases, the goal is to compare a set of competing models $f_1, f_2, \ldots$ to determine which provides the most parsimonious explanation for a dataset. The quantitative representation of "effects" in these models—the influence of each input on the output—is often assumed to be linear, and in the frequentist context, the goal is often to determine if the coeffecient corresponding with an input is non-zero to determine its "significance" in influencing the outcome. Models designed for inference have utility, however, in order for ecology to develop as a predictive science (Evans, Norris, and Benton 2012), interest has grown in developing models that are used not just for description of data, but also for prediction. Predictive models are based in *the forward problem*, where the aim is to predict new values of the output y given an input x and our estimate value of θ (Stouffer 2019). Because the forward problem relies on an estimate of θ, then, the problem of inference is nested within the forward problem (fig. 3).

3.1.2 What do you need to build a predictive model? In order to build a predictive model under the Bayesian paradigm, one needs the following: first, **data**, split into features $\hat{x}$ and labels $\hat{y}$ (fig. 3). Second, a **model** f, which maps features x to labels y as a function of parameters θ, i.e. $y = f(x, \theta)$. Third, a loss function $L(\hat{y}, y)$, which describes how far a model's prediction y is from an empirical estimate $\hat{y}$. Lastly, **priors** on parameters, $P(\theta)$. Often an important step before fitting a model is feature engineering: adjusting and reworking the predictors to better uncover predictor-response relationships (Kuhn and Johnson 2019). This can include projecting the predictors into a lower dimensional space, as in our proof-of-concept. Then, when a model is fitted (synonymous with parameter inference or the inverse problem, see fig. 3), a fitting algorithm attempts to estimate the values of θ that minimizes the mean value of loss function $L(\hat{y}, y)$ for all labels y in the provided data Y. These typically rely on drawing candidate parameter values from priors and applying some form of Bayesian sampling to generate a posterior estimate of parameters, $P(\theta|\hat{x}, \hat{y})$.

3.1.3 How do we validate a predictive model? After model fitting, we inevitably want to see how "good" it is. One of the context for validation is *model comparison*, where we aim to see which of a competing set of models provides the best explanation for a data set. A naive initial approach is to simply compute the average error between the model's prediction and the true data we have, and choose the model with the smallest error—however this approach inevitably results in *overfitting*. One approach to avoid overfitting is using information criteria (*e.g.* AIC, BIC, MDL) based around the heuristic that good models maximize the ratio of information provided by the model to the number of parameters it has. However, when the intended use-case of a model is prediction the relevant form of validation is *predictive accuracy*, which should be tested with *crossvalidation*. Crossvalidation methods divide the original dataset into two—one which is used to fit the model (called the *training* set) and one used to validate its predictive accuracy on the data that it hasn't "seen" yet (called the *test* set) (Bishop 2006). This procedure is often repeated for different subdivisions of the dataset (Arlot and Celisse 2010).

In the proof-of-concept, we used a neural-network to perform binary classification by predicting the presence/absence of an interaction between any two species. Many different metrics exist to validate the performance of a binary classifier. One approach is *accuracy*, the proportion of values it got correct. However, consider what we know about interaction networks: they are often vary sparse, with connectance between 0.1 and 0.3. There are two ways for the model to be right: the model predicts an interaction and there is one, or the model predicts no interaction and there isn't one. If we built a model that always guesses there will be no interaction between two species, it will be correct in the majority of cases because the majority of potential interactions in a network typically do not exist. Therefore this "empty-matrix" model would always have an *accuracy* of $1 - C$, where C is the observed connectance, which would almost always be greater than 50%! This emphasizes the importance of considering null models when validating a model's performance. One way to avoid this phenomena is to only consider the true-positive rate, which is the proportion of actually observed interaction that the model predicts correctly. A different metric is the true-skill statistic (TSS; Allouche, Tsoar, and Kadmon (2006)), which is related to the ability to avoid both false-negative and false-positives. The performance of this proof-of-concept model in each of the metrics (accuracy, true positive, TSS) is shown in fig. 4, and reflects that the proof-of-concept model works well with limited data, yielding TSS ≈ 0.5. This is similar to the skill levels derived from a predictive model of food-webs that uses a niche model parameterized with allometry (Gravel et al. 2013); that our model reaches a much higher accuracy with fewer initial data is a strong argument in favor of augmenting the training set with external data sources, as we argue in this manuscript.

3.2. Networks and Interactions

3.2.1 What is an interaction, really? Interactions between species can be conceptualized in a multitude of ways (mutualistic vs. antagonistic, strong vs. weak, symmetric vs. asymmetric, direct vs. indirect) (Jordano 2016a; Morales-Castilla et al. 2015). What is common to all definitions of interaction is that *at least* one of the species is affected by the presence of another, either positively or negatively (Morales-Castilla et al. 2015). Networks can be used to represent a variety of interaction types, including: *unipartite networks*, where each species can be linked to other species (these are typically used to represent food webs), *bipartite networks* where there are two pools of species, and all interactions occur between species in each pool, are typically used for pairwise interactions (e.g. hosts and parasites), and *k-partite networks,* which serve as a way to expand to more than two discrete sets of interacting species (e.g. some parasitoid webs, seed dispersal networks, and pollination networks) (Pocock, Evans, and Memmott 2012).

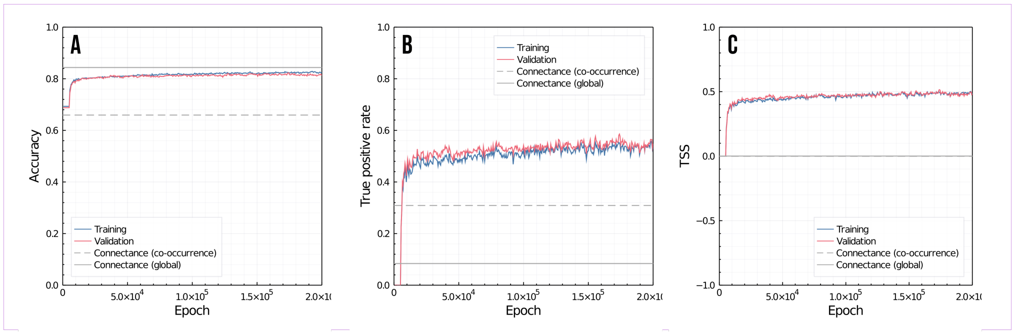

Figure 4 Example validation plots from the proof-of-concept. (A) Accuracy for the neural network model on the training set (blue) and validation set (red), and the null model accuracy for both global connectance (solid gray) and cooccuring connectance (dashed gray). (B) True-positive rate for the neural network model on the training set (blue) and validation set (red), and null model true-positive rate for both global connectance (solid gray) and cooccuring connectance (dashed gray) (C) True-Skill Statistic (TSS) for the neural network model on the training set (blue) and validation set (red), and null model true-positive rate for both global connectance and cooccuring connectance (both gray lines at 0).

3.2.2 What about interaction* strength*? Species interaction networks can also be used as a means to quantify and understand *interaction strength*. Interaction strength, unlike the qualitative presence or absence of an interaction, is a continuous measurement which attempts to quantify the effect of one species on another. Interaction strength can generally be divided into two main categories (as suggested by Berlow et al. (2004)): 1) the strength of an interaction between individuals of each species, or 2) the effect that changes in one species population has on the dynamics of the other species. It can be measured as the effect over a period of time (in the units of biomass or energy flux (Barnes et al. 2018; Brown et al. 2004)) or the relative importance of one species on another (Heleno et al. 2014; Berlow et al. 2004; Wootton and Emmerson 2005). One recurring observation is that networks are often composed of many weak interactions and few strong interactions (Berlow et al. 2004). The distribution of interaction strength within a network effects its stability (Neutel 2002; Ruiter, Neutel, and Moore 1995) and functioning (Duffy 2002; Montoya, Rodríguez, and Hawkins 2003), and serves to benefit multispecies models (Wootton and Emmerson 2005).

3.2.3 Why predict networks and interactions at the same time? Ecological networks are quite sparse (MacDonald, Banville, and Poisot 2020)—composed of a set of interactions, but also a larger set of non-interactions. If we aim to predict the structure of networks from the "bottom-up"— by considering each pairwise combination of S different species—we are left with S^2 interaction values to estimate. Instead, we can use our existing understanding of the mechanisms that structure ecological networks to whittle down the set of feasible adjacency matrices, thereby reducing the amount of information we must predict, and making the problem of predicting interactions less daunting. The processes that structure ecological networks do not only occur at the scale of interactions—there are also processes at the network level which limit what interactions are possible. The realized structure of a network is the synthesis of the interactions forming the basis for network structure, and the network structure refining the possible interactions—"Part makes whole, and whole makes part" (Levins and Lewontin 1987).

3.2.4 What network properties should we use to inform our predictions of interactions? There are many dimensions of network structure (Delmas et al. 2018), yet there are two reasons to begin with a single property, connectance (the ratio of actual edges to possible edges in the network). First, connectance is ecologically informative—it relates to resilience to invasion (Baiser, Russell, and Lockwood 2010; Smith-Ramesh, Moore, and Schmitz 2016), can increase robustness to extinction in food webs (J. Dunne, Williams, and Martinez 2002), while decreasing it in mutualistic networks (Vieira and Almeida-Neto 2015), and connectance relates to network stability (Landi et al. 2018). Second, most (if not all) network properties co-vary with connectance (Poisot and Gravel 2014; J. A. Dunne, Williams, and Martinez 2002). We have models to estimate species richness over space (Jenkins, Pimm, and Joppa 2013), and because we can predict connectance from species richness, (MacDonald, Banville, and Poisot 2020), we can then derive distributions of network properties from estimates of richness alone. Therefore we suggest that predicting the value of network connectance across space (and eventually time) is most likely to be the most practical to formulate at the moment.

3.2.5 How do we predict how species that we have never observed together will interact? A neutral approach would assume the probability of an interaction is the same as the likelihood of co-occurrence (Poisot, Stouffer, and Gravel 2015; Pichler et al. 2020), and that the effect of abundances and traits would have no effect (Canard et al. 2012). However, functional-trait based proxies could enable better predictions of ecological interactions. Selection on functional traits could cause interactions to be conserved at some evolutionary scales, and therefore predictions of interaction could be informed by phylogenetic analyses (Davies 2021; Elmasri et al. 2020; Gómez, Verdú, and Perfectti 2010). Phylogenetic matching in bipartite networks is consistent across scales (Poisot and Stouffer 2018), even in the absence of strong selective pressure (Coelho, Rodrigues, and Rangel 2017).

A separate family of methods are based on network embedding (as in the proof-of-concept). A network embedding projects each node of the network into a lower-dimensional latent space. This enables us to represent the structure of a network, which previously required the S^2 dimensions of an adjacency matrix, with a smaller number of dimensions. The position of each node in this lower dimensional space is then treated as a latent measurement corresponding to the role of that species in the network (Becker et al. 2020). Species close together in the latent space should interact with similar set of species (Rossberg et al. 2006; Rohr et al. 2010). However, these models are sensitive to sampling biases as they are limited to species for which there is already interaction data (Becker et al. 2020), and as a result a methodological breakthough is needed to extend these models to species for which there is little or no interaction data.

3.2.6 How do we determine what interaction networks are feasible? For several decades, ecologists have aimed to understand how networks of many interacting species persist through time. The diversity-stability paradox, first explored by May (1974), shows that under a neutral set of assumptions ecological networks should become decreasingly stable as the number of species increases. Yet, in the natural world we observe networks of interactions that consist of far more species than May's model predicts (Albouy et al. 2019). As a result, understanding what aspects of the neutral assumptions of May's model are incorrect has branched many investigations into the relationship between ecological network structure and persistence (Allesina and Tang 2012). These assumptions can be split into dynamical assumptions and topological assumptions. Topologically, we know that ecological networks are not structured randomly. Some properties, like the aforementioned connectance, are highly predictable (MacDonald, Banville, and Poisot 2020). Generative models of food-webs (based on network embeddings) fit empirical networks more effectively than random models (Allesina, Alonso, and Pascual 2008). These models have long used allometry as a single-dimensional niche space—naturally we want to extend this to traits in general. The second approach stability is through *dynamics*. Early models of community dynamics rely on the assumption of linear interaction effects, but in recent years models of bioenergetic community dynamics have shown promise in basing our understanding of energy flow in food-webs in the understood relationship between allometry and metabolism (Delmas et al. 2017). An additional consideration is the multidimensional nature of "stability" and "feasibility" (e.g resilience to environmental change vs extinctions) (Domínguez-García, Dakos, and

Kéfi 2019) and how different disturbances propagate across levels of biological organization (Kéfi et al. 2019; Gravel, Massol, and Leibold 2016).

3.2.7 How are interaction strengths actually estimated? In some contexts, interaction strength can be estimated via functional foraging (Portalier et al. 2019), where the primary basis for inferring interaction is foraging behavior like searching, capture and handling times. In food-webs, metabolic based models use body mass, metabolic demands, and energy loss to infer energy fluxes between organisms (Yodzis and Innes 1992; Berlow et al. 2009). Food-web energetics models can be incorporated at various resolutions for a specific network, ranging from individual-based data to more lumped data at the species level or trophic group, depending on data availability (Barnes et al. 2018; Berlow et al. 2009).

3.2.8 What taxonomic scales are suitable for the prediction of species interactions? If we use different trait-based proxies to predict potential interactions between species. The choice of such proxies should be theoretically linked to the taxonomic and spatial scale we are using in our prediction (Wiens 1989). At some scales we can use morphological traits of co-occurring species to assess the probability of interaction between them (Bartomeus et al. 2016). On broader taxonomic scales we can infer interaction probability through the phylogenetic distance, assuming that functional traits themselves are conserved (Gómez, Verdú, and Perfectti 2010). In this case, we can think of the probability that one species will interact with another as the distance between them in niche-space (Desjardins-Proulx et al. 2017), and this can be modeled by simulating neutral expectations of trait variation on phylogenetic tree (Davies 2021). At the narrowest scales, we may be interested in predicting behavioral traits like foraging behavior (Bartomeus et al. 2016), and at this scale we may need to consider abundance's effect on probability of an encounter (Wells and O'Hara 2013).

3.2.9 What about indirect and higher-order interactions? Although network ecology often assumes that interactions go strictly from one node to the other, the web of life is made up of a variety of interactions. Indirect interactions—either higher-order interactions between species, or interaction strengths that themselves interact — have gained interest in recent years (Golubski et al. 2016; Golubski and Abrams 2011). One mathematical tool to describe these situations is hypergraphs: hypergraphs are the generalization of a graph, allowing a broad yet manageable approach to complex interactions (Carletti, Fanelli, and Nicoletti 2020), allowing for particular interactions to occur beyond a pair of nodes. An additional degree of complexity is introduced by multi-layer networks (Hutchinson et al. 2019). Multi-layer networks include edges across "variants" of the networks (timepoints, locations, or environments). These can be particularly useful to account for the metacommunity structure (Gross et al. 2020), or to understand how dispersal can inform conservation action (Albert et al. 2017). Ecological networks are intrinsically multi-layered (Pilosof et al. 2017). However, *prima facie*, increasing the dimensionality of the object we need to predict (the multiple layers rather than a single network) makes the problem more complicated. Yet, mutli-layer approaches improve prediction in social networks (Jalili et al. 2017; Najari et al. 2019; Yasami and Safaei 2018), and they may prove useful going forward.

3.3. Space Although networks were initially used to describe the interactions *within* a community, interest in the last decade has shifted towards understanding their structure and variation over space (Trøjelsgaard and Olesen 2016; Baiser et al. 2019), and has established network ecology as an important emerging component of biogeography and macroecology.

3.3.1 How much do networks vary over space? Networks can vary across space either in their structural properties (e.g. connectance or degree distribution) or in their composition (identity of nodes and edges). Interestingly, variation in the structural properties of ecological networks primarily responds to changes in the size of the network. The number of links in ecological networks scales with the number of species (MacDonald, Banville, and Poisot 2020; Brose et al. 2004), and connectance and size drive the rest of network structure (Poisot and Gravel 2014; J. A. Dunne, Williams, and Martinez 2002; Riede et al. 2010). Species turnover in space results in changes in the composition of ecological networks. But, this is not the only reason network composition varies (Poisot, Stouffer, and Gravel 2015). Intraspecific variation can result in interaction turnovers without changes in species composition (Bolnick et al. 2011). Similarly, changes in species abundances can lead to variation in interaction strengths (Canard et al. 2014; Vázquez et al. 2007). Variation in the abiotic environment and indirect interactions (Golubski et al. 2016) could modify the occurrence and strength of individual interactions. Despite this, empirical networks tend to share a common backbone (Mora et al. 2018) and functional composition (Dehling et al. 2020) across space.

3.3.2 How do we predict what the species pool at a particular location is? As the species pool forms the basis for network structure, predicting which species are present at a particular location is essential to predict networks across space. Species distribution models (SDMs) are increasingly ubiquitous in macroecology— these models predict the range of a species based on known occurrences and environmental conditions, such as climate and land cover (Guisan and Thuiller 2005; Elith et al. 2006). Including interactions or co-occurrences in SDMs generally improves predictive performance (Wisz et al. 2013). Several approaches exist to combine multiple SDMs: community assemblage at a particular site can be predicted either by combining independent single-species SDMs (stacked-SDMs, SSDMs) or by directly modelling the entire species assemblage and multiple species at the same time (joint SDMs, JSDMs) (Norberg et al. 2019). Building on the JSDM framework, hierarchical modeling of species communities (Ovaskainen et al. 2017) has the advantage of capturing processes that structure communities. Spatially Explicit Species Assemblage Modeling (SESAM) constrains SDM predictions using macro-ecological models (Guisan and Rahbek 2011) — for example, variation in species richness across space can constrain assemblage predictions (D'Amen et al. 2015).

The next step is to constrain distribution predictions using network properties. This builds on previous calls to adopt a probabilistic view: a probabilistic species pool (Karger et al. 2016), and probabilistic interactions through Bayesian networks (Staniczenko et al. 2017). Blanchet, Cazelles, and Gravel (2020) argue that the probabilistic view avoids confusion between interactions and co-occurrences, but that it requires prior knowledge of interactions. This could potentially be solved through our framework of predicting networks first, interactions next, and finally the realized species pool.

3.3.3 How do we combine spatial and network predictions? In order to predict networks across space, we need to combine multiple models—one which predicts what the species pool will be at a given location, and one to predict what interaction networks composed from this species pool are likely to be (see fig. 2). Both of these models contain uncertainty, and when we combine them the uncertainty from each model should be propagated into the combined model. The Bayesian paradigm provides a convenient solution to this—if we have a chain of models where each model feeds into the next, we can sample from the posterior of the input models. A different approach is *ensemble modeling* which combines the predictions made be several models, where each model is predicting the same thing (Parker 2013). Error propagation, an important step in building any ecological model, describes the effect of the uncertainty of input variables on the uncertainty of output variables (Draper 1995; Parysow, Gertner, and Westervelt 2000). Benke et al. (2018) identifies two broad approaches to model error propagation: analytically using differential equations or stochastically using Monte-Carlo simulation methods.

Errors induced by the spatial or temporal extrapolation of data also need to be taken into account when estimating the uncertainty of a model's output (Peters and Herrick 2004).

3.4. Time

3.4.1 Why should we forecast species interaction networks? Forecasting species interactions are critical for informing ecosystem management (Harvey et al. 2017) and systematic conservation prioritization (Pollock et al. 2020), and for anticipating extinctions and their consequences (McDonald-Madden et al. 2016; McWilliams et al. 2019). Ecological interactions shape species distributions at both local and broad spatial scales, and including interactions in SDM models typically improves predictive performance (M. B. Araújo and Luoto 2007; Wisz et al. 2013; Pigot and Tobias 2013). However, these tend to rely on approaches involving estimating pairwise dependencies based on cooccurrence, using surrogates for biotic-interaction gradients, and hybridizing SDMs with dynamic models (Wisz et al. 2013). Most existing models to predict the future distribution of species ignore interactions (Urban et al. 2016). Changes in species ranges and phenology will inevitably create spatiotemporal mismatches and affect encounter rates between species (Gilman et al. 2010), which will further shift the distribution of species across space. New interactions will also appear between species that are not currently co-occuring (Gilman et al. 2010). Only by forecasting how species will interact can we hope to have an accurate portrait of how biodiversity will be distributed under the future climate.

Forecasting how climate change will alter biodiversity is also crucial for maximizing conservation outcomes. Improving SDMs through interactions is crucial for conservation, as nearly 30% of models in SDM studies are used to assess population declines or landscape ability to support populations (M. B. Araújo et al. 2019). Reliable predictions about how ecological networks will change over time will give us critical information that could be communicated to decision-makers and the scientific community about what are future environmental risks awaiting and how to mitigate them (Kindsvater et al. 2018). Not only this, but how biodiversity is structured influence the functioning of the whole ecosystem, community stability and persistence (Thompson et al. 2012; Stouffer and Bascompte 2010). Will climate change impact the distribution of network properties (e.g. connectance)? If so, which regions or species groups need special conservation efforts? These overarching questions are yet to be answered (but see Albouy et al. 2013; Kortsch et al. 2015; Hattab et al. 2016). We believe that the path toward forecasting ecological networks provides useful guidelines to ultimately better predict how climate change will affect the different dimensions of biodiversity and ecosystem functioning.

3.4.2 How do we turn a predictive model into a forecasting model? On some scales, empirical time-series encode enough information about ecological processes for machine-learning approaches to make accurate forecasts. However, there is an intrinsic limit to the predictability of ecological time-series (Pennekamp et al. 2019). A forecast inherently has a *resolution limit* in space, time, and organization. For example, one could never hope to predict the precise abundance of every species on Earth on every day hundreds of years into the future. There is often a trade-off between the resolution and horizon of forecast, *e.g.*, a lower resolution forecast, like primary production will be at a maximum in the summer, is likely to be true much further into the future than a higher resolution forecast. If we want to forecast the structure of ecological networks beyond the forecasting horizon of time-series based methods, we need forecasts of our predictive model's inputs— a forecast of the distribution of both environmental conditions and the potential species pool across space (fig. 3).

3.4.3 How can we validate a forecasting model? Often the purpose of building a forecasting model is to inform *present* action (Dietze et al. 2018). Yet, the nature of forecasting—trying to predict the future—is that you can only know if a forecast is “right” once it is too late to change it. If we want to maximize the chance that reality falls within a forecasting model’s predictions, there are two directions to approach this problem: the first is to extend model validation techniques to a forecasting context, and the second is to attempt to maximize the amount of uncertainty in the forecast without compromising its resolution. Crossvalidation (see *How do we validate a predictive model?*) can be used to test the efficacy of a forecasting model. Given a time-series of N observations, a model can iteratively be trained on the first n time-points of data, and the forecasting model’s accuracy can be evaluated on the remaining time-points it hasn’t “seen” (Bishop 2006). This enables us to understand both how much temporal data is required for a model to be robust, and also enables us to explore the *forecasting horizon* of a process. Further, this approach can also be applied in the opposite temporal direction— if we have reliable data from the past, “hindcasting” can also be used to test a forecast’s robustness.

However, these methods inevitably bump into a hard-limitation on what is feasible for a forecasting model. The future is uncertain. Any empirical time-series we use to validate a model was collected in past conditions that may not persist into the future. Any system we wish to forecast will undergo only one of many possible scenarios, yet we can only observe the realized outcome of the system under the scenario that actually unfolds. It is therefore impossible to assess the quality of a forecasting model in scenarios that remain hypothetical. If the goal is to maximize the probability that reality will fall within the forecast’s estimates, forecasts should incorporate as much uncertainty about the future scenario as possible—one way to do this is ensemble modeling (Parker 2013). However, as we increase the amount of uncertainty we incorporate into a forecasting model, the resolution of the forecast’s predictions could shrink (Lei and Whitaker 2017), and therefore the modeler should be mindful of the trade-off between resolution and accuracy when developing any forecast.

4

Conclusion: why should we predict species interaction networks?

Because we almost can, and because we definitely should. A better understanding of species interactions, and the networks they form, would help unify the fields of community, network, and spatial ecology; improve the quantification of the functional relationships between species (Dehling and Stouffer 2018; O’Connor et al. 2020); re-evaluate metacommunities in light of network structure (Guzman et al. 2019); and enable a new line of research into the biogeography of species interactions (Massol et al. 2017; Braga et al. 2019) which incorporates a synthesis of both Eltonian and Grinnellian niche (Gravel et al. 2019). Further, the ability to reliably predict and forecast species interactions would inform conservation efforts for protecting species, communities, and ecosystems. Integration of species interactions into the assessment of vulnerability to climate change is a needed methodological advance (Foden and Young 2016). International panels draw on models to establish scientific consensus (M. B. Araújo et al. 2019), and they can be improved through more effective prediction of species distributions and interactions (Syfert et al. 2014). Further, recent studies argue for a shift in focus from species to interaction networks for biodiversity conservation to better understand ecosystem processes (Harvey et al. 2017).

We should invest in network prediction because the right conditions to do so reliably and rapidly, including forecasting, are beginning to emerge. Given the possible benefits to a variety of ecological disciplines that would result from an increased ability to predict ecological networks and their structure, we feel strongly that the research agenda we outline here should be picked up by the community. Although novel technologies are bringing massive amounts of data to some parts of ecology (primarily environmental DNA and remote sensing, but now more commonly image analysis and bioacoustics), it is even more important to be intentional about *reconciling* data. This involves not only the work of understanding the processes encoded within data, but also the groundwork of developing pipelines to bridge the ever-expanding gap between "high-throughput" and "low-throughput" sampling methods. An overall increase in the volume of data will not result in an increase of our predictive capacity as long as this data increase is limited to specific aspects of the problem. In the areas we highlight in fig. 2, many data steps are still limiting: documenting empirical interactions is natural history work that doesn't lend itself to systematic automation; expert knowledge is by design a social process that may be slightly accelerated by text mining and natural language processing (but is not yet, or not routinely or at scale). These limitations are affecting our ability to reconstruct networks.

But the tools to which we feed these data, incomplete as they may be, are gradually getting better; that is, they can do predictions faster, they handle uncertainty and propagate it well, and they can accomodate data volumes that are lower than we may expect (Pichler et al. 2020). It is clear attempting to predict the structure of ecological networks at any scale is a methodological and ecological challenge; yet it will result in qualitative changes in our understanding of complex adaptive systems, as well as changes to our ability to leverage information about network structure for conservation decision. It is perhaps even more important to forecast the structure of ecological networks because it is commonly neglected as a facet of biodiversity that can (and should) be managed. In fact, none of the Aichi targets mention biostructure or its protection, despite this being recognized as an important task (McCann 2007), either implicitely or explicitely. Being able to generate reliable datasets on networks in space or time will make this information more actionable.

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References

Aguiar, Marcus A. M. de, Erica A. Newman, Mathias M. Pires, Justin D. Yeakel, Carl Boettiger, Laura A. Burkle, Dominique Gravel, et al. 2019. "Revealing Biases in the Sampling of Ecological Interaction Networks." *PeerJ* 7: e7566. `https://doi.org/10.7717/peerj.7566`.

Albert, Cécile H., Bronwyn Rayfield, Maria Dumitru, and Andrew Gonzalez. 2017. "Applying Network Theory to Prioritize Multispecies Habitat Networks That Are Robust to Climate and Land-Use Change: Prioritizing a Network for Biodiversity." *Conservation Biology* 31 (6): 1383–96. `https://doi.org/10.1111/cobi.12943`.

Albouy, Camille, Philippe Archambault, Ward Appeltans, Miguel B. Araújo, David Beauchesne, Kevin Cazelles, Alyssa R. Cirtwill, et al. 2019. "The Marine Fish Food Web Is Globally Connected." *Nature Ecology & Evolution* 3 (8): 1153–61. `https://doi.org/10.1038/s41559-019-0950-y`.

Albouy, Camille, François Guilhaumon, Fabien Leprieur, Frida Ben Rais Lasram, Samuel Somot, Roland Aznar, Laure Velez, François Le Loc'h, and David Mouillot. 2013. "Projected Climate Change and the Changing Biogeography of Coastal Mediterranean Fishes." Edited by Peter Pearman. *Journal of Biogeography* 40 (3): 534–47. `https://doi.org/10.1111/jbi.12013`.

Albrecht, Jörg, Alice Classen, Maximilian G. R. Vollstädt, Antonia Mayr, Neduvoto P. Mollel, David Schellenberger Costa, Hamadi I. Dulle, et al. 2018. "Plant and Animal Functional Diversity Drive Mutualistic Network Assembly Across an Elevational Gradient." *Nature Communications* 9 (1): 3177. https://doi.org/10.1038/s41467-018-05610-w.

Allesina, Stefano, David Alonso, and Mercedes Pascual. 2008. "A General Model for Food Web Structure." *Science* 320 (5876): 658–61. https://doi.org/10.1126/science.1156269.

Allesina, Stefano, and Si Tang. 2012. "Stability Criteria for Complex Ecosystems." *Nature* 483 (7388): 205–8. https://doi.org/10.1038/nature10832.

Allouche, Omri, Asaf Tsoar, and Ronen Kadmon. 2006. "Assessing the Accuracy of Species Distribution Models: Prevalence, Kappa and the True Skill Statistic (TSS)." *Journal of Applied Ecology* 43 (6): 1223–32. https://doi.org/10.1111/j.1365-2664.2006.01214.x.

Antoniou, Antreas, Amos Storkey, and Harrison Edwards. 2018. "Data Augmentation Generative Adversarial Networks." *arXiv:1711.04340 [cs, Stat]*. http://arxiv.org/abs/1711.04340.

Araújo, Márcio S., Paulo R. Guimarães, Richard Svanbäck, Aluisio Pinheiro, Paulo Guimarães, Sérgio F. dos Reis, and Daniel I. Bolnick. 2008. "Network Analysis Reveals Contrasting Effects of Intraspecific Competition on Individual Vs. Population Diets." *Ecology* 89 (7): 1981–93. https://doi.org/10.1890/07-0630.1.

Araújo, Miguel B., Robert P. Anderson, A. Márcia Barbosa, Colin M. Beale, Carsten F. Dormann, Regan Early, Raquel A. Garcia, et al. 2019. "Standards for Distribution Models in Biodiversity Assessments." *Science Advances* 5 (1): eaat4858. https://doi.org/10.1126/sciadv.aat4858.

Araújo, Miguel B., and Miska Luoto. 2007. "The Importance of Biotic Interactions for Modelling Species Distributions Under Climate Change." *Global Ecology and Biogeography* 16 (6): 743–53. https://doi.org/10.1111/j.1466-8238.2007.00359.x.

Arlot, Sylvain, and Alain Celisse. 2010. "A Survey of Cross-Validation Procedures for Model Selection." *Statistics Surveys* 4: 40–79. https://doi.org/10.1214/09-SS054.

Baiser, Benjamin, Dominique Gravel, Alyssa R. Cirtwill, Jennifer A. Dunne, Ashkaan K. Fahimipour, Luis J. Gilarranz, Joshua A. Grochow, et al. 2019. "Ecogeographical Rules and the Macroecology of Food Webs." *Global Ecology and Biogeography* 28 (9): 1204–18. https://doi.org/10.1111/geb.12925.

Baiser, Benjamin, Gareth J. Russell, and Julie L. Lockwood. 2010. "Connectance Determines Invasion Success via Trophic Interactions in Model Food Webs." *Oikos* 119 (12): 1970–76. https://doi.org/10.1111/j.1600-0706.2010.18557.x.

Barnes, Andrew D., Malte Jochum, Jonathan S. Lefcheck, Nico Eisenhauer, Christoph Scherber, Mary I. O'Connor, Peter de Ruiter, and Ulrich Brose. 2018. "Energy Flux: The Link Between Multitrophic Biodiversity and Ecosystem Functioning." *Trends in Ecology & Evolution* 33 (3): 186–97. https://doi.org/10.1016/j.tree.2017.12.007.

Bartomeus, Ignasi, Dominique Gravel, Jason M. Tylianakis, Marcelo A. Aizen, Ian A. Dickie, and Maud Bernard-Verdier. 2016. "A Common Framework for Identifying Linkage Rules Across Different Types of Interactions." *Functional Ecology* 30 (12): 1894–1903. https://doi.org/10.1111/1365-2435.12666.

Becker, Daniel J., Gregory F. Albery, Anna R. Sjodin, Timothée Poisot, Tad A. Dallas, Evan A. Eskew, Maxwell J. Farrell, et al. 2020. "Predicting Wildlife Hosts of Betacoronaviruses for SARS-CoV-2 Sampling Prioritization." *bioRxiv*, 2020.05.22.111344. https://doi.org/10.1101/2020.05.22.111344.

Benke, K. K., S. Norng, N. J. Robinson, L. R. Benke, and T. J. Peterson. 2018. "Error Propagation in Computer Models: Analytic Approaches, Advantages, Disadvantages and Constraints." *Stochastic Environmental Research and Risk Assessment* 32 (10): 2971–85. https://doi.org/10.1007/s00477-018-1555-8.

Bennett, Alison E., Darren M. Evans, and Jeff R. Powell. 2019. "Potentials and Pitfalls in the Analysis of Bipartite Networks to Understand Plantmicrobe Interactions in Changing Environments." *Functional Ecology* 33 (1): 107–17. https://doi.org/10.1111/1365-2435.13223.

Berlow, Eric L., Jennifer Dunne, Neo D. Martinez, Philip B. Stark, Richard J. Williams, and Ulrich Brose. 2009. "Simple Prediction of Interaction Strengths in Complex Food Webs." *Proceedings of the National Academy of Sciences* 106 (1): 187–91. https://doi.org/10.1073/pnas.0806823106.

Berlow, Eric L., Anje-Margiet Neutel, Joel E. Cohen, Peter C. de Ruiter, Bo Ebenman, Mark Emmerson, Jeremy W. Fox, et al. 2004. "Interaction Strengths in Food Webs: Issues and Opportunities." *Journal of Animal Ecology* 73 (3): 585–98. https://doi.org/10.1111/j.0021-8790.2004.00833.x.

Bezanson, J., A. Edelman, S. Karpinski, and V. Shah. 2017. "Julia: A Fresh Approach to Numerical Computing." *SIAM Review* 59 (1): 65–98. https://doi.org/10.1137/141000671.

Bishop, Christopher M. 2006. *Pattern Recognition and Machine Learning*. Information Science and Statistics. New York: Springer.

Blanchet, F. Guillaume, Kevin Cazelles, and Dominique Gravel. 2020. "Co-Occurrence Is Not Evidence of Ecological Interactions." *Ecology Letters* 23 (7): 1050–63. https://doi.org/10.1111/ele.13525.

Bohan, David A., Geoffrey Caron-Lormier, Stephen Muggleton, Alan Raybould, and Alireza Tamaddoni-Nezhad. 2011. "Automated Discovery of Food Webs from Ecological Data Using Logic-Based Machine Learning." *PLOS ONE* 6 (12): e29028. https://doi.org/10.1371/journal.pone.0029028.

Bohan, David A., Corinne Vacher, Alireza Tamaddoni-Nezhad, Alan Raybould, Alex J. Dumbrell, and Guy Woodward. 2017. "Next-Generation Global Biomonitoring: Large-Scale, Automated Reconstruction of Ecological Networks." *Trends in Ecology & Evolution* 32 (7): 477–87. https://doi.org/10.1016/j.tree.2017.03.001.

Bolnick, Daniel I., Priyanga Amarasekare, Márcio S. Araújo, Reinhard Bürger, Jonathan M. Levine, Mark Novak, Volker H. W. Rudolf, Sebastian J. Schreiber, Mark C. Urban, and David A. Vasseur. 2011. "Why Intraspecific Trait Variation Matters in Community Ecology." *Trends in Ecology & Evolution* 26 (4): 183–92. https://doi.org/10.1016/j.tree.2011.01.009.

Braga, J, Laura J. Pollock, C. Barros, J. Montoya, Dominique Gravel, Luigi Maiorano, Gentile Francesco Ficetola, Stéphane Dray, and Wilfried Thuiller. 2019. "Spatial Analyses of Multi-Trophic Terrestrial Vertebrate Assemblages in Europe." *Global Ecology and Biogeography* 28 (11): 1636–48.

Brose, Ulrich, Annette Ostling, Kateri Harrison, and Neo D. Martinez. 2004. "Unified Spatial Scaling of Species and Their Trophic Interactions." *Nature* 428 (6979): 167–71. https://doi.org/10.1038/nature02297.

Brown, James H., James F. Gillooly, Andrew P. Allen, Van M. Savage, and Geoffrey B. West. 2004. "Toward a Metabolic Theory of Ecology." *Ecology* 85 (7): 1771–89. https://doi.org/10.1890/03-9000.

Burkle, L. A., and R. Alarcon. 2011. "The Future of Plant-Pollinator Diversity: Understanding Interaction Networks Across Time, Space, and Global Change." *American Journal of Botany* 98 (3): 528–38. https://doi.org/10.3732/ajb.1000391.

Burkle, L. A., J. C. Marlin, and T. M. Knight. 2013. "Plant-Pollinator Interactions over 120 Years: Loss of Species, Co-Occurrence, and Function." *Science* 339 (6127): 1611–15. https://doi.org/10.1126/science.1232728.

Canard, Elsa, N. Mouquet, D. Mouillot, M. Stanko, D. Miklisova, and D. Gravel. 2014. "Empirical Evaluation of Neutral Interactions in Host-Parasite Networks." *The American Naturalist* 183 (4): 468–79. https://doi.org/10.1086/675363.

Canard, Elsa, Nicolas Mouquet, Lucile Marescot, Kevin J. Gaston, Dominique Gravel, and David Mouillot. 2012. "Emergence of Structural Patterns in Neutral Trophic Networks." *PLOS ONE* 7 (8): e38295. https://doi.org/10.1371/journal.pone.0038295.

Carletti, Timoteo, Duccio Fanelli, and Sara Nicoletti. 2020. "Dynamical Systems on Hypergraphs." *Journal of Physics: Complexity* 1 (3): 035006. https://doi.org/10.1088/2632-072X/aba8e1.

Carpenter, Stephen R. 2002. "Ecological Futures: Building an Ecology of the Long Now." *Ecology* 83 (8): 2069–83.

Chawla, Nitesh V. 2010. "Data Mining for Imbalanced Datasets: An Overview." In *Data Mining and Knowledge Discovery Handbook*, edited by Oded Maimon and Lior Rokach, 875–86. Boston, MA: Springer US. https://doi.org/10.1007/978-0-387-09823-4_45.

Christin, Sylvain, Éric Hervet, and Nicolas Lecomte. 2019. "Applications for Deep Learning in Ecology." *Methods in Ecology and Evolution* 10 (10): 1632–44. https://doi.org/10.1111/2041-210X.13256.

Chuang, Kangway V., and Michael J. Keiser. 2018. "Adversarial Controls for Scientific Machine Learning." *Acs Chemical Biology* 13 (10): 2819–21. https://doi.org/10.1021/acschembio.8b00881.

Coelho, Marco Túlio Pacheco, João Fabrício Mota Rodrigues, and Thiago F. Rangel. 2017. "Neutral Biogeography of Phylogenetically Structured Interaction Networks." *Ecography* 40 (12): 1467–74. https://doi.org/10.1111/ecog.02780.

Creer, Simon, Kristy Deiner, Serita Frey, Dorota Porazinska, Pierre Taberlet, W. Kelley Thomas, Caitlin Potter, and Holly M. Bik. 2016. "The Ecologist's Field Guide to Sequence-Based Identification of Biodiversity." *Methods in Ecology and Evolution* 7 (9): 1008–18. https://doi.org/10.1111/2041-210X.12574.

Cutler, D. Richard, Thomas C. Edwards, Karen H. Beard, Adele Cutler, and Kyle T. Hess. 2007. "Random Forests for Classification in Ecology." *Ecology* 88 (11): 2783–92. https://doi.org/10.1890/07-0539.1.

D'Amen, Manuela, Anne Dubuis, Rui F. Fernandes, Julien Pottier, Loïc Pellissier, and Antoine Guisan. 2015. "Using Species Richness and Functional Traits Predictions to Constrain Assemblage Predictions from Stacked Species Distribution Models." *Journal of Biogeography* 42 (7): 1255–66. https://doi.org/10.1111/jbi.12485.

Davies, T. Jonathan. 2021. "Ecophylogenetics Redux." *Ecology Letters* n/a. https://doi.org/10.1111/ele.13682.

Dehling, D. Matthias, Guadalupe Peralta, Irene M. A. Bender, Pedro G. Blendinger, Katrin Böhning-Gaese, Marcia C. Muñoz, Eike Lena Neuschulz, et al. 2020. "Similar Composition of Functional Roles in Andean Seed-Dispersal Networks, Despite High Species and Interaction Turnover." *Ecology* 101 (7). https://doi.org/10.1002/ecy.3028.

Dehling, D. Matthias, and Daniel B. Stouffer. 2018. "Bringing the Eltonian Niche into Functional Diversity." *Oikos* 127 (12): 1711–23. https://doi.org/10.1111/oik.05415.

Delmas, Eva, Mathilde Besson, Marie-Hélène Brice, Laura A. Burkle, Giulio V. Dalla Riva, Marie-Josée Fortin, Dominique Gravel, et al. 2018. "Analysing Ecological Networks of Species Interactions." *Biological Reviews*, 112540. https://doi.org/10.1111/brv.12433.

Delmas, Eva, Ulrich Brose, Dominique Gravel, Daniel B. Stouffer, and Timothée Poisot. 2017. "Simulations of Biomass Dynamics in Community Food Webs." *Methods in Ecology and Evolution* 8 (7): 881–86. https://doi.org/10.1111/2041-210X.12713.

Desjardins-Proulx, Philippe, Idaline Laigle, Timothée Poisot, and Dominique Gravel. 2017. "Ecological Interactions and the Netflix Problem." *PeerJ* 5: e3644. https://doi.org/10.7717/peerj.3644.

Desjardins-Proulx, Philippe, Timothée Poisot, and Dominique Gravel. 2019. "Artificial Intelligence for Ecological and Evolutionary Synthesis." *Frontiers in Ecology and Evolution* 7. https://doi.org/10.3389/fevo.2019.00402.

Dickinson, Janis L., Benjamin Zuckerberg, and David N. Bonter. 2010. "Citizen Science as an Ecological Research Tool: Challenges and Benefits." *Annual Review of Ecology, Evolution, and Systematics* 41 (1): 149–72. https://doi.org/10.1146/annurev-ecolsys-102209-144636.

Dietze, Michael C., Andrew Fox, Lindsay M. Beck-Johnson, Julio L. Betancourt, Mevin B. Hooten, Catherine S. Jarnevich, Timothy H. Keitt, et al. 2018. "Iterative Near-Term Ecological Forecasting: Needs, Opportunities, and Challenges." *Proceedings of the National Academy of Sciences* 115 (7): 1424–32. https://doi.org/10.1073/pnas.1710231115.

Domínguez-García, Virginia, Vasilis Dakos, and Sonia Kéfi. 2019. "Unveiling Dimensions of Stability in Complex Ecological Networks." *Proceedings of the National Academy of Sciences* 116 (51): 25714–20. https://doi.org/10.1073/pnas.1904470116.

Draper, D. 1995. "Assessment and Propagation of Model Uncertainty." *Journal of the Royal Statistical Society Series B-Statistical Methodology* 57 (1): 45–97. https://doi.org/10.1111/j.2517-6161.1995.tb02015.x.

Duffy, J. Emmett. 2002. "Biodiversity and Ecosystem Function: The Consumer Connection." *Oikos* 99 (2): 201–19. https://doi.org/10.1034/j.1600-0706.2002.990201.x.

Dunne, Jennifer. 2006. "The Network Structure of Food Webs." In *Ecological Networks: Linking Structure to Dynamics in Food Webs*, 27–86.

Dunne, Jennifer A., Richard J. Williams, and Neo D. Martinez. 2002. "Food-Web Structure and Network Theory: The Role of Connectance and Size." *Proceedings of the National Academy of Sciences* 99 (20): 12917–22. https://doi.org/10.1073/pnas.192407699.

Dunne, Jennifer, Richard J Williams, and Néo D Martinez. 2002. "Network Structure and Biodiversity Loss in Food Webs: Robustness Increases with Connectance." *Ecol. Lett.* 5 (4): 558–67.

Elith, Jane, Catherine H. Graham, Robert P. Anderson, Miroslav Dudík, Simon Ferrier, Antoine Guisan, Robert J. Hijmans, et al. 2006. "Novel Methods Improve Prediction of Species' Distributions from Occurrence Data." *Ecography* 29 (2): 129–51. https://doi.org/10.1111/j.2006.0906-7590.04596.x.

Elmasri, Mohamad, Maxwell J. Farrell, T. Jonathan Davies, and David A. Stephens. 2020. "A Hierarchical Bayesian Model for Predicting Ecological Interactions Using Scaled Evolutionary Relationships." *The Annals of Applied Statistics* 14 (1): 221–40. https://doi.org/10.1214/19-AOAS1296.

Evans, Matthew R., Ken J. Norris, and Tim G. Benton. 2012. "Predictive Ecology: Systems Approaches." *Philosophical Transactions of the Royal Society B: Biological Sciences* 367 (1586): 163–69. https://doi.org/10.1098/rstb.2011.0191.

Foden, Wendy B., and Bruce E. Young. 2016. *IUCN SSC Guidelines for Assessing Species' Vulnerability to Climate Change*. IUCN Cambridge, England and Gland, Switzerland.

Fontaine, Colin, Paulo R. Guimarães, Sonia Kéfi, Nicolas Loeuille, Jane Memmott, Wim H. van der Putten, Frank J. F. van Veen, and Elisa Thébault. 2011. "The Ecological and Evolutionary Implications of Merging Different Types of Networks." *Ecology Letters* 14 (11): 1170–81. https://doi.org/10.1111/j.1461-0248.2011.01688.x.

Gilman, Sarah E., Mark C. Urban, Joshua Tewksbury, George W. Gilchrist, and Robert D. Holt. 2010. "A Framework for Community Interactions Under Climate Change." *Trends in Ecology & Evolution* 25 (6): 325–31. https://doi.org/10.1016/j.tree.2010.03.002.

Golubski, Antonio J., and Peter A. Abrams. 2011. "Modifying Modifiers: What Happens When Interspecific Interactions Interact?" *Journal of Animal Ecology* 80 (5): 1097–1108. https://doi.org/10.1111/j.1365-2656.2011.01852.x.

Golubski, Antonio J., Erik E. Westlund, John Vandermeer, and Mercedes Pascual. 2016. "Ecological Networks over the Edge: Hypergraph Trait-Mediated Indirect Interaction (TMII) Structure." *Trends in Ecology & Evolution* 31 (5): 344–54. https://doi.org/10.1016/j.tree.2016.02.006.

Goodfellow, Ian, Yoshua Bengio, and Aaron Courville. 2016. *Deep Learning*. Adaptive Computation and Machine Learning. Cambridge, Massachusetts: The MIT Press.

Gómez, José M., Miguel Verdú, and Francisco Perfectti. 2010. "Ecological Interactions Are Evolutionarily Conserved Across the Entire Tree of Life." *Nature* 465 (7300): 918–21. https://doi.org/10.1038/nature09113.

Gravel, Dominique, Benjamin Baiser, Jennifer A. Dunne, Jens-Peter Kopelke, Neo D. Martinez, Tommi Nyman, Timothée Poisot, et al. 2019. "Bringing Elton and Grinnell Together: A Quantitative Framework to Represent the Biogeography of Ecological Interaction Networks." *Ecography* 42 (3): 401–15. https://doi.org/10.1111/ecog.04006.

Gravel, Dominique, François Massol, and Mathew A. Leibold. 2016. "Stability and Complexity in Model Meta-Ecosystems." *Nature Communications* 7 (1): 12457. https://doi.org/10.1038/ncomms12457.

Gravel, Dominique, Timothée Poisot, Camille Albouy, Laure Velez, and David Mouillot. 2013. "Inferring Food Web Structure from Predatorprey Body Size Relationships." *Methods in Ecology and Evolution* 4 (11): 1083–90. https://doi.org/10.1111/2041-210X.12103.

Gross, Thilo, Korinna T. Allhoff, Bernd Blasius, Ulrich Brose, Barbara Drossel, Ashkaan K. Fahimipour, Christian Guill, Justin D. Yeakel, and Fanqi Zeng. 2020. "Modern Models of Trophic Meta-Communities." *Philosophical Transactions of the Royal Society B: Biological Sciences* 375 (1814): 20190455. https://doi.org/10.1098/rstb.2019.0455.

Guimarães, Paulo R. 2020. "The Structure of Ecological Networks Across Levels of Organization." *Annual Review of Ecology, Evolution, and Systematics* 51 (1): 433–60. https://doi.org/10.1146/annurev-ecolsys-012220-120819.

Guisan, Antoine, and Carsten Rahbek. 2011. "SESAM a New Framework Integrating Macroecological and Species Distribution Models for Predicting Spatio-Temporal Patterns of Species Assemblages." *Journal of Biogeography* 38 (8): 1433–44. https://doi.org/10.1111/j.1365-2699.2011.02550.x.

Guisan, Antoine, and Wilfried Thuiller. 2005. “Predicting Species Distribution: Offering More Than Simple Habitat Models.” *Ecology Letters* 8 (9): 993–1009. `https://doi.org/10.1111/j.1461-0248.2005.00792.x`.

Guzman, Laura Melissa, Rachel M. Germain, Coreen Forbes, Samantha Straus, Mary I. O’Connor, Dominique Gravel, Diane S. Srivastava, and Patrick L. Thompson. 2019. “Towards a Multi-Trophic Extension of Metacommunity Ecology.” *Ecology Letters* 22 (1): 19–33. `https://doi.org/10.1111/ele.13162`.

Hadfield, Jarrod D., Boris R. Krasnov, Robert Poulin, and Shinichi Nakagawa. 2014. “A Tale of Two Phylogenies: Comparative Analyses of Ecological Interactions.” *The American Naturalist* 183 (2): 174–87. `https://doi.org/10.1086/674445`.

Harvey, Eric, Isabelle Gounand, Colette L. Ward, and Florian Altermatt. 2017. “Bridging Ecology and Conservation: From Ecological Networks to Ecosystem Function.” *Journal of Applied Ecology* 54 (2): 371–79. `https://doi.org/10.1111/1365-2664.12769`.

Hattab, Tarek, Fabien Leprieur, Frida Ben Rais Lasram, Dominique Gravel, François Le Loc’h, and Camille Albouy. 2016. “Forecasting Fine-Scale Changes in the Food-Web Structure of Coastal Marine Communities Under Climate Change.” *Ecography* 39 (12): 1227–37. `https://doi.org/10.1111/ecog.01937`.

Heleno, Ruben, Cristina Garcia, Pedro Jordano, Anna Traveset, José Maria Gómez, Nico Blüthgen, Jane Memmott, et al. 2014. “Ecological Networks: Delving into the Architecture of Biodiversity.” *Biology Letters* 10 (1). `https://doi.org/10.1098/rsbl.2013.1000`.

Hortal, Joaquín, Francesco de Bello, José Alexandre F. Diniz-Filho, Thomas M. Lewinsohn, Jorge M. Lobo, and Richard J. Ladle. 2015. “Seven Shortfalls That Beset Large-Scale Knowledge of Biodiversity.” *Annual Review of Ecology, Evolution, and Systematics* 46 (1): 523–49. `https://doi.org/10.1146/annurev-ecolsys-112414-054400`.

Hutchinson, Matthew C., Bernat Bramon Mora, Shai Pilosof, Allison K. Barner, Sonia Kéfi, Elisa Thébault, Pedro Jordano, and Daniel B. Stouffer. 2019. “Seeing the Forest for the Trees: Putting Multilayer Networks to Work for Community Ecology.” Edited by Oscar Godoy. *Functional Ecology* 33 (2): 206–17. `https://doi.org/10.1111/1365-2435.13237`.

Ings, Thomas C., José M. Montoya, Jordi Bascompte, Nico Blüthgen, Lee Brown, Carsten F. Dormann, François Edwards, et al. 2009. “Ecological Networks–Beyond Food Webs.” *The Journal of Animal Ecology* 78 (1): 253–69. `https://doi.org/10.1111/j.1365-2656.2008.01460.x`.

Innes, Mike. 2018. “Flux: Elegant Machine Learning with Julia.” *Journal of Open Source Software* 3 (25): 602. `https://doi.org/10.21105/joss.00602`.

Jalili, Mahdi, Yasin Orouskhani, Milad Asgari, Nazanin Alipourfard, and Matjaž Perc. 2017. “Link Prediction in Multiplex Online Social Networks.” *Royal Society Open Science* 4 (2): 160863. `https://doi.org/10.1098/rsos.160863`.

Jeliazkov, Alienor, Darko Mijatovic, Stéphane Chantepie, Nigel Andrew, Raphaël Arlettaz, Luc Barbaro, Nadia Barsoum, et al. 2020. “A Global Database for Metacommunity Ecology, Integrating Species, Traits, Environment and Space.” *Scientific Data* 7 (1): 6. `https://doi.org/10.1038/s41597-019-0344-7`.

Jenkins, Clinton N., Stuart L. Pimm, and Lucas N. Joppa. 2013. “Global Patterns of Terrestrial Vertebrate Diversity and Conservation.” *Proceedings of the National Academy of Sciences* 110 (28): E2602–10. `https://doi.org/10.1073/pnas.1302251110`.

Jordano, Pedro. 2016a. “Chasing Ecological Interactions.” *PLOS Biology* 14 (9): e1002559. `https://doi.org/10.1371/journal.pbio.1002559`.

———. 2016b. “Sampling Networks of Ecological Interactions.” *Functional Ecology*. https://doi.org/10.1111/1365-2435.12763.

Karger, Dirk Nikolaus, Anna F. Cord, Michael Kessler, Holger Kreft, Ingolf Kühn, Sven Pompe, Brody Sandel, et al. 2016. “Delineating Probabilistic Species Pools in Ecology and Biogeography.” *Global Ecology and Biogeography* 25 (4): 489–501. https://doi.org/10.1111/geb.12422.

Kéfi, Sonia, Virginia Domínguez-García, Ian Donohue, Colin Fontaine, Elisa Thébault, and Vasilis Dakos. 2019. “Advancing Our Understanding of Ecological Stability.” *Ecology Letters* 22 (9): 1349–56. https://doi.org/10.1111/ele.13340.

Kindsvater, Holly K., Nicholas K. Dulvy, Cat Horswill, Maria-José Juan-Jordá, Marc Mangel, and Jason Matthiopoulos. 2018. “Overcoming the Data Crisis in Biodiversity Conservation.” *Trends in Ecology & Evolution* 33 (9): 676–88. https://doi.org/10.1016/j.tree.2018.06.004.

Kissling, W. Daniel, Jorge A. Ahumada, Anne Bowser, Miguel Fernandez, Nestor Fernandez, Enrique Alonso Garcia, Robert P. Guralnick, et al. 2018. “Building Essential Biodiversity Variables (EBVs) of Species Distribution and Abundance at a Global Scale.” *Biological Reviews* 93 (1): 600–625. https://doi.org/10.1111/brv.12359.

Kortsch, Susanne, Raul Primicerio, Maria Fossheim, Andrey V. Dolgov, and Michaela Aschan. 2015. “Climate Change Alters the Structure of Arctic Marine Food Webs Due to Poleward Shifts of Boreal Generalists.” *Proceedings of the Royal Society B: Biological Sciences* 282 (1814): 20151546. https://doi.org/10.1098/rspb.2015.1546.

Krizhevsky, Alex, Ilya Sutskever, and Geoffrey E. Hinton. 2017. “ImageNet Classification with Deep Convolutional Neural Networks.” *Communications of the ACM* 60 (6): 84–90. https://doi.org/10.1145/3065386.

Kuhn, Max, and Kjell Johnson. 2019. *Feature Engineering and Selection : A Practical Approach for Predictive Models*. Chapman and Hall/CRC. https://doi.org/10.1201/9781315108230.

Landi, Pietro, Henintsoa O. Minoarivelo, Åke Brännström, Cang Hui, and Ulf Dieckmann. 2018. “Complexity and Stability of Ecological Networks: A Review of the Theory.” *Population Ecology* 60 (4): 319–45. https://doi.org/10.1007/s10144-018-0628-3.

Lausch, A., L. Bannehr, M. Beckmann, C. Boehm, H. Feilhauer, J. M. Hacker, M. Heurich, et al. 2016. “Linking Earth Observation and Taxonomic, Structural and Functional Biodiversity: Local to Ecosystem Perspectives.” *Ecological Indicators*, Navigating Urban Complexity: Advancing Understanding of Urban Social Ecological Systems for Transformation and Resilience, 70: 317–39. https://doi.org/10.1016/j.ecolind.2016.06.022.

Lei, Lili, and Jeffrey S. Whitaker. 2017. “Evaluating the Trade-Offs Between Ensemble Size and Ensemble Resolution in an Ensemble-Variational Data Assimilation System.” *Journal of Advances in Modeling Earth Systems* 9 (2): 781–89. https://doi.org/10.1002/2016MS000864.

Levin, Simon A. 1998. “Ecosystems and the Biosphere as Complex Adaptive Systems.” *Ecosystems* 1 (5): 431–36. https://doi.org/10.1007/s100219900037.

Levins, Richard, and Richard Charles Lewontin. 1987. *The Dialectical Biologist*. Cambridge, Mass.: Harvard University Press.

MacDonald, Arthur Andrew Meahan, Francis Banville, and Timothée Poisot. 2020. “Revisiting the Links-Species Scaling Relationship in Food Webs.” *Patterns* 1 (7). https://doi.org/10.1016/j.patter.2020.100079.

Makiola, Andreas, Zacchaeus G. Compson, Donald J. Baird, Matthew A. Barnes, Sam P. Boerlijst, Agnès Bouchez, Georgina Brennan, et al. 2020. “Key Questions for Next-Generation

Biomonitoring." *Frontiers in Environmental Science* 7. `https://doi.org/10.3389/fenvs.2019.00197`.

Massol, F., M. Dubart, V. Calcagno, K. Cazelles, C. Jacquet, S. Kéfi, and D. Gravel. 2017. "Chapter Four - Island Biogeography of Food Webs." In *Advances in Ecological Research*, edited by David A. Bohan, Alex J. Dumbrell, and François Massol, 56:183–262. Networks of Invasion: A Synthesis of Concepts. Academic Press. `https://doi.org/10.1016/bs.aecr.2016.10.004`.

May, Robert M. 1974. *Stability and Complexity in Model Ecosystems*. Vol. 1. Princeton University Press. `https://doi.org/10.2307/j.ctvs32rq4`.

McCann, Kevin. 2007. "Protecting Biostructure." *Nature* 446 (7131): 29–29. `https://doi.org/10.1038/446029a`.

McDonald-Madden, E., R. Sabbadin, E. T. Game, P. W. J. Baxter, I. Chadès, and H. P. Possingham. 2016. "Using Food-Web Theory to Conserve Ecosystems." *Nature Communications* 7 (1): 10245. `https://doi.org/10.1038/ncomms10245`.

McWilliams, Chris, Miguel Lurgi, Jose M. Montoya, Alix Sauve, and Daniel Montoya. 2019. "The Stability of Multitrophic Communities Under Habitat Loss." *Nature Communications* 10 (1): 2322. `https://doi.org/10.1038/s41467-019-10370-2`.

Michalska-Smith, Matthew J., and Stefano Allesina. 2019. "Telling Ecological Networks Apart by Their Structure: A Computational Challenge." *PLOS Computational Biology* 15 (6): e1007076. `https://doi.org/10.1371/journal.pcbi.1007076`.

Montoya, José M., Miguel A. Rodríguez, and Bradford A. Hawkins. 2003. "Food Web Complexity and Higher-Level Ecosystem Services." *Ecology Letters* 6 (7): 587–93. `https://doi.org/10.1046/j.1461-0248.2003.00469.x`.

Mora, Bernat Bramon, Dominique Gravel, Luis J. Gilarranz, Timothée Poisot, and Daniel B. Stouffer. 2018. "Identifying a Common Backbone of Interactions Underlying Food Webs from Different Ecosystems." *Nature Communications* 9 (1): 1–8. `https://doi.org/10.1038/s41467-018-05056-0`.

Morales-Castilla, Ignacio, Miguel G. Matias, Dominique Gravel, and Miguel B. Araújo. 2015. "Inferring Biotic Interactions from Proxies." *Trends in Ecology & Evolution* 30 (6): 347–56. `https://doi.org/10.1016/j.tree.2015.03.014`.

Najari, Shaghayegh, Mostafa Salehi, Vahid Ranjbar, and Mahdi Jalili. 2019. "Link Prediction in Multiplex Networks Based on Interlayer Similarity." *Physica A: Statistical Mechanics and Its Applications* 536: 120978. `https://doi.org/10.1016/j.physa.2019.04.214`.

Neutel, A.-M. 2002. "Stability in Real Food Webs: Weak Links in Long Loops." *Science* 296 (5570): 1120–23. `https://doi.org/10.1126/science.1068326`.

Norberg, Anna, Nerea Abrego, F. Guillaume Blanchet, Frederick R. Adler, Barbara J. Anderson, Jani Anttila, Miguel B. Araújo, et al. 2019. "A Comprehensive Evaluation of Predictive Performance of 33 Species Distribution Models at Species and Community Levels." *Ecological Monographs* 89 (3): e01370. `https://doi.org/10.1002/ecm.1370`.

Novak, Mark, and J. Timothy Wootton. 2008. "Estimating Nonlinear Interaction Strengths: An Observation-Based Method for Species-Rich Food Webs." *Ecology* 89 (8): 2083–89. `https://doi.org/10.1890/08-0033.1`.

O'Connor, Louise M. J., Laura J. Pollock, João Braga, Gentile Francesco Ficetola, Luigi Maiorano, Camille Martinez-Almoyna, Alessandro Montemaggiori, Marc Ohlmann, and Wilfried Thuiller. 2020. "Unveiling the Food Webs of Tetrapods Across Europe Through the Prism of the Eltonian Niche." *Journal of Biogeography* 47 (1): 181–92. https://doi.org/10.1111/jbi.13773.

Olden, Julian D., Joshua J. Lawler, and N. LeRoy Poff. 2008. "Machine Learning Methods Without Tears: A Primer for Ecologists." *The Quarterly Review of Biology* 83 (2): 171–93. https://doi.org/10.1086/587826.

Ovaskainen, Otso, Gleb Tikhonov, Anna Norberg, F. Guillaume Blanchet, Leo Duan, David Dunson, Tomas Roslin, and Nerea Abrego. 2017. "How to Make More Out of Community Data? A Conceptual Framework and Its Implementation as Models and Software." *Ecology Letters* 20 (5): 561–76. https://doi.org/10.1111/ele.12757.

Parker, Wendy S. 2013. "Ensemble Modeling, Uncertainty and Robust Predictions." *WIREs Climate Change* 4 (3): 213–23. https://doi.org/10.1002/wcc.220.

Parysow, Pablo, George Gertner, and James Westervelt. 2000. "Efficient Approximation for Building Error Budgets for Process Models." *Ecological Modelling* 135 (2): 111–25. https://doi.org/10.1016/S0304-3800(00)00347-1.

Pascual, Mercedes, and Jennifer A. Dunne. 2006. *Ecological Networks: Linking Structure to Dynamics in Food Webs*. Oxford University Press, USA.

Pennekamp, Frank, Alison C. Iles, Joshua Garland, Georgina Brennan, Ulrich Brose, Ursula Gaedke, Ute Jacob, et al. 2019. "The Intrinsic Predictability of Ecological Time Series and Its Potential to Guide Forecasting." *Ecological Monographs* 89 (2): e01359. https://doi.org/10.1002/ecm.1359.

Petchey, O. L., A. P. Beckerman, J. O. Riede, and P. H. Warren. 2008. "Size, Foraging, and Food Web Structure." *Proceedings of the National Academy of Sciences* 105 (11): 4191–96. https://doi.org/10.1073/pnas.0710672105.

Peters, Debra P. C., and Jeffrey E. Herrick. 2004. "Strategies for Ecological Extrapolation." *Oikos* 106 (3): 627–36. https://doi.org/10.1111/j.0030-1299.2004.12869.x.

Pérez-Harguindeguy, N., S. Díaz, E. Garnier, S. Lavorel, H. Poorter, P. Jaureguiberry, M. S. Bret-Harte, et al. 2013. "New Handbook for Standardised Measurement of Plant Functional Traits Worldwide." *Australian Journal of Botany* 61 (3): 167. https://doi.org/10.1071/BT12225.

Pichler, Maximilian, Virginie Boreux, Alexandra-Maria Klein, Matthias Schleuning, and Florian Hartig. 2020. "Machine Learning Algorithms to Infer Trait-Matching and Predict Species Interactions in Ecological Networks." *Methods in Ecology and Evolution* 11 (2): 281–93. https://doi.org/10.1111/2041-210X.13329.

Pigot, Alex L., and Joseph A. Tobias. 2013. "Species Interactions Constrain Geographic Range Expansion over Evolutionary Time." Edited by Colleen Webb. *Ecology Letters* 16 (3): 330–38. https://doi.org/10.1111/ele.12043.

Pilosof, Shai, Mason A. Porter, Mercedes Pascual, and Sonia Kéfi. 2017. "The Multilayer Nature of Ecological Networks." *Nature Ecology & Evolution* 1 (4): 101. https://doi.org/10.1038/s41559-017-0101.

Pocock, Michael J. O., Darren M. Evans, and Jane Memmott. 2012. "The Robustness and Restoration of a Network of Ecological Networks." *Science* 335 (6071): 973–77. https://doi.org/10.1126/science.1214915.

Poelen, Jorrit H., James D. Simons, and Chris J. Mungall. 2014. "Global Biotic Interactions: An Open Infrastructure to Share and Analyze Species-Interaction Datasets." *Ecological Informatics* 24: 148–59. https://doi.org/10.1016/j.ecoinf.2014.08.005.

Poisot, Timothée, Benjamin Baiser, Jennifer Dunne, Sonia Kéfi, François Massol, Nicolas Mouquet, Tamara N. Romanuk, Daniel B. Stouffer, Spencer A. Wood, and Dominique Gravel. 2016. “Mangal Making Ecological Network Analysis Simple.” *Ecography* 39 (4): 384–90. https://doi.org/10.1111/ecog.00976.

Poisot, Timothée, Gabriel Bergeron, Kevin Cazelles, Tad Dallas, Dominique Gravel, Andrew Macdonald, Benjamin Mercier, Clément Violet, and Steve Vissault. 2020. “Environmental Biases in the Study of Ecological Networks at the Planetary Scale.” *bioRxiv*, 2020.01.27.921429. https://doi.org/10.1101/2020.01.27.921429.

Poisot, Timothée, and Dominique Gravel. 2014. “When Is an Ecological Network Complex? Connectance Drives Degree Distribution and Emerging Network Properties.” *PeerJ* 2: e251. https://doi.org/10.7717/peerj.251.

Poisot, Timothée, and Daniel B. Stouffer. 2018. “Interactions Retain the Co-Phylogenetic Matching That Communities Lost.” *Oikos* 127 (2): 230–38. https://doi.org/10.1111/oik.03788.

Poisot, Timothée, Daniel B. Stouffer, and Dominique Gravel. 2015. “Beyond Species: Why Ecological Interaction Networks Vary Through Space and Time.” *Oikos* 124 (3): 243–51. https://doi.org/10.1111/oik.01719.

Pollock, Laura J., Louise M. J. O’Connor, Karel Mokany, Dan F. Rosauer, Matthew V. Talluto, and Wilfried Thuiller. 2020. “Protecting Biodiversity (in All Its Complexity): New Models and Methods.” *Trends in Ecology & Evolution* 35 (12): 1119–28. https://doi.org/10.1016/j.tree.2020.08.015.

Pomeranz, Justin PF, Ross M. Thompson, Timothée Poisot, and Jon S. Harding. 2018. “Inferring Predator-Prey Interactions in Food Webs.” *Methods in Ecology and Evolution* 0 (ja). https://doi.org/10.1111/2041-210X.13125.

Portalier, Sébastien M. J., Gregor F. Fussmann, Michel Loreau, and Mehdi Cherif. 2019. “The Mechanics of Predatorprey Interactions: First Principles of Physics Predict Predatorprey Size Ratios.” *Functional Ecology* 33 (2): 323–34. https://doi.org/10.1111/1365-2435.13254.

Porter, John, Peter Arzberger, Hans-Werner Braun, Pablo Bryant, Stuart Gage, Todd Hansen, Paul Hanson, et al. 2005. “Wireless Sensor Networks for Ecology.” *BioScience* 55 (7): 561–72. https://doi.org/10.1641/0006-3568(2005)055%5B0561:WSNFE%5D2.0.CO;2.

Rackauckas, Christopher, Yingbo Ma, Julius Martensen, Collin Warner, Kirill Zubov, Rohit Supekar, Dominic Skinner, Ali Ramadhan, and Alan Edelman. 2020. “Universal Differential Equations for Scientific Machine Learning.”

Riede, Jens O., Björn C. Rall, Carolin Banasek-Richter, Sergio A. Navarrete, Evie A. Wieters, Mark C. Emmerson, Ute Jacob, and Ulrich Brose. 2010. “Scaling of Food-Web Properties with Diversity and Complexity Across Ecosystems.” In *Advances in Ecological Research*, 42:139–70. Elsevier. https://doi.org/10.1016/B978-0-12-381363-3.00003-4.

Rohr, Rudolf Philippe, Heike Scherer, Patrik Kehrli, Christian Mazza, and Louis-Félix Bersier. 2010. “Modeling Food Webs: Exploring Unexplained Structure Using Latent Traits.” *The American Naturalist* 176 (2): 170–77. https://doi.org/10.1086/653667.

Rossberg, A. G., H. Matsuda, T. Amemiya, and K. Itoh. 2006. “Food Webs: Experts Consuming Families of Experts.” *Journal of Theoretical Biology* 241 (3): 552–63. https://doi.org/10.1016/j.jtbi.2005.12.021.

Ruiter, Peter C. de, Anje-Margriet Neutel, and John C. Moore. 1995. “Energetics, Patterns of Interaction Strengths, and Stability in Real Ecosystems.” *Science* 269 (5228): 1257–60. https://doi.org/10.1126/science.269.5228.1257.

Sala, Enric, and Michael H. Graham. 2002. "Community-Wide Distribution of Predatorprey Interaction Strength in Kelp Forests." *Proceedings of the National Academy of Sciences* 99 (6): 3678–83. https://doi.org/10.1073/pnas.052028499.

Sander, Elizabeth L., J. Timothy Wootton, and Stefano Allesina. 2017. "Ecological Network Inference from Long-Term Presence-Absence Data." *Scientific Reports* 7 (1): 7154. https://doi.org/10.1038/s41598-017-07009-x.

Scholes, Robert J, Michele Walters, Eren Turak, Hannu Saarenmaa, Carlo HR Heip, Éamonn Ó Tuama, Daniel P Faith, et al. 2012. "Building a Global Observing System for Biodiversity." *Current Opinion in Environmental Sustainability*, Open issue, 4 (1): 139–46. https://doi.org/10.1016/j.cosust.2011.12.005.

Segar, Simon T., Tom M. Fayle, Diane S. Srivastava, Thomas M. Lewinsohn, Owen T. Lewis, Vojtech Novotny, Roger L. Kitching, and Sarah C. Maunsell. 2020. "The Role of Evolution in Shaping Ecological Networks." *Trends in Ecology & Evolution* 35 (5): 454–66. https://doi.org/10.1016/j.tree.2020.01.004.

Seibold, Sebastian, Marc W. Cadotte, J. Scott MacIvor, Simon Thorn, and Jörg Müller. 2018. "The Necessity of Multitrophic Approaches in Community Ecology." *Trends in Ecology & Evolution* 33 (10): 754–64. https://doi.org/10.1016/j.tree.2018.07.001.

Skidmore, Andrew K., and Nathalie Pettorelli. 2015. "Agree on Biodiversity Metrics to Track from Space: Ecologists and Space Agencies Must Forge a Global Monitoring Strategy." *Nature* 523 (7561): 403–6.

Smith-Ramesh, Lauren M., Alexandria C. Moore, and Oswald J. Schmitz. 2016. "Global Synthesis Suggests That Food Web Connectance Correlates to Invasion Resistance." *Global Change Biology*, n/a–. https://doi.org/10.1111/gcb.13460.

Staniczenko, Phillip P. A., Prabu Sivasubramaniam, K. Blake Suttle, and Richard G. Pearson. 2017. "Linking Macroecology and Community Ecology: Refining Predictions of Species Distributions Using Biotic Interaction Networks." *Ecology Letters* 20 (6): 693–707. https://doi.org/10.1111/ele.12770.

Stephenson, PJ. 2020. "Technological Advances in Biodiversity Monitoring: Applicability, Opportunities and Challenges." *Current Opinion in Environmental Sustainability* 45: 36–41. https://doi.org/10.1016/j.cosust.2020.08.005.

Stouffer, Daniel B. 2019. "All Ecological Models Are Wrong, but Some Are Useful." *Journal of Animal Ecology* 88 (2): 192–95. https://doi.org/10.1111/1365-2656.12949.

Stouffer, Daniel B., and Jordi Bascompte. 2010. "Understanding Food-Web Persistence from Local to Global Scales." *Ecology Letters* 13 (2): 154–61. https://doi.org/10.1111/j.1461-0248.2009.01407.x.

Syfert, Mindy M., Lucas Joppa, Matthew J. Smith, David A. Coomes, Steven P. Bachman, and Neil A. Brummitt. 2014. "Using Species Distribution Models to Inform IUCN Red List Assessments." *Biological Conservation* 177: 174–84. https://doi.org/10.1016/j.biocon.2014.06.012.

Thompson, Ross M., Ulrich Brose, Jennifer Dunne, Robert O. Hall, Sally Hladyz, Roger L. Kitching, Neo D. Martinez, et al. 2012. "Food Webs: Reconciling the Structure and Function of Biodiversity." *Trends in Ecology & Evolution* 27 (12): 689–97. https://doi.org/10.1016/j.tree.2012.08.005.

Tinker, M. Tim, Paulo R. Guimarães, Mark Novak, Flavia Maria Darcie Marquitti, James L. Bodkin, Michelle Staedler, Gena Bentall, and James A. Estes. 2012. "Structure and Mechanism of Diet Specialisation: Testing Models of Individual Variation in Resource Use with

Sea Otters." *Ecology Letters* 15 (5): 475–83. https://doi.org/10.1111/j.1461-0248.2012.01760.x.

Tipping, Michael E., and Christopher M. Bishop. 1999. "Probabilistic Principal Component Analysis." *Journal of the Royal Statistical Society: Series B (Statistical Methodology)* 61 (3): 611–22. https://doi.org/10.1111/1467-9868.00196.

Trøjelsgaard, Kristian, and Jens M. Olesen. 2016. "Ecological Networks in Motion: Micro- and Macroscopic Variability Across Scales." *Functional Ecology* 30 (12): 1926–35. https://doi.org/10.1111/1365-2435.12710.

Urban, M. C., G. Bocedi, A. P. Hendry, J.- B. Mihoub, G. Peer, A. Singer, J. R. Bridle, et al. 2016. "Improving the Forecast for Biodiversity Under Climate Change." *Science* 353 (6304): aad8466–66. https://doi.org/10.1126/science.aad8466.

Vazquez, Diego P., Nico Bluethgen, Luciano Cagnolo, and Natacha P. Chacoff. 2009. "Uniting Pattern and Process in Plant-Animal Mutualistic Networks: A Review." *Annals of Botany* 103 (9): 1445–57. https://doi.org/10.1093/aob/mcp057.

Vázquez, Diego P., Carlos J. Melián, Neal M. Williams, Nico Blüthgen, Boris R. Krasnov, and Robert Poulin. 2007. "Species Abundance and Asymmetric Interaction Strength in Ecological Networks." *Oikos* 116 (7): 1120–27. https://doi.org/10.1111/j.0030-1299.2007.15828.x.

Vieira, Marcos Costa, and Mário Almeida-Neto. 2015. "A Simple Stochastic Model for Complex Coextinctions in Mutualistic Networks: Robustness Decreases with Connectance." *Ecology Letters* 18 (2): 144–52. https://doi.org/10.1111/ele.12394.

Wells, Konstans, and Robert B. O'Hara. 2013. "Species Interactions: Estimating Per-Individual Interaction Strength and Covariates Before Simplifying Data into Per-Species Ecological Networks." *Methods in Ecology and Evolution* 4 (1): 1–8. https://doi.org/10.1111/j.2041-210x.2012.00249.x.

Wiens, J. A. 1989. "Spatial Scaling in Ecology." *Functional Ecology* 3 (4): 385–97. https://doi.org/10.2307/2389612.

Wisz, Mary Susanne, Julien Pottier, W. Daniel Kissling, Loïc Pellissier, Jonathan Lenoir, Christian F. Damgaard, Carsten F. Dormann, et al. 2013. "The Role of Biotic Interactions in Shaping Distributions and Realised Assemblages of Species: Implications for Species Distribution Modelling." *Biological Reviews* 88 (1): 15–30. https://doi.org/10.1111/j.1469-185X.2012.00235.x.

Wootton, J. Timothy. 1997. "Estimates and Tests of Per Capita Interaction Strength: Diet, Abundance, and Impact of Intertidally Foraging Birds." *Ecological Monographs* 67 (1): 45–64. https://doi.org/10.1890/0012-9615(1997)067%5B0045:EATOPC%5D2.0.CO;2.

Wootton, J. Timothy, and Mark Emmerson. 2005. "Measurement of Interaction Strength in Nature." *Annual Review of Ecology, Evolution, and Systematics* 36 (1): 419–44. https://doi.org/10.1146/annurev.ecolsys.36.091704.175535.

Yasami, Yasser, and Farshad Safaei. 2018. "A Novel Multilayer Model for Missing Link Prediction and Future Link Forecasting in Dynamic Complex Networks." *Physica A: Statistical Mechanics and Its Applications* 492: 2166–97. https://doi.org/10.1016/j.physa.2017.11.134.

Yodzis, P., and S. Innes. 1992. "Body Size and Consumer-Resource Dynamics." *The American Naturalist* 139 (6): 1151–75. https://doi.org/10.1086/285380.