

A Roadmap Toward Prediction of Ecological Networks Across Space and Time

Tanya Strydom^{1,2} Michael David Catchen^{3,2} Francis Banville^{1,4,2} Dominique Caron^{3,2} Gabriel Dansereau^{1,2}
Norma Forero^{1,2} Gracielle Higino⁵ Benjamin Mercier^{4,2} Andrew Gonzalez^{3,2} 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

* timothee.poisot@umontreal.ca

Abstract: Ecological networks can capture meaningful information on the structure of ecological communities. Yet the scarcity of existing data, and the difficulty associated with comprehensively sampling ecological interactions, means that to describe the structure, variation, and change of ecological networks over time and space, we need to rely on modelling tools with the capacity to make accurate predictions about how species interact. In this review, we offer a roadmap aimed at guiding the development and integration of these tools, with the specific purpose of boosting our predictive ability. By working from first principles on the mechanisms involved in structuring ecological networks, we make recommendations about the scale at which we can predict networks across both biological organization as well as space and time. In so doing, we show that multiple sources of data and quantitative approaches, including statistical, dynamical, and inferential models, can and must be integrated to deliver forecasts of ecological networks. Importantly, we argue that ecological forecasting applied to networks will provide benefits to other fields of ecology: it will notably improve the integration between network ecology and metacommunity theory and highlight the interoperability between different data sources. Here, we take a question driven approach to review our current understanding of ecological networks, sketch the path forward for this research program.

1 Introduction

2 Ecosystems *are* interactions – organisms interact with one-another and with their environment,
3 either directly or indirectly. Between organisms, these interactions form networks of varying
4 complexity, drive ecological and evolutionary dynamics, and maintain ecosystem diversity and
5 functioning (Delmas et al. 2018; Landi et al. 2018; Albrecht et al. 2018). Networks of species
6 interactions underpin our understanding of key ecological processes (Pascual and Dunne 2006;
7 Heleno et al. 2014). Yet, even basic knowledge of species interactions (like being able to list
8 them, or guess which ones may exist) is one of the most severe shortfalls in biodiversity science
9 (Hortal et al. 2015). This is due in large part to the tedious, time-consuming, and expensive
10 data collection process. As with many ecological systems, networks of species interactions
11 have entered their “long now” (Carpenter 2002), where contemporary actions have long-term,
12 low-predictability consequences (Burkle, Marlin, and Knight 2013).

13 Therefore, our field needs a conceptual path forward toward models that enable prediction (for
14 the present) and forecasting (for the future) of species interactions and the networks they form
15 (McCann 2007; Seibold et al. 2018). Here we provide a data-driven illustration to show how ma-
16 chine learning approaches can enable unreasonably effective prediction of interactions whereby
17 we construct a metaweb of host-parasite interactions across space, which serves as a proof-of-
18 concept for this conceptual framework. We then propose a roadmap forward for how to improve
19 predictions using this approach, and provide a primer on the relevant tools and methods that
20 could be incorporated into models of this type in the future in order to account for the spatial,
21 temporal, and climatic dimensions of network prediction (Burkle and Alarcon 2011).

22 Proof-of-Concept: can we predict ecological networks?

23 The core premise of this manuscript is that ecological networks can be predicted. In this section,
24 we provide a proof-of-concept, in which we (i) aggregate a series of networks collected across
25 space into a metaweb, (ii) extract features based on species co-occurrence, (iii) use these features
26 to train a neural network to predict interactions, and (iv) apply this classifier to the original fea-
27 tures to predict possibly missing interactions across the entire species pool. The entire analysis

28 is presented in fig. 1, and the code to reproduce it is available at **TODO OSF LINK**; the entire
29 example was carried out in *Julia 1.5.3* (Bezanson et al. 2017), and notably uses the *Flux* ma-
30 chine learning framework (Innes 2018). Note that this analysis is meant to serve as an *example*
31 *only*, and should in practice be fined-tuned according to the state of the art (*e.g.* Goodfellow,
32 Bengio, and Courville 2016).

33 We used data from Hadfield et al. (2014), describing 51 host-parasite networks, where not all
34 species pairs co-occur across sites. This implies that there are “negative associations” that might
35 be biologically feasible but not observed because the two species have not been observed in co-
36 occurrence. As this dataset has no features like species traits on which to base a predictive
37 model, we have aggregated all interactions into a binary metaweb (J. Dunne 2006). We then
38 transformed the (undirected) metaweb through a probabilistic PCA (Tipping and Bishop 1999),
39 so as to create a number of latent features for the species in a context where the dataset is both
40 unbalanced and likely to have many missing values. This frames the problem as predicting a
41 binary outcome, the interaction M_{xy} represented as true or false based on a features vector
42 $v_{xy} = [v_x, v_y]$ where v_x is the values of the selected features for the parasite and v_y is the
43 features of the host. In the following example, we used the first 15 components of the latent
44 sub-space created by the probabilistic PCA. This features vector is then fed into the input layer
45 of a neural network, which uses three hidden layers with appropriate dropout rates (0.5), and
46 finally a two-neurons output layer whose result is softmaxed to pick the most likely outcome,
47 *i.e.* the interaction bit describing an interaction when equal to 1, and no interaction when equal
48 to 0.

49 [Figure 1 about here.]

50 During the training of this neural network, we exploited ecological constraints in two ways.
51 First, the selection of features was done so that absent interactions in a species pair with no co-
52 occurrence were removed from the data. This ensures that the network is trained only on the
53 subset of the data for which we have minimal ecological information. Second, the batches of 16
54 items used for training were constrained to have at least 10 positive interactions. The reasoning
55 for this choice was made based on three observations: the network is sparse (*i.e.* the prevalence

56 of interactions is low); negative interactions have a chance of being false negatives due to lack of
57 reporting in the field; there are no true negative interactions reported, *i.e.* interactions for which
58 we know that they almost never happen. Therefore, slightly inflating the dataset with positive
59 interactions enables us to counterbalance these biases.

60 After the training (2.5×10^4 epochs in fig. 1), our model reached an accuracy of ≈ 0.8 , with no
61 marked deviation between the training and testing sets (respectively 80% and 20% of the data),
62 suggesting no to minimal overfitting. Applying this model to the entire dataset (including species
63 pairs never observed co-occurring in the dataset) identified 1831 new possible interactions – 382
64 of which were in species pairs where the pair of species was never considered prior. This suggests
65 that meaningful information about ecological interaction is structured within network data, and
66 our core argument here is that we should embrace the prediction of species interaction networks
67 as a worthy topic of concept , and specifically strive to adopt an explicitly spatial and temporal
68 perspective on this question. Now, the question becomes: how do we make our prediction of
69 ecological networks *better*?

70 **A Roadmap Toward Better Prediction of Ecological Networks across 71 Space and Time**

72 Below we focus on and discuss integrating what we envisage to be the conceptual and method-
73 ological pathway towards better prediction of ecological networks (fig. 2).

74 **Challenges: the many constraints on prediction**

75 **Ecological network data are scarce and hard to obtain**

76 At the moment, our understanding of the structure of ecological networks is limited by the avail-
77 ability of data. Although we have seen a growth in species occurrence data, this growth is much
78 slower for ecological interactions because species interactions are challenging to sample com-
79 prehensively (Bennett, Evans, and Powell 2019; Jordano 2016b) and sampling methodology
80 has strong effects on the resulting data (de Aguiar et al. 2019). In turn, the difficulty of sam-

pling 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 (or environmental conditions) (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, the analysis of interaction strength from empirical estimation is highly prone to bias as existing data quantifying interaction strength are 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). Furthermore, interaction strength is extremely variable and context dependent and can be influenced by density dependence and spatiotemporal variation in abundances and community composition (Wootton and Emmerson 2005). A better understanding of interaction strengths in communities is a key step in linking species interactions to ecosystem processes and functioning.

103 **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 that can be found in existing datasets. Species interaction datasets 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

109 or predict networks of *underrepresented* interaction types or when trying to integrate networks
110 of different types (Fontaine et al. 2011), especially given the inherent structural variation of eco-
111 logical networks (Michalska-Smith and Allesina 2019). This stresses the need for an integrated,
112 flexible, and data-efficient set of computational tools which will allow us to predict ecological
113 networks accurately from existing and imperfect datasets, but also enable us to perform model
114 validation and comparison with more flexibility than existing tools. We argue that fig. 1 is an
115 example of the promise of these tools *even* when facing datasets of small size. When carefully
116 controlling for overfitting machine learning systems are at least adequate at generalizing. The
117 ability to extract and engineer features also serves to bolster our predictive power. In short,
118 the current lack of massive datasets must not be an obstacle to prediction; it is an ideal testing
119 ground to understand how little data is sufficient to obtain actionable predictions.

120 Scaling-up predictions requires scaled-up data

121 We are also currently limited by the the level of biological organisation at which we can describe
122 ecological networks. For instance, our understanding of individual based networks (*e.g.* M. S.
123 Araújo et al. 2008; Tinker et al. 2012) is still in its infancy (Guimarães 2020) and acts as a
124 resolution-limit. On the note of scale, the resolution of environmental (or landscape) data would
125 also limit our ability to predict networks at finer scales, although current trends in *e.g.* remote
126 sensing would suggest that with time this would become less of a hindrance (Makiola et al.
127 2020). Ecosystems are a quintessential complex-adaptive-system (Levin 1998) with a myriad
128 of ways in which processes at different spatial, temporal, and organizational scales can influence
129 and respond to one another. Understanding how the product of these different processes drive the
130 properties of ecosystem across different scales remains a central challenge of ecological research,
131 and we should strive to work on methods that will integrate different empirical “snapshots” of
132 this larger system.

133 Opportunities: the emerging ecosystem of open tools and data

134 If we wish to predict the interactions between species we have not observed together, using our
135 knowledge of the structure of ecological networks to interact in a particular ecosystem is one

136 of our most useful assets. We are able to infer species interactions using proxies such as traits,
137 phylogenies, geographical data and other frameworks (Morales-Castilla et al. 2015). Drawing
138 on elements that contribute to the realization of an interaction such as abundance and traits
139 matching in space and time, and the combination of these elements allow us to infer potential
140 from realized interactions and empirical data about populations (Poisot, Cirtwill, et al. 2016).
141 In turn, this effort is supported by a thriving ecosystem of data sources and computational tools.
142 In this section, we give a brief overview of these resources.

143 Open Data

144 The acquisition of biodiversity and environmental data has tremendously increased over the
145 past decades thanks to the rise of citizen science (Dickinson, Zuckerberg, and Bonter 2010) and
146 of novel technology (Stephenson 2020), including wireless sensors (Porter et al. 2005), next-
147 generation DNA sequencing (Creer et al. 2016), and remote sensing (Skidmore and Pettorelli
148 2015; Lausch et al. 2016). Open access databases, such as [GBIF](#) (for biodiversity data), [NCBI](#)
149 (for taxonomic and genomics data), [TreeBASE](#) (for phylogenetics data), [CESTE](#) (Jeliazkov et
150 al. 2020) (for metacommunity ecology and species traits data), and [WorldClim](#) (for bioclimatic
151 data) contain millions of data points that can be integrated to monitor and model biodiversity at
152 the global scale. For species interactions data, at the moment [Mangal](#) is the most comprehensive
153 open database of published ecological networks (Poisot, Baiser, et al. 2016), and [GloBI](#) is an
154 extensive database of realized and potential species interactions (Poelen, Simons, and Mungall
155 2014). Developing standard practices in data integration and quality control (Kissling et al.
156 2018) and in next-generation biomonitoring (NGB; Makiola et al. 2020) would improve our
157 ability to make reliable predictions of ecosystem properties on increasing spatial and temporal
158 scales. The advancement of prediction techniques coupled with a movement towards standar-
159 dising data collection protocols (e.g. Pérez-Harguindeguy et al. (2013) for plant functional
160 traits) and metadata (e.g. [DarwinCore](#))—which facilitates interoperability and integration of
161 datasets—as well as a growing interest at the government level (Scholes et al. 2012) paints a
162 positive picture for data access and usability in the coming years.

163 **Open Tools and Methods**

164 Machine learning encompasses a broad variety of techniques applied with or without human
165 supervision. These techniques can often be more flexible and perform better than classical sta-
166 tistical methods, and can achieve a very high level of accuracy in many predictive and classifi-
167 cation tasks in a relatively short amount of time (e.g. Cutler et al. 2007; Krizhevsky, Sutskever,
168 and Hinton 2017). Increasing computing power combined with recent advances in machine
169 learning techniques and applications shows promise in ecology and environmental science (see
170 Christin, Hervet, and Lecomte (2019) for an overview). Moreover, ongoing developments in
171 the field of artificial intelligence are aimed at using deep learning more efficiently in low-data
172 regimes (e.g. Antoniou, Storkey, and Edwards 2018) and with unbalanced datasets (Chawla
173 2010). Machine learning is emerging as the new standard in computational ecology in general
174 (Olden, Lawler, and Poff 2008; Christin, Hervet, and Lecomte 2019), and in network ecology
175 in-particular (Bohan et al. 2017), as long as sufficient relevant data are available. Many ecologi-
176 cal and evolutionary processes underlie species interactions and the structure of their ecological
177 networks (e.g. Vazquez et al. 2009; Segar et al. 2020). It can thus be difficult to choose rel-
178 evant variables and model species interactions networks explicitly. A promising application of
179 machine learning in natural sciences is Scientific-Machine Learning (SciML), a framework that
180 combines machine learning with mechanistic models (Chuang and Keiser 2018; Rackauckas et
181 al. 2020). Considering the current biases in network ecology (Poisot et al. 2020) and the scarcity
182 of data of species interactions, the prediction of ecological networks will undoubtedly benefit
183 from these improvements. Many studies have used machine learning models specifically with
184 ecological interactions. Relevant examples include species traits used to predict interactions
185 and infer trait-matching rules (Desjardins-Proulx et al. 2017; Pichler et al. 2020), automated
186 discovery of food webs (Bohan et al. 2011), reconstruction of ecological networks using next-
187 generation sequencing data (Bohan et al. 2017), and network inference from presence-absence
188 data (Sander, Wootton, and Allesina 2017).

189 [Figure 2 about here.]

190 **A Primer on Predictive Network Ecology**

191 Below we provide a primer on the current state of predictive network ecology, with particular
192 focus on using machine learning approaches in the modelling process. Here adopt a question-
193 driven approach to serve as a guide through the path toward building models to predict and
194 forecast the structure of ecological networks across space, and to identify the next steps in the
195 research regime.

196 **Models**

197 **What is a predictive model?**

198 Models are used for many purposes, and the term “model” embodies a wide variety of meanings
199 in scientific discourse. All models can be thought of as a function, f , that takes a set of inputs
200 x (also called features, descriptors, or independent variables) and some parameters θ , and maps
201 them to predicted output states y (also called label, response, or dependent variable) based on the
202 input to the model: $y = f(x, \theta)$. However, any given model f can be used for either descriptive
203 or predictive purposes. Many forms of scientific inquiry are based around using models *descrip-*
204 *tively* (also called inference, the inverse problem, fitting a model, or training a model) (Stouffer
205 2019). In this context, the goal of using a model is to estimate the parameters, θ , that best explain
206 a set of empirical observations, $\{\hat{x}, \hat{y}\}$. In some cases, these parameter values are themselves
207 of interest (e.g the strength of selection, intrinsic growth rate, dispersal distance), but in others
208 cases, the goal is to compare a set of competing models f_1, f_2, \dots to determine which provides
209 the most parsimonious explanation for a dataset. The quantitative representation of “effects” in
210 these models—the influence of each input on the output—is often assumed to be linear, and in
211 the frequentist context, the goal is often to determine if the coefficient corresponding with an in-
212 put is non-zero to determine its “significance” in influencing the outcome. Models designed for
213 inference have utility, however, in order for ecology to develop as a predictive science (Evans,
214 Norris, and Benton 2012), interest has grown in developing models that are used not just for
215 description of data, but also for prediction. Predictive models use *the forward problem*, where
216 the aim is to predict new values of the output y given an input x and our estimate value of θ

217 (Stouffer 2019). Because the forward problem relies on an estimate of θ , then, the problem of
218 inference is nested within the forward problem (fig. 3).

219 [Figure 3 about here.]

220 What do you need to build a predictive model?

221 In order to build a predictive machine-learning model, one needs the following: first, **data**, split
222 into features \hat{x} and labels \hat{y} (Box Figure Label). Second, a **model** f , which maps features x to
223 labels y as a function of parameters θ , i.e. $y = f(x, \theta)$. Third, a loss function $L(\hat{y}, y)$, which
224 describes how far a model’s prediction y is from an empirical estimate \hat{y} . Lastly, **priors** on pa-
225 rameters, $P(\theta)$. Another important step before fitting a model is feature engineering: adjusting
226 and reworking the predictors to better uncover predictor-response relationships (Kuhn and John-
227 son 2019). This can include projecting the predictors into a lower dimensional space, as in our
228 proof-of-concept.

229 How do we validate a predictive model?

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

243 **Networks and Interactions**

244 **Why predict networks and interactions at the same time?**

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

257 **What network properties should we should use to inform our predictions of interactions?**

258 There are many dimensions of network structure (Delmas et al. 2018). This might make the task
259 of network structure prediction look daunting, as the number of properties one could predict is
260 immense. Yet there are two reasons to begin with a single property, connectance (the ratio of
261 actual edges to possible edges in the network). First, connectance is ecologically informative—
262 it relates to resilience to invasion (Baiser, Russell, and Lockwood 2010; Smith-Ramesh, Moore,
263 and Schmitz 2016), can increase robustness to extinction in food webs (Jennifer A. Dunne,
264 Williams, and Martinez 2002), while decreasing it in mutualistic networks (Vieira and Almeida-
265 Neto 2015), and connectance relates to network stability (Landi et al. 2018). Second, most (if not
266 all) network properties co-vary with connectance (Poisot and Gravel 2014; Jennifer A. Dunne,
267 Williams, and Martinez 2002). We have models to estimate species richness over space (Jen-
268 kins, Pimm, and Joppa 2013), and because we can predict connectance from species richness,
269 (MacDonald, Banville, and Poisot 2020), we can then derive distributions of network properties

270 from estimates of richness alone. Therefore we suggest that predicting the value of network con-
271 nectance across space (and eventually time) is most likely to be the most practical to formulate
272 at the moment.

273 **How do we predict how species that have never co-occurred will interact?**

274 The probability of an interaction occurring depends on the likelihood of co-occurrence in space
275 and time (Poisot, Stouffer, and Gravel 2015; Pichler et al. 2020). Given two species co-occur,
276 a neutral approach to probabilistic interactions would assume that the effect of abundances and
277 trait matching would have no effect (E. Canard et al. 2012). However, functional-trait based
278 proxies could enable better predictions of ecological interactions. Selection on functional traits
279 could cause interactions to be conserved at some evolutionary scales, and therefore predictions
280 of interaction could be informed by phylogenetic analyses. (Elmasri et al. 2020; Gómez, Verdú,
281 and Perfectti 2010). Phylogenetic matching in bipartite networks is consistent across scales
282 (Poisot and Stouffer 2018), even absent strong selective pressure (Coelho, Rodrigues, and Rangel
283 2017).

284 A separate family of methods are based on network embedding (as in the proof-of-concept). A
285 network embedding projects each node of the network into a lower-dimensional latent space.
286 This enables us to represent the structure of a network, which previously required the S^2 dimen-
287 sions of an adjacency matrix, with a smaller number of dimensions. The position of each node
288 in this lower dimensional space is then treated as a latent measurement corresponding to the role
289 of that species in the network (Becker et al. 2020). Species close together in the latent space
290 should interact with similar set of species (Rossberg et al. 2006; Rohr et al. 2010). However,
291 these models are sensitive to sampling biases as they are limited to species for which there is
292 already interaction data (Becker et al. 2020).

293 **What is an interaction, really?**

294 Interactions between species can be conceptualized in a multitude of ways (mutualistic vs. antag-
295 onistic, strong vs. weak, symmetric vs. asymmetric, direct vs. indirect) (Jordano 2016a; Morales-

296 Castilla et al. 2015). What is common to all definitions of interaction is that *at least* one of the
297 species is affected by the presence of another, either positively or negatively (Morales-Castilla et
298 al. 2015). Networks can be used to represent a variety of interaction types, including: *unipartite*
299 *networks*, where each species can be linked to any other species, species (these are typically used
300 to represent food webs), *bipartite networks* where there are two pools of species, and all interac-
301 tions occur between species in each pool, are typically used for pairwise interactions (e.g. hosts
302 and parasites), and *k-partite networks*; which serve as a way to expand to more than two dis-
303 crete sets of interacting species (e.g. parasitoid webs, seed dispersal networks, and pollination
304 networks) (Pocock, Evans, and Memmott 2012).

305 **What about interaction strength?**

306 Species interaction networks can also be used as means to quantify and understand *interaction*
307 *strength*. Interaction strength, unlike the qualitative presence or absence of an interaction, is a
308 continuous measurement which attempts to quantify the effect of one species on another. In-
309 teraction strength can generally be divided into two main categories (as suggested by Berlow
310 et al. (2004)): either the strength of an interaction between individuals of each species, or the
311 effect that changes in one species population has on the dynamics of the other species. Further,
312 it can be measured either as the direct effect of one species on another over a period of time
313 (often in the units of biomass) or the relative importance of one species on another (Heleno
314 et al. 2014; Berlow et al. 2004; Wootton and Emmerson 2005). One recurring observation
315 throughout studies of interaction strengths is that networks are often composed of many weak
316 links and few strong links (Berlow et al. 2004). The distribution of interaction strength within
317 a network informs on its stability (Neutel 2002; Ruiter, Neutel, and Moore 1995), influences
318 on the ecosystem functioning (Duffy 2002; Montoya, Rodríguez, and Hawkins 2003) and our
319 potential to improve multispecies models (Wootton and Emmerson 2005). Seeing interaction
320 strength within a network as energy fluxes could also possibly lead to its integration within
321 the Biodiversity-Ecosystem Functioning (BEF) framework, which could in return further im-
322 prove even our understanding of community dynamics and ecosystem functioning (Barnes et al.
323 2018a).

324 **How are interaction strengths actually estimated?**

325 Before we attempt to make inferences from data, we must adapt a conceptual framework to model
326 interaction strength. One such framework is functional foraging (Portalier et al. 2019), where
327 the primary basis for inferring interaction is based on an organism's traits, the environment, and
328 foraging behavior like searching, capture and handling times. A different conceptual alternative,
329 applicable in food-webs, is metabolic based models, where body mass, metabolic demands, and
330 energy loss are used to infer energetic energy fluxes between organisms (Yodzis and Innes 1992;
331 Berlow et al. 2009). Energy can be seen as the common currency that links every level of biology
332 from individual organisms to the whole ecosystem (Brown et al. 2004; Barnes et al. 2018b).
333 A (metabolically) bottom-up approach first estimates basal species biomasses and compute the
334 higher trophic-level species biomasses and energetic demands from there (Berlow et al. 2009).
335 Alternatively, a metabolically top-down approach computes energy fluxes starting from the top
336 consumer downward toward producers (Barnes et al. 2018a). Food-web energetics models can
337 be incorporated at various resolutions for a specific network, ranging from individual-based data
338 to more lumped data at the species level or trophic group, depending on data availability (Barnes
339 et al. 2018a).

340 **What about indirect and higher-order interactions?**

341 Although network ecology often assumes that interactions go strictly from one node to the other,
342 the web of life is made up of a variety of interactions. Indirect interactions—either higher-order
343 interactions between species, or interaction strengths that themselves interact — has gained in-
344 terest in recent years (Golubski et al. 2016; Golubski and Abrams 2011). One mathematical tool
345 to describe these situations is hypergraphs: hypergraphs are the generalization of a graph, al-
346 lowing a broad yet manageable approach to complex interactions (Carletti, Fanelli, and Nicoletti
347 2020), allowing for particular interactions to occur beyond a pair of nodes. An additional degree
348 of complexity is introduced by multi-layer networks (Hutchinson et al. 2019). Multi-layer net-
349 works include edges across “variants” of the networks (timepoints, locations, or environments).
350 These can be particularly useful to account for the metacommunity structure (Gross et al. 2020),
351 or to understand how dispersal can inform conservation action (Albert et al. 2017). Ecological

352 networks are intrinsically multi-layered (Pilosof et al. 2017). *Prima facie*, increasing the di-
353 mensionality of the object we need to predict (the multiple layers rather than a single network)
354 may make the problem complicated. But multi-layer networks encode ecological constraints –
355 of dispersal, of evolution, and of niche suitability. It is worth investigating if the multi-layer
356 structure of ecological networks could improve the predictability of interactions, as in social
357 networks (Jalili et al. 2017; Najari et al. 2019; Yasami and Safaei 2018).

358 **How do we determine what interaction networks are feasible?**

359 For several decades, ecologists have aimed to understand how networks of many interacting
360 species persist through time. The diversity-stability paradox, first explored by May (1974),
361 shows that under a neutral set of assumptions, ecological networks should become decreasingly
362 stable as the number of species increases. However, in the natural world we observe networks
363 of interactions that consist of far more species than May’s model predicts (Albouy et al. 2019).
364 As a result, understanding what aspects of the neutral assumptions of May’s model are incorrect
365 has branched many investigations into the relationship between ecological network structure and
366 persistence (Allesina and Tang 2012). These assumptions can be split into dynamical assump-
367 tions and topological assumptions.

368 Topologically, we know that ecological networks are not structured randomly. Some properties,
369 like the aforementioned connectance, are highly predictable (MacDonald, Banville, and Poisot
370 2020). Various generative models of food-webs have been shown to fit empirical networks more
371 effectively than random models. These typically rely on network embeddings, where each node
372 (species) in the network is assigned a value in a latent space, and the resulting network topology
373 is generated stochastically based on properties of the position of nodes in that latent space. Gen-
374 erative network models have long used allometry as a single-dimensional latent space—naturally
375 we want to extend this to traits in general (Allesina, Alonso, and Pascual 2008). The second ap-
376 proach to understand stability is through *dynamics*. Early models of community dynamics rely
377 on the assumption of linear interaction effects. However, models of bioenergetic community
378 dynamics have shown promise in basing our understanding of dynamics in food-webs, where
379 the functional response of one species on another is grounded in the understood relationship

380 between allometry and metabolism (Delmas et al. 2017). An additional consideration is the
381 multidimensional nature of “stability” and “feasibility” (e.g resilience to environmental change
382 vs extinctions) (Domínguez-García, Dakos, and Kéfi 2019) and how different disturbances prop-
383 agate across levels of biological organization (Kéfi et al. 2019; Gravel, Massol, and Leibold
384 2016).

385 Space

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

390 How much do networks vary over space?

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

406 **How do we predict what the species pool at a particular location is?**

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

421 The next step is to constrain distribution predictions using network properties. This would
422 also build on previous calls to adopt a probabilistic view: there have been calls for a proba-
423 bilistic species pool (Karger et al. 2016), and more importantly including interactions through
424 Bayesian networks and propagating conditional dependencies has generated better range pre-
425 dictions (Staniczenko et al. 2017). Blanchet, Cazelles, and Gravel (2020) argue that the proba-
426 bilistic view avoids confusion between interactions and co-occurrences, but that it requires prior
427 knowledge of interactions. This could potentially be solved through our framework of predicting
428 networks first, interactions next, and finally the realized species pool.

429 **How do we combine spatial and network predictions?**

430 In order to predict networks across space, we need to combine multiple models—one which
431 predicts what the species pool will be at a given location, and one to predict what interaction
432 networks composed from this species pool are likely (see fig. 2). Both of these models contain

433 uncertainty, and when we combine them our uncertainty from each to propagate into the com-
434 bined model. The Bayesian paradigm provides a convenient solution to this—if we have a chain
435 of models where each model feeds into the next, we can sample from the posterior of the input
436 models. A different approach is *ensemble modeling* which combines the predictions made by
437 several models, where each model is predicting the same thing (Parker 2013). Error propagation,
438 an important step in building any ecological model, describes the effect of the uncertainty
439 of input variables on the uncertainty of output variables (Draper 1995; Parysow, Gertner, and
440 Westervelt 2000). Benke et al. (2018) identifies two broad approaches to model error propa-
441 gation: analytically using differential equations or stochastically using Monte-Carlo simulation
442 methods. Errors induced by the spatial or temporal extrapolation of data also need to be taken
443 into account when estimating the uncertainty of a model’s output (Peters and Herrick 2004).

444 **What is the spatial scale suitable for the prediction of species interactions?**

445 As described above, we can use different trait-based proxies to predict potential interactions.
446 The choice of such proxies should be theoretically linked to the spatial scale we are using in our
447 prediction (Wiens 1989). At some scales we can use morphological traits of co-occurring species
448 to assess the probability of interaction between them (Bartomeus et al. 2016). This translates to
449 a spatial extent that does not necessarily capture the entire distribution of a given set of species,
450 with a resolution that is sufficient to capture the phenotypical variability of the species. At some
451 scales, we can infer interactions through the phylogenetic similarity between species, assuming
452 their functional traits are themselves conserved (Gómez, Verdú, and Perfectti 2010). On
453 evolutionary scales where the niche is conserved, we can think of the probability that one species
454 will interact with another as the distance between them in niche-space (Desjardins-Proulx et al.
455 2017). At the smallest scales, we may be interested in predicting behavioral traits like foraging
456 behavior (Bartomeus et al. 2016). At this point, the spatial resolution in this case should be fine
457 enough that a model may be precise in a given system, but much less generalizable. At this
458 scale it is also important to consider abundance’s effect on probability of an encounter (Wells
459 and O’Hara 2013).

460 **Time**

461 **Why should we forecast species interaction networks?**

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

477 Forecasting how climate change will alter biodiversity is also crucial for maximizing conserva-
478 tion outcomes. Improving SDMs through interactions is crucial for conservation, as nearly 30%
479 of models in SDM studies are used to assess population declines or landscape ability to support
480 populations (M. B. Araújo et al. 2019). Reliable predictions about how ecological networks
481 will change over time will give us critical information that could be communicated to decision-
482 makers and the scientific community about what are future environmental risks awaiting and
483 how to mitigate them (Kindvater et al. 2018). Not only this, but how biodiversity is structured
484 influence the functioning of the whole ecosystem, community stability and persistence Stouf-
485 fer and Bascompte (2010). Will climate change impact the distribution of network properties
486 (e.g. connectance)? If so, which regions or species groups need special conservation efforts?
487 These overarching questions are yet to be answered (but see Albouy et al. 2013; Kortsch et al.

488 2015; Hattab et al. 2016). We believe that the path toward forecasting ecological networks pro-
489 vides useful guidelines to ultimately better predict how climate change will affect the different
490 dimensions of biodiversity and ecosystem functioning.

491 **How do we turn a predictive model into a forecasting model?**

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

503 **How can we validate a forecasting model?**

504 Often the purpose of building a forecasting model to inform *present* action (Dietze et al. 2018).
505 Yet, the nature of forecasting—trying to predict the future—is that you can only know if a fore-
506 cast is “right” once it is too late to change it. If we want to maximize the chance that reality
507 falls within a forecasting model’s predictions, there are two directions to approach this problem:
508 the first is to extend model validation techniques to a forecasting context, and the second is to
509 attempt to maximize the amount of uncertainty in the forecast without compromising its reso-
510 lution. Crossvalidation (see *How do we validate a predictive model?*) can be used to test the
511 efficacy of a forecasting model. Given a time-series of N observations, a model can iteratively
512 be trained on the first n time-points of data, and the forecasting model’s accuracy can be eval-
513 uated on the remaining time-points it hasn’t “seen” (Bishop 2006). This enables us to understand
514 both how much temporal data is required for a model to be robust, and also enables us to explore

515 the *forecasting horizon* of a process. Further, this approach can also be applied in the opposite
516 temporal direction—if we have reliable data from the past, “hindcasting” can also be used to
517 test a forecast’s robustness.

518 However, these methods inevitably bump into a hard-limitation on what is feasible for a forecast-
519 ing model. The future is uncertain. Any empirical time-series we use to validate a model was
520 collected in past conditions that may not persist into the future. Any system we wish to forecast
521 will undergo only one of many possible scenarios, yet we can only observe the realized outcome
522 of the system under the scenario that actually unfolds. It is therefore impossible to assess the
523 quality of a forecasting model in scenarios that remain hypothetical. If the goal is to maximize
524 the probability that reality will fall within the forecast’s estimates, forecasts should incorporate
525 as much uncertainty about the future scenario as possible—one way to do this is ensemble mod-
526 eling (Parker 2013). However, as we increase the amount of uncertainty we incorporate into a
527 forecasting model, the resolution of the forecast’s predictions could shrink (Lei and Whitaker
528 2017), and therefore the modeler be mindful of the trade-off between resolution and accuracy
529 where developing any forecast.

530 Conclusion: why should we predict species interaction networks?

531 Because we almost can, and because we definitely should. A better understanding of species
532 interactions, and the networks they form, would help unify the fields of community, network,
533 and spatial ecology; improve the quantification of the functional relationships between species
534 (Dehling and Stouffer 2018; O’Connor et al. 2020); re-evaluate metacommunities in light of
535 network structure (Guzman et al. 2019); and enable a new line of research into the biogeog-
536 raphy of species interactions (Massol et al. 2017; Braga et al. 2019) which incorporates a
537 synthesis of both Eltonian and Grinnellian niche (Gravel et al. 2019). Further, the ability to re-
538 liably predict and forecast species interactions would inform conservation efforts for protecting
539 species, communities, and ecosystems. Integration of species interactions into the assessment of
540 vulnerability to climate change is a needed methodological advance (Foden and Young 2016).
541 International panels draw on models to establish scientific consensus (M. B. Araújo et al. 2019),

542 and they can be improved through more effective prediction of species distributions and inter-
543 actions (Syfert et al. 2014). Further, recent studies argue for a shift in focus from species to
544 interaction networks for biodiversity conservation to better ecosystem processes (Harvey et al.
545 2017).

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

563 But the tools to which we feed these data, incomplete as they may be, are gradually getting bet-
564 ter; that is, they can do predictions faster, they handle uncertainty and propagate it well, and
565 they can accomodate data volumes than are lower than we may expect (Pichler et al. 2020). It is
566 clear attempting to predict the structure of ecological networks at any scale is a methodological
567 and ecological challenge; yet it will result in qualitative changes in our understanding of com-
568 plex adaptive systems, as well as changes to our ability to leverage information about network
569 structure for conservation decision. It is perhaps even more important to forecast the structure
570 of ecological networks because it is commonly neglected as a facet of biodiversity that can (and

571 should) be managed. In fact, none of the Aichi targets mention biostructure or its protection, de-
572 spite this being recognized as an important task (McCann 2007), either implicitly or explicitly.
573 Being able to generate reliable datasets on networks in space or time will make this information
574 more actionable.

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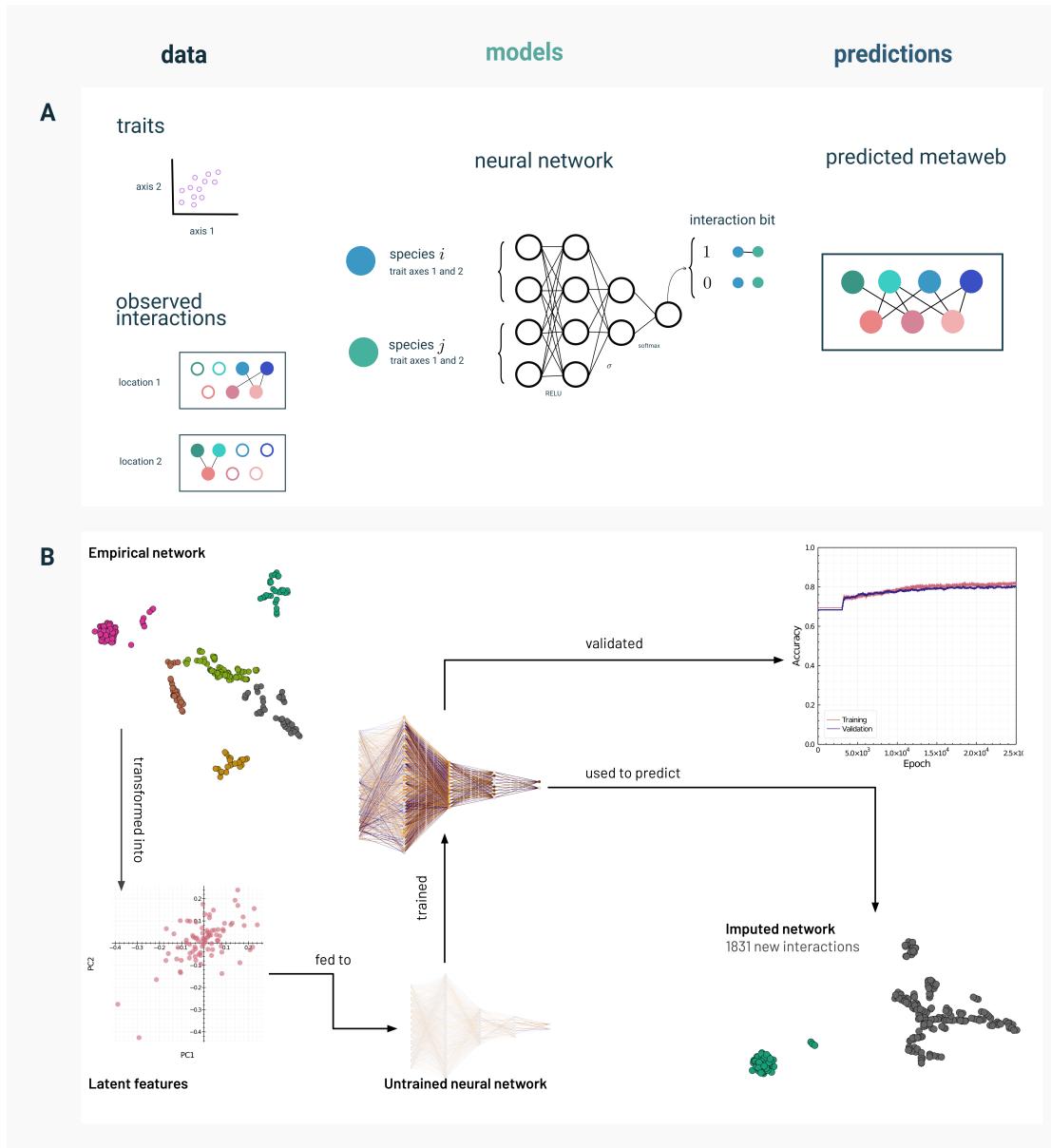


Figure 1: (A) A conceptual overview of the process of network prediction. Beginning with data of observed interaction between species, we aim to predict the metaweb of interaction across the entire species pool, even those that have not been observed together. (B) Proof-of-Concept: An empirical network (from Hadfield et al. 2014) is converted into 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.

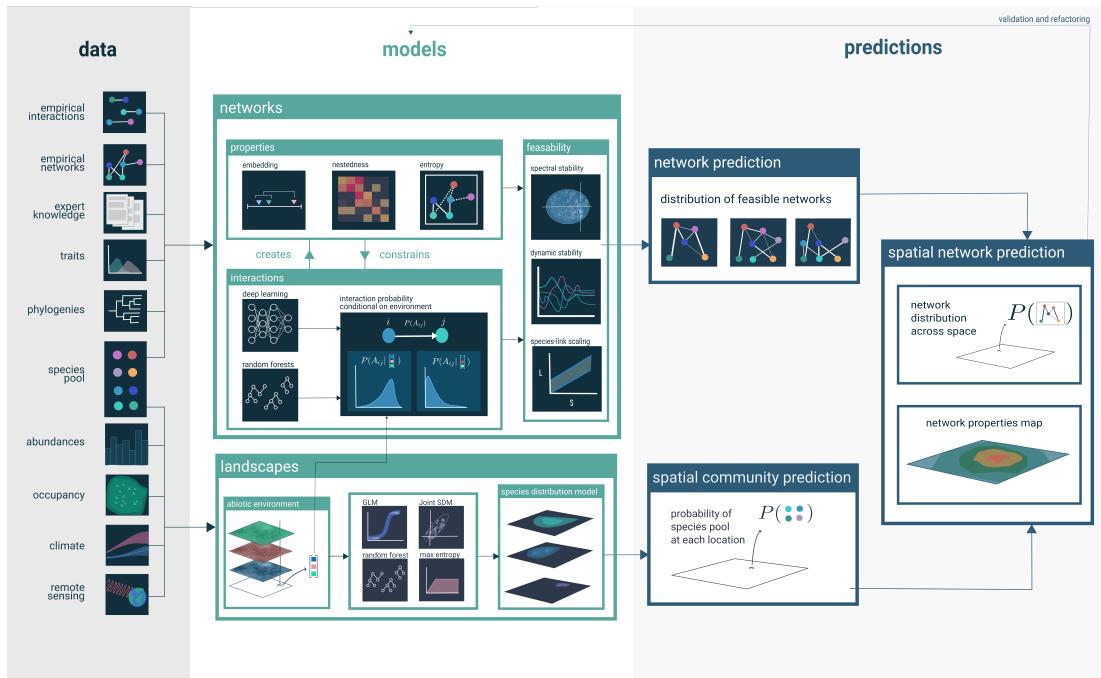


Figure 2: A conceptual roadmap highlighting key areas for the prediction of ecological networks. Starting with the input of data from multiple sources, followed by a modelling framework for ecological networks and the landscape, which are then ultimately combined to allow for the prediction of spatially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

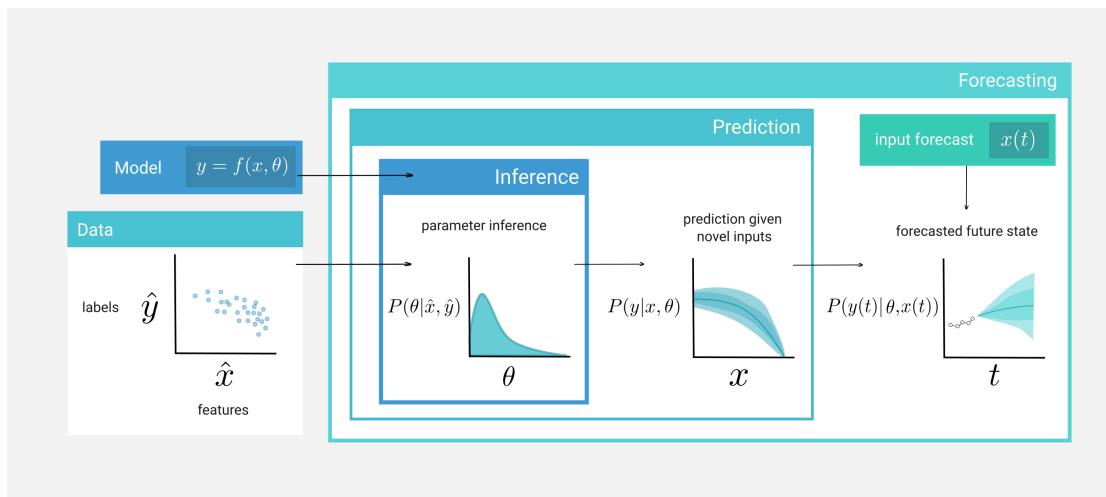


Figure 3: The nested nature of developing predictive and forecasting models, showcases the *forward problem* and how this relies on a hierarchical structure of the modelling process.