

Food web reconstruction through phylogenetic transfer of low-rank network representation

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their importance in many ecological processes, collecting data and information on ecological interactions is an exceedingly challenging task. For this reason, large parts of the world have a data deficit when it comes to species interactions, and how the resulting networks are structured. As data collection alone is unlikely to be sufficient, community ecologists must adopt predictive methods. present a methodological framework that uses graph embedding and transfer learning to assemble a predicted list of trophic interactions of a species pool for which their interactions are unknown. Specifically, we ‘learn’ the information from a known interaction network by inferring the latent traits of species and infer the latent traits of a species pool for which we have no *a priori* interaction data based on their phylogenetic relatedness to species from the known network. The latent traits can then be used to predict interactions and construct an interaction network. we assembled a metaweb for Canadian mammals derived from interactions in the European food web, despite only 4% of common species being shared between the two locations. The results of the predictive model are compared against databases of recorded pairwise interactions, showing that we correctly recover 91% of known interactions. framework itself is robust even when the known network is incomplete or contains spurious interactions making it an ideal candidate as a tool for filling gaps when it comes to species interactions. We provide guidance on how this framework can be adapted by substituting some approaches or predictors in order to make it more generally applicable.

1 Introduction

2 There are two core challenges we are faced with in furthering our understanding of ecological networks
3 across space, particularly at macro-ecologically relevant scales (e.g. Trøjelsgaard & Olesen, 2016). First,
4 ecological networks within a location are difficult to sample properly (Jordano, 2016a, 2016b), resulting in
5 a widespread “Eltonian shortfall” (Hortal et al., 2015), *i.e.* a lack of knowledge about inter- and intra-
6 specific relationships. This first challenge has been, in large part, addressed by the recent emergence of a
7 suite of methods aiming to predict interactions within *existing* networks, many of which are reviewed in
8 Strydom, Catchen, et al. (2021). Second, recent analyses based on collected data (Poisot, Bergeron, et al.,
9 2021) or metadata (Cameron et al., 2019) highlight that ecological networks are currently studied in a
10 biased subset of space and bioclimates, which impedes our ability to generalize any local understanding of
11 network structure. Meaning that, although the framework to address incompleteness *within* networks
12 exists, there would still be regions for which, due to a *lack* of local interaction data, we are unable to infer
13 potential species interactions. Having a general solution for inferring *potential* interactions (despite the
14 unavailability of interaction data) could be the catalyst for significant breakthroughs in our ability to start
15 thinking about species interaction networks over large spatial scales. In a recent overview of the field of
16 ecological network prediction, Strydom, Catchen, et al. (2021) identified two challenges of interest to the
17 prediction of interactions at large scales. First, there is a relative scarcity of relevant data in most places
18 globally – paradoxically, this restricts our ability to infer interactions to locations where inference is
19 perhaps the least required; second, accurate predictions often demand accurate predictors, and the lack of
20 methods that can leverage small amount of data is a serious impediment to our predictive ability globally.

21 Here, we present a general method to recommend potential trophic interactions, relying on the transfer
22 learning of network representations, specifically by using similarities of species in a
23 biologically/ecologically relevant proxy space (e.g. shared morphology or ancestry). Transfer learning is a
24 machine learning methodology that uses the knowledge gained from solving one problem and applying it
25 to a related (destination) problem (Pan & Yang, 2010; Torrey & Shavlik, 2010). In this instance, we solve
26 the problem of predicting trophic interactions between species, based on knowledge extracted from
27 another species pool for which interactions are known by using phylogenetic structure as a medium for
28 transfer. There is a plurality of measures of species similarities that can be used for inferring *potential*
29 species interactions *i.e.* metaweb reconstruction (see *e.g.* Morales-Castilla et al., 2015); however,

30 phylogenetic proximity has several desirable properties when working at large scales. Gerhold et al. (2015)
31 made the point that phylogenetic signal captures diversification of characters (large macro-evolutionary
32 process), but not necessarily community assembly (fine ecological process); Dormann et al. (2010)
33 previously found very similar conclusions. Interactions tend to reflect a phylogenetic signal because they
34 have a conserved pattern of evolutionary convergence that encompasses a wide range of ecological and
35 evolutionary mechanisms (Cavender-Bares et al., 2009; Mouquet et al., 2012), and - most importantly -
36 retain this signal even when it is not detectable at the community scale (Hutchinson et al., 2017; Poisot &
37 Stouffer, 2018). Finally, species interactions at macro-ecological scales seem to respond mostly to
38 macro-evolutionary processes (Price, 2003); which is evidenced by the presence of conserved backbones in
39 food webs (Dalla Riva & Stouffer, 2016; Mora et al., 2018), strong evolutionary signature on prey choice
40 (Stouffer et al., 2012), and strong phylogenetic signature in food web intervalty (Eklöf & Stouffer, 2016).
41 Phylogenetic reconstruction has also previously been used within the context of ecological networks,
42 namely understanding ancestral plant-insect interactions (Braga et al., 2021). Taken together, these
43 considerations suggest that phylogenies can reliably be used to transfer knowledge on species interactions.

44 [Figure 1 about here.]

45 Our methodology is outlined in fig. 1, where we provide an illustration based on learning the embedding
46 of a metaweb of trophic interactions for European mammals (known interactions; Maiorano et al., 2020a,
47 2020b) and, based on phylogenetic relationships between mammals globally (*i.e.*, phylogenetic tree
48 Upham et al., 2019), infer a metaweb for the Canadian mammalian species pool (interactions are treated
49 as unknown in this instance). Following the definition of Dunne (2006), a metaweb is a network analogue
50 to the regional species pool; specifically, it is an inventory of all *potential* interactions between species from
51 a spatially delimited area (and so captures the γ diversity of interactions). The metaweb is, therefore, *not* a
52 prediction of the food web at a specific locale within the spatial area it covers, and will have a different
53 structure (notably by having a larger connectance; see *e.g.* Wood et al., 2015). These local food webs
54 (which captures the α diversity of interactions) are a subset of the metaweb's species and interactions, and
55 have been called "metaweb realizations" (Poisot et al., 2015). Differences between local food web and their
56 metaweb are due to chance, species abundance and co-occurrence, local environmental conditions, and
57 local distribution of functional traits, among others.
58 Because the metaweb represents the joint effect of functional, phylogenetic, and macroecological

59 processes (Morales-Castilla et al., 2015), it holds valuable ecological information. Specifically, it is the
60 “upper bounds” on what the composition of the local networks can be (see e.g. McLeod et al., 2021). These
61 local networks, in turn, can be reconstructed given appropriate knowledge of local species composition,
62 providing information on structure of food webs at finer spatial scales. This has been done for example for
63 tree-galler-parasitoid systems (Gravel et al., 2018), fish trophic interactions (Albouy et al., 2019), tetrapod
64 trophic interactions (O’Connor et al., 2020), and crop-pest networks (Grünig et al., 2020). Whereas the
65 original metaweb definition, and indeed most past uses of metawebs, was based on the presence/absence
66 of interactions, we focus on *probabilistic* metawebs where interactions are represented as the chance of
67 success of a Bernoulli trial (see e.g. Poisot et al., 2016); therefore, not only does our method recommend
68 interactions that may exist, it gives each interaction a score, allowing us to properly weigh them.

69 Our case study shows that phylogenetic transfer learning is an effective approach to the generation of
70 probabilistic metawebs. This showcases that although the components (species) that make up the
71 Canadian and European communities may be *minimally* shared (the overall species overlap is less than
72 4%), if the medium (proxy space) selected in the transfer step is biologically plausible, we can still
73 effectively learn from the known network and make biologically relevant predictions of interactions.

74 Indeed, as we detail in the results, when validated against known but fractional data of trophic
75 interactions between Canadian mammals, our model achieves a predictive accuracy of approximately 91%.
76 It should be reiterated that the framework presented in fig. 1 is amenable to changes; notably, the measure
77 of similarity may not be phylogeny, and can be replaced by information on foraging (Beckerman et al.,
78 2006), cell-level mechanisms (Boeckaerts et al., 2021), or a combination of traits and phylogenetic
79 structure (Stock, 2021). Most importantly, although we focus on a trophic system, it is an established fact
80 that different (non-trophic) interactions do themselves interact with and influence the outcome of trophic
81 interactions (see e.g. Kawatsu et al., 2021; Kéfi et al., 2012). Future development of metaweb inference
82 techniques should cover the prediction of multiple interaction types.

83 Data used for the case study

84 We use data from the European metaweb assembled by Maiorano et al. (2020a). This was assembled using
85 data extracted from scientific literature (including published papers, books, and grey literature) from the
86 last 50 years and includes all terrestrial tetrapods (mammals, breeding birds, reptiles and amphibians)

87 occurring on the European sub-continent (and Turkey) - with the caveat that only species introduced in
88 historical times and currently naturalized being included. This metaweb itself is a network of binary (*i.e.*
89 presence/absence), potential two-way interactions between species pairs.

90 We filtered down the European metaweb to create a subgraph corresponding to all mammals by matching
91 species names in the original network to the Global Biodiversity Information Facility (GBIF) taxonomic
92 backbone (GBIF Secretariat, 2021) and retaining all those who matched to mammals. This serves a dual
93 purpose 1) to extract only mammals from the European network and 2) to match and standardize species
94 names when aggregating the different data sources further downstream (which is an important
95 consideration when combining datasets (Grenié et al., 2021)). All nodes had valid matches to GBIF at this
96 step, and so this backbone is used for all name reconciliation steps as outlined below.

97 The European metaweb represents the knowledge we want to learn and transfer; the phylogenetic
98 similarity of mammals here represents the information for transfer (*i.e.* the transfer medium). We used the
99 mammalian consensus supertree by Upham et al. (2019), for which all approximatively 6000 names have
100 been similarly matched to their GBIF valid names. This step allows us to place each node of the
101 mammalian European metaweb in the phylogeny.

102 The destination problem to which we want to transfer knowledge is the trophic interactions between
103 mammals in Canada. We obtained the list of extant species from the International Union for Conservation
104 of Nature (IUCN) checklist, and selected the terrestrial and semi-aquatic species (this corresponds to the
105 same selection that was applied by Maiorano et al. (2020a) in the European metaweb). The IUCN names
106 were, as previously, reconciled against GBIF to have an exact match to the taxonomy.

107 After taxonomic cleaning and reconciliation as outlined in the following sections, the mammalian
108 European metaweb has 260 species, and the Canadian species pool has 163; of these, 17 (about 4% of the
109 total) are shared, and 89 species from Canada (54%) had at least one congeneric species in Europe. The
110 similarity for both species pools predictably increases with higher taxonomic order, with 19% of shared
111 genera, 47% of shared families, and 75% of shared orders; for the last point, Canada and Europe each had a
112 single unique order (*Didelphimorphia* for Canada, *Erinaceomorpha* for Europe).

113 In the following sections, we describe the representational learning step applied to European data, the
114 transfer step through phylogenetic similarity, and the generation of a probabilistic metaweb for the
115 destination species pool.

116 **Method description**

117 The core point of our method is the transfer of knowledge of a known ecological network, in order to
118 predict interactions between species from another location at which the network is unknown (or partially
119 known). In fig. 1, we give a high-level overview of the approach; in the example around which this
120 manuscript is built (leveraging detailed knowledge about binary trophic interactions between Mammalia
121 in Europe to predict the less known trophic interactions between closely phylogenetically related
122 Mammalia in Canada), we use a series of specific steps for network embedding, trait inference, network
123 prediction and thresholding.

124 Specifically, our approach can be summarized as follows: from the known network in Europe, we use a
125 truncated Singular Value Decomposition (t-SVD; Halko et al., 2011) to generate latent traits representing a
126 low-dimensional embedding of the network. As an aside, most ecologists are indirectly familiar with SVD:
127 Principal Component Analysis is a special case of SVD, which is more sensitive to numerical instabilities
128 (see notably Shlens, 2014). The latent traits give an unbiased estimate of the node's position in the latent
129 feature spaces and can be mapped onto a reference phylogeny (other distance-based measures of species
130 proximity that allow for the inference of features in the latent space can be used, for example the
131 dissimilarity in functional traits). Based on the reconstructed latent traits for species in the destination
132 species pool, a Random Dot Product Graph model (hereafter RDPG; S. J. Young & Scheinerman, 2007)
133 predicts the interaction between species through a function of the nodes' features through matrix
134 multiplication. Thus, from latent traits and node position, we can infer interactions.

135 The method we develop is, ecologically speaking, a “black box,” *i.e.* an algorithm that can be understood
136 mathematically, but whose component parts are not always directly tied to ecological processes. There is a
137 growing realization in machine learning that (unintentional) black box algorithms are not necessarily a
138 bad thing (Holm, 2019), as long as their constituent parts can be examined (which is the case with our
139 method). But more importantly, data hold more information than we might think; as such, even
140 algorithms that are disconnected from the model can make correct guesses most of the time (Halevy et al.,
141 2009); in fact, in an instance of ecological forecasting of spatio-temporal systems, model-free approaches
142 (*i.e.* drawing all of their information from the data) outperformed model-informed ones (Perretti et al.,
143 2013).

144 **Implementation and code availability**

145 The entire pipeline is implemented in *Julia* 1.6 (Bezanson et al., 2017) and is available under the
146 permissive MIT License at <https://osf.io/2zwqm/>. The taxonomic cleanup steps are done using GBIF.jl
147 (Dansereau & Poisot, 2021). The network embedding and analysis is done using EcologicalNetworks.jl
148 (Banville et al., 2021; Poisot et al., 2019). The phylogenetic simulations are done using PhyloNetworks.jl
149 (Solís-Lemus et al., 2017) and Phylo.jl (Reeve et al., 2016). A complete Project.toml file specifying the
150 full tree of dependencies is available alongside the code. This material also includes a fully annotated copy
151 of the entire code required to run this project (describing both the intent of the code and discussing some
152 technical implementation details), a vignette for every step of the process, and a series of Jupyter
153 notebooks with the text and code. The pipeline can be executed on a laptop in a matter of minutes, and
154 therefore does not require extensive computational power.

155 **Step 1: Learning the origin network representation**

156 The first step in transfer learning is to learn the structure of the original dataset. In order to do so, we rely
157 on an approach inspired from representational learning, where we learn a *representation* of the metaweb
158 (in the form of the latent subspaces), rather than a list of interactions (species *a* eats *b*). This approach is
159 conceptually different from other metaweb-scale predictions (e.g. Albouy et al., 2019), in that the metaweb
160 representation is easily transferable. Specifically, we use RDPG to create a number of latent variables that
161 can be combined into an approximation of the network adjacency matrix. RDPG results are known to
162 have strong phylogenetic signal, and to capture the evolutionary backbone of food webs (Dalla Riva &
163 Stouffer, 2016); in other words, the latent variables of an RDPG can be mapped onto a phylogenetic tree,
164 and phylogenetically similar predators should share phylogenetically similar preys. In addition, recent
165 advances show that the latent variables produced this way can be used to predict *de novo* network edges.
166 Interestingly, the latent variables do not need to be produced by decomposing the network itself; in a
167 recent contribution, Runghen et al. (2021) showed that deep artificial neural networks are able to
168 reconstruct the left and right subspaces of an RDPG, in order to predict human movement networks from
169 individual/location metadata. This is an exciting opportunity, as it opens up the possibility of using
170 additional metadata as predictors.

171 The latent variables are created by performing a truncated Singular Value Decomposition (t-SVD) on the

172 adjacency matrix. SVD is an appropriate embedding of ecological networks, which has recently been
173 shown to both capture their complex, emerging properties (Strydom, Dalla Riva, et al., 2021) and to allow
174 highly accurate prediction of the interactions within a single network (Poisot, Ouellet, et al., 2021). Under
175 SVD, an adjacency matrix \mathbf{A} (where $\mathbf{A}_{m,n} \in \mathbb{B}$ where 1 indicates predation and 0 an absence thereof) is
176 decomposed into three components resulting in $\mathbf{A} = \mathbf{U}\Sigma\mathbf{V}'$. Here, Σ is a $m \times n$ diagonal matrix and
177 contains only singular (σ) values along its diagonal, \mathbf{U} is a $m \times m$ unitary matrix, and \mathbf{V}' a $n \times n$ unitary
178 matrix. Truncating the SVD removes additional noise in the dataset by omitting non-zero and/or smaller
179 σ values from Σ using the rank of the matrix. Under a t-SVD $\mathbf{A}_{m,n}$ is decomposed so that Σ is a square $r \times r$
180 diagonal matrix (whith $1 \leq r \leq r_{full}$ where r_{full} is the full rank of \mathbf{A} and r the rank at which we truncate
181 the matrix) containing only non-zero σ values. Additionally, \mathbf{U} is now a $m \times r$ semi unitary matrix and \mathbf{V}'
182 a $n \times r$ semi-unitary matrix.

183 The specific rank at which the SVD ought to be truncated is a difficult question. The purpose of SVD is to
184 remove the noise (expressed at high dimensions) and to focus on the signal, (expressed at low dimensions).
185 In datasets with a clear signal/noise demarcation, a scree plot of Σ can show a sharp drop at the rank where
186 noise starts (Zhu & Ghodsi, 2006). Because the European metaweb is almost entirely known, the amount
187 of noise (uncertainty) is low; this is reflected in fig. 2 (left), where the scree plot shows no important drop,
188 and in fig. 2 (right) where the proportion of variance explained increases smoothly at higher dimensions.
189 For this reason, we default back to a threshold that explains 60% of the variance in the underlying data,
190 corresponding to 12 dimensions - *i.e.* a tradeoff between accuracy and a reduced number of features.

191 An RDPG estimates the probability of observing interactions between nodes (species) as a function of the
192 nodes' latent variables, and is a way to turn a SVD (which decompose one matrix into three) into two
193 matrices that can be multiplied to provide an approximation of the network. The latent variables used for
194 the RDPG, called the left and right subspaces, are defined as $\mathcal{L} = \mathbf{U}\sqrt{\Sigma}$, and $\mathcal{R} = \sqrt{\Sigma}\mathbf{V}'$ – using the full
195 rank of \mathbf{A} , $\mathcal{L}\mathcal{R} = \mathbf{A}$, and using any smaller rank results in $\mathcal{L}\mathcal{R} \approx \mathbf{A}$. Using a rank of 1 for the t-SVD
196 provides a first-order approximation of the network. One advantage of using a RDPG rather than a SVD is
197 that the number of components to estimate decreases; notably, one does not have to estimate the singular
198 values of the SVD. Furthermore, the two subspaces can be directly multiplied to yield a network.

199 [Figure 2 about here.]
200 Because RDPG relies on matrix multiplication, the higher dimensions essentially serve to make specific

interactions converge towards 0 or 1; therefore, for reasonably low ranks, there is no guarantee that the values in the reconstructed network will be within the unit range. In order to determine what constitutes an appropriate threshold for probability, we performed the RDPG approach on the European metaweb, and evaluated the probability threshold by treating this as a binary classification problem, specifically assuming that both 0 and 1 in the European metaweb are all true. Given the methodological details given in Maiorano et al. (2020a) and O'Connor et al. (2020), this seems like a reasonable assumption, although one that does not hold for all metawebs. We used the thresholding approach presented in Poisot, Ouellet, et al. (2021), and picked a cutoff that maximized Youden's J statistic (a measure of the informedness (trust) of predictions; Youden (1950)); the resulting cutoff was 0.22, and gave an accuracy above 0.99. In Supp. Mat. 1, we provide several lines of evidence that using the entire network to estimate the threshold does not lead to overfitting; that using a subset of species would yield the same threshold; that decreasing the quality of the original data by adding or removing interactions would minimally affect the predictive accuracy of RDPG applied to the European metaweb; and that the networks reconstructed from artificially modified data are reconstructed with the correct ecological properties.

The left and right subspaces for the European metaweb, accompanied by the threshold for prediction, represent the knowledge we seek to transfer. In the next section, we explain how we rely on phylogenetic similarity to do so.

Steps 2 and 3: Transfer learning through phylogenetic relatedness

In order to transfer the knowledge from the European metaweb to the Canadian species pool, we performed ancestral character estimation using a Brownian motion model, which is a conservative approach in the absence of strong hypotheses about the nature of phylogenetic signal in the network decomposition (Litsios & Salamin, 2012). This uses the estimated feature vectors for the European mammals to create a state reconstruction for all species (conceptually something akin to a trait-based mammalian phylogeny using latent generality and vulnerability traits) and allows us to impute the missing (latent) trait data for the Canadian species that are not already in the European network; as we are focused on predicting contemporary interactions, we only retained the values for the tips of the tree. We assumed that all traits (*i.e.* the feature vectors for the left and right subspaces) were independent, which is a reasonable assumption as every trait/dimension added to the t-SVD has an *additive* effect to the one before it. Note that the Upham et al. (2019) tree itself has some uncertainty associated to inner nodes of

230 the phylogeny. In this case study, we have decided to not propagate this uncertainty, as it would
231 complexify the process. The Brownian motion algorithm returns the *average* value of the trait, and its
232 upper and lower bounds. Because we do not estimate other parameters of the traits' distributions, we
233 considered that every species trait is represented as a uniform distribution between these bounds. The
234 choice of the uniform distribution was made because the algorithm returns a minimum and maximum
235 point estimate for the value, and given this information, the uniform distribution is the one with
236 maximum entropy. Had all mean parameters estimates been positive, the exponential distribution would
237 have been an alternative, but this is not the case for the subspaces of an RDPG. In order to examine the
238 consequences of the choice of distribution, we estimated the variance per latent variable per node to use a
239 Normal distribution; as we show in Supp. Mat. 2, this decision results in dramatically over-estimating the
240 number and probability of interactions, and therefore we keep the discussions in the main text to the
241 uniform case. The inferred left and right subspaces for the Canadian species pool ($\hat{\mathcal{L}}$ and $\hat{\mathcal{R}}$) have entries
242 that are distributions, representing the range of values for a given species at a given dimension.

243 These objects represent the transferred knowledge, which we can use for prediction of the Canadian
244 metaweb.

245 **Step 4: Probabilistic prediction of the destination network**

246 The phylogenetic reconstruction of $\hat{\mathcal{L}}$ and $\hat{\mathcal{R}}$ has an associated uncertainty, represented by the breadth of
247 the uniform distribution associated to each of their entries. Therefore, we can use this information to
248 assemble a *probabilistic* metaweb in the sense of Poisot et al. (2016), *i.e.* in which every interaction is
249 represented as a single, independent, Bernoulli event of probability p .

250 [Figure 3 about here.]

251 Specifically, we have adopted the following approach. For every entry in $\hat{\mathcal{L}}$ and $\hat{\mathcal{R}}$, we draw a value from
252 its distribution. This results in one instance of the possible left ($\hat{\ell}$) and right (\hat{r}) subspaces for the
253 Canadian metaweb. These can be multiplied, to produce one matrix of real values. Because the entries in
254 $\hat{\ell}$ and \hat{r} are in the same space where \mathcal{L} and \mathcal{R} were originally predicted, it follows that the threshold ρ
255 estimated for the European metaweb also applies. We use this information to produce one random
256 Canadian metaweb, $N = \hat{\mathcal{L}}\hat{\mathcal{R}}' \geq \rho$. As we can see in (fig. 3), the European and Canadian metawebs are

257 structurally similar (as would be expected given the biogeographic similarities) and the two (left and right)
258 subspaces are distinct *i.e.* capturing predation (generality) and prey (vulnerability) latent traits.

259 Because the intervals around some trait values can be broad (in fact, probably broader than what they
260 would actually be, see *e.g.* Garland et al., 1999), we repeat the above process 2×10^5 times, which results in
261 a probabilistic metaweb P , where the probability of an interaction (here conveying our degree of trust that
262 it exists given the inferred trait distributions) is given by the number of times where it appears across all
263 random draws N , divided by the number of samples. An interaction with $P_{i,j} = 1$ means that these two
264 species were predicted to interact in all 2×10^5 random draws.

265 It must be noted that despite bringing in a large amount of information from the European species pool
266 and interactions, the Canadian metaweb has distinct structural properties. Following an approach similar
267 to Vermaat et al. (2009), we show in Supp. Mat. 3 that not only can we observe differences in a
268 multivariate space between the European and Canadian metaweb, we can also observe differences in the
269 same space between random subgraphs from these networks. These results line up with the studies
270 spatializing metawebs that have been discussed in the introduction: changes in the species pool are
271 driving local structural changes in the networks.

272 **Data cleanup, discovery, validation, and thresholding**

273 Once the probabilistic metaweb for Canada has been produced, we followed a number of data inflation
274 steps to finalize it. This step is external to the actual transfer learning framework but rather serves as a
275 way to augment and validate the predicted metaweb.

276 [Figure 4 about here.]

277 First, we extracted the subgraph corresponding to the 17 species shared between the European and
278 Canadian pools and replaced these interactions with a probability of 0 (non-interaction) or 1 (interaction),
279 according to their value in the European metaweb. This represents a minute modification of the inferred
280 network (about 0.8% of all species pairs from the Canadian web), but ensures that we are directly re-using
281 knowledge from Europe.

282 Second, we looked for all species in the Canadian pool known to the Global Biotic Interactions (GloBI)
283 database (Poelen et al., 2014), and extracted their known interactions. Because GloBI aggregates observed

interactions, it is not a *networks* data source, and therefore the only information we can reliably extract from it is that a species pair *was reported to interact at least once*. This last statement should yet be taken with caution, as some sources in GLoBI (e.g. Thessen & Parr, 2014) are produced through text analysis, and therefore may not document direct evidence of the interaction. Nevertheless, should the predictive model work, we would expect that a majority of interactions known to GLoBI would also be predicted. We retrieved 366 interactions between mammals from the Canadian species pool from GLoBI, 33 of which were not predicted by the model; this results in a success rate of 91%. After performing this check, we set the probability of all interactions known to GLoBI to 1.

Finally, we downloaded the data from Strong & Leroux (2014), who mined various literature sources to identify trophic interactions in Newfoundland. This dataset documented 25 interactions between mammals, only two of which were not part of our (Canada-level) predictions, resulting in a success rate of 92%. These two interactions were added to our predicted metaweb with a probability of 1. A table listing all interactions in the predicted Canadian metaweb can be found in the supplementary material.

[Figure 5 about here.]

Because the confidence intervals on the inferred trait space are probably over-estimates, we decided to apply a thresholding step to the interactions after the data inflation (fig. 5). Cirtwill & Hambäck (2021) proposed a number of strategies to threshold probabilistic networks. Their methods assume the underlying data to be tag-based sequencing, which represents interactions as co-occurrences of predator and prey within the same tags; this is conceptually identical to our Bernoulli-trial based reconstruction of a probabilistic network. We performed a full analysis of the effect of various cutoffs, and as they either resulted in removing too few interactions, or removing enough interactions that species started to be disconnected from the network, we set this threshold for a probability equivalent to 0 to the largest possible value that still allowed all species to have at least one interaction with a non-zero probability. The need for this slight deviation from the Cirtwill & Hambäck (2021) method highlights the need for additional development on network thresholding.

309 **Results and discussion of the case study**

310 In fig. 5, we examine the effect of varying the cutoff on $P(i \rightarrow j)$ on the number of links, species, and
311 connectance. Determining a cutoff using the maximum curvature, or central difference approximation of
312 the second order partial derivative, as suggested by e.g. Cirtwill & Hambäck (2021), results in species being
313 lost, or almost all links being kept. We therefore settled on the value that allowed all species to remain
314 with at least one interaction. This result, in and of itself, suggests that additional methodological
315 developments for the thresholding of probabilistic networks are required.

316 [Figure 6 about here.]

317 The t-SVD embedding is able to learn relevant ecological features for the network. fig. 6 shows that the
318 first rank correlates linearly with generality and vulnerability (Schoener, 1989), *i.e.* the number of preys
319 and predators for each species. Importantly, this implies that a rank 1 approximation represents the
320 configuration model for the metaweb, *i.e.* a set of random networks generated from a given degree
321 sequence (Park & Newman, 2004). Accounting for the probabilistic nature of the degrees, the rank 1
322 approximation also represents the *soft* configuration model (van der Hoorn et al., 2018). Both models are
323 maximum entropy graph models (Garlaschelli et al., 2018), with sharp (all network realizations satisfy the
324 specified degree sequence) and soft (network realizations satisfy the degree sequence on average) local
325 constraints, respectively. The (soft) configuration model is an unbiased random graph model widely used
326 by ecologists in the context of null hypothesis significance testing of network structure (e.g. Bascompte et
327 al., 2003) and can provide informative priors for Bayesian inference of network structure (e.g. J.-G. Young
328 et al., 2021). It is noteworthy that for this metaweb, the relevant information was extracted at the first
329 rank. Because the first rank corresponds to the leading singular value of the system, the results of fig. 6
330 have a straightforward interpretation: degree-based processes are the most important in structuring the
331 mammalian food web.

332 **Discussion**

333 One important aspect in which Europe and Canada differ (despite their comparable bioclimatic
334 conditions) is the degree of the legacy of human impacts, which have been much longer in Europe.

335 Nenzén et al. (2014) showed that even at small scales (the Iberian peninsula), mammal food webs retain
336 the signal of both climate change and human activity, even when this human activity was orders of
337 magnitude less important than it is now. Similarly, Yeakel et al. (2014) showed that changes in human
338 occupation over several centuries can lead to food web collapse. Megafauna in particular seems to be very
339 sensitive to human arrival (Pires et al., 2015). In short, there is well-substantiated support for the idea that
340 human footprint affects more than the risk of species extinction (Marco et al., 2018), and can lead to
341 changes in interaction structure. Yet, owing to the inherent plasticity of interactions, there have been
342 documented instances of food webs undergoing rapid collapse/recovery cycles over short periods of time
343 (Pedersen et al., 2017). The embedding of a network, in a sense, embeds its macro-evolutionary history,
344 especially as RDPG captures ecological signal (Dalla Riva & Stouffer, 2016); at this point, it is important to
345 recall that a metaweb is intended as a catalogue of all potential interactions, which should then be filtered
346 (Morales-Castilla et al., 2015). In practice (and in this instance) the reconstructed metaweb will predict
347 interactions that are plausible based on the species' evolutionary history, however some interactions
348 would/would not be realized due to human impact.

349 Dallas et al. (2017) suggested that most links in ecological networks may be cryptic, *i.e.* uncommon or
350 otherwise hard to observe. This argument essentially echoes Jordano (2016b): the sampling of ecological
351 interactions is difficult because it requires first the joint observation of two species, and then the
352 observation of their interaction. In addition, it is generally expected that weak or rare links would be more
353 common in networks (Csermely, 2004), compared to strong, persistent links; this is notably the case in
354 food chains, wherein many weaker links are key to the stability of a system (Neutel et al., 2002). In the
355 light of these observations, the results in fig. 4 are not particularly surprising: we expect to see a surge in
356 these low-probability interactions under a model that has a good predictive accuracy. Because the
357 predictions we generate are by design probabilistic, then one can weigh these rare links appropriately. In a
358 sense, that most ecological interactions are elusive can call for a slightly different approach to sampling:
359 once the common interactions are documented, the effort required in documenting each rare interaction
360 may increase exponentially. Recent proposals suggest that machine learning algorithms, in these
361 situations, can act as data generators (Hoffmann et al., 2019): in this perspective, high quality
362 observational data can be supplemented with synthetic data coming from predictive models, which
363 increases the volume of information available for inference. Indeed, Strydom, Catchen, et al. (2021)
364 suggested that knowing the metaweb may render the prediction of local networks easier, because it fixes

365 an “upper bound” on which interactions can exist; indeed, with a probabilistic metaweb, we can consider
366 that the metaweb represents an aggregation of informative priors on the interactions.

367 Related to the last point, Cirtwill et al. (2019) showed that network inference techniques based on
368 Bayesian approaches would perform far better in the presence of an interaction-level informative prior;
369 the desirable properties of such a prior would be that it is expressed as a probability, preferably
370 representing a Bernoulli event, the value of which would be representative of relevant biological processes
371 (probability of predation in this case). We argue that the probability returned at the very last step of our
372 framework may serve as this informative prior; indeed, the output of our analysis can be used in
373 subsequent steps, also possibly involving expert elicitation to validate some of the most strongly
374 recommended interactions. One important *caveat* to keep in mind when working with interaction
375 inference is that interactions can never really be true negatives (in the current state of our methodological
376 framework and data collection limitations); this renders the task of validating a model through the usual
377 application of binary classification statistics very difficult (although see Strydom, Catchen, et al., 2021 for a
378 discussion of alternative suggestions). The other way through which our framework can be improved is by
379 substituting the predictors that are used for transfer. For example, in the presence of information on
380 species traits that are known to be predictive of species interactions, one might want to rely on functional
381 rather than phylogenetic distances – in food webs, body size (and allometrically related variables) has
382 been established as such a variable (Brose et al., 2006); the identification of relevant functional traits is
383 facilitated by recent methodological developments (Rosado et al., 2013). It should be noted that Xing &
384 Fayle (2021) highlight phylogenetic relatedness as one of the core components of network comparison at
385 the global scale. In this case study, we have embedded the original metaweb using t-SVD, because it lends
386 itself to an RDPG reconstruction, which is known to capture the consequences of evolutionary processes
387 (Dalla Riva & Stouffer, 2016); this being said, there are other ways to embed graphs (Arsov & Mirceva,
388 2019; Cai et al., 2017; Cao et al., 2019), which can be used as alternatives.

389 As Herbert (1965) rightfully pointed out, “[y]ou can’t draw neat lines around planet-wide problems”; in
390 this regard, our approach (and indeed, any inference of a metaweb at large scales) must contend with
391 several interesting and interwoven families of problems. The first is the limit of the metaweb to embed
392 and transfer. If the initial metaweb is too narrow in scope, notably from a taxonomic point of view, the
393 chances of finding another area with enough related species to make a reliable inference decreases; this
394 would likely be indicated by large confidence intervals during ancestral character estimation, but the lack

of well documented metawebs is currently preventing the development of more concrete guidelines. The question of phylogenetic relatedness and dispersal is notably true if the metaweb is assembled in an area with mostly endemic species, and as with every predictive algorithm, there is room for the application of our best ecological judgement. Conversely, the metaweb should be reliably filled, which assumes that the S^2 interactions in a pool of S species have been examined, either through literature surveys or expert elicitation. Supp. Mat. 1 provides some guidance as to the type of sampling effort that should be prioritized. Although RDPG was able to maintain very high predictive power when interactions were missing, the addition of false positive interactions was immediately detected; this suggests that it may be appropriate to err on the side of “too many” interactions when constructing the initial metaweb to be transferred. The second series of problems are related to determining which area should be used to infer the new metaweb in, as this determines the species pool that must be used. In our application, we focused on the mammals of Canada. The upside of this approach is that information at the country level is likely to be required by policy makers and stakeholders for their biodiversity assessment, as each country tends to set goals at the national level (Buxton et al., 2021) for which quantitative instruments are designed (Turak et al., 2017), with specific strategies often enacted at smaller scales (Ray et al., 2021). And yet, we do not really have a satisfying answer to the question of “where does a food web stop”; the current most satisfying solutions involve examining the spatial consistency of network area relationships (Fortin et al., 2021; see e.g. Galiana et al., 2018, 2019, 2021), which is of course impossible in the absence of enough information about the network itself. This suggests that an *a posteriori* refinement of the results may be required, based on a downscaling of the metaweb. The final family of problems relates less to the availability of data or quantitative tools, and more to the praxis of spatial ecology. Operating under the context of national divisions, in large parts of the world, reflects nothing more than the legacy of settler colonialism. Indeed, the use of ecological data is not an apolitical act (Nost & Goldstein, 2021), as data infrastructures tend to be designed to answer questions within national boundaries, and their use both draws upon and reinforces territorial statecraft; as per Machen & Nost (2021), this is particularly true when the output of “algorithmic thinking” (e.g. relying on machine learning to generate knowledge) can be re-used for governance (e.g. enacting conservation decisions at the national scale). We therefore recognize that methods such as we propose operate under the framework that contributed to the ongoing biodiversity crisis (Adam, 2014), reinforced environmental injustice (Choudry, 2013; Domínguez & Luoma, 2020), and on Turtle Island especially, should be replaced by Indigenous principles of land

425 management (Eichhorn et al., 2019; No'kmaq et al., 2021). As we see AI/ML being increasingly mobilized
426 to generate knowledge that is lacking for conservation decisions (e.g. Lamba et al., 2019; Mosebo
427 Fernandes et al., 2020), our discussion of these tools need to go beyond the technical, and into the
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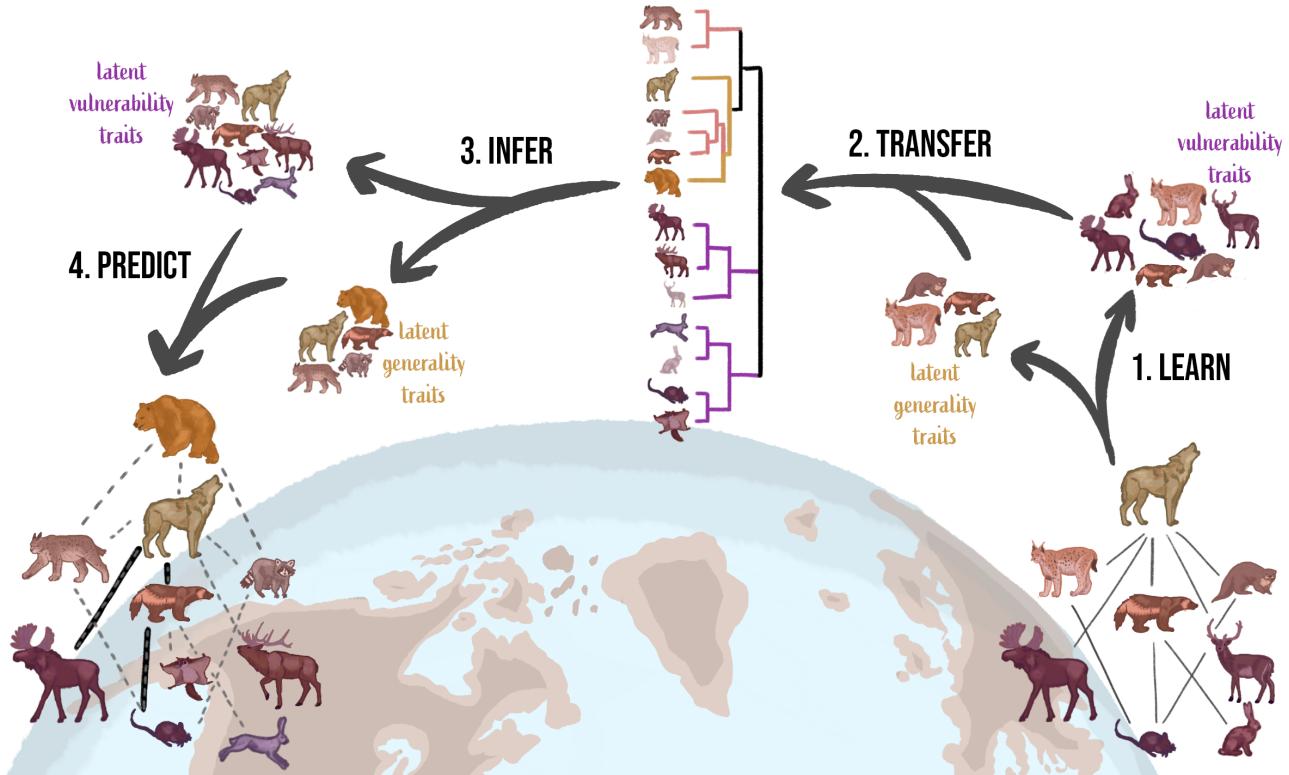


Figure 1: Overview of the phylogenetic transfer learning (and prediction) of species interaction networks. Starting from an initial, known, network, we learn its representation through a graph embedding step (here, a truncated Singular Value Decomposition; Step 1), yielding a series of latent traits (latent vulnerability traits are more representative of species at the lower trophic-level and latent generality traits are more representative of species at higher trophic-levels; *sensu* Schoener (1989)); second, for the destination species pool, we perform ancestral character estimation using a phylogeny (here, using a Brownian model for the latent traits; Step 2); we then sample from the reconstructed distribution of latent traits (Step 3) to generate a probabilistic metaweb at the destination (here, assuming a uniform distribution of traits), and threshold it to yield the final list of interactions (Step 4).

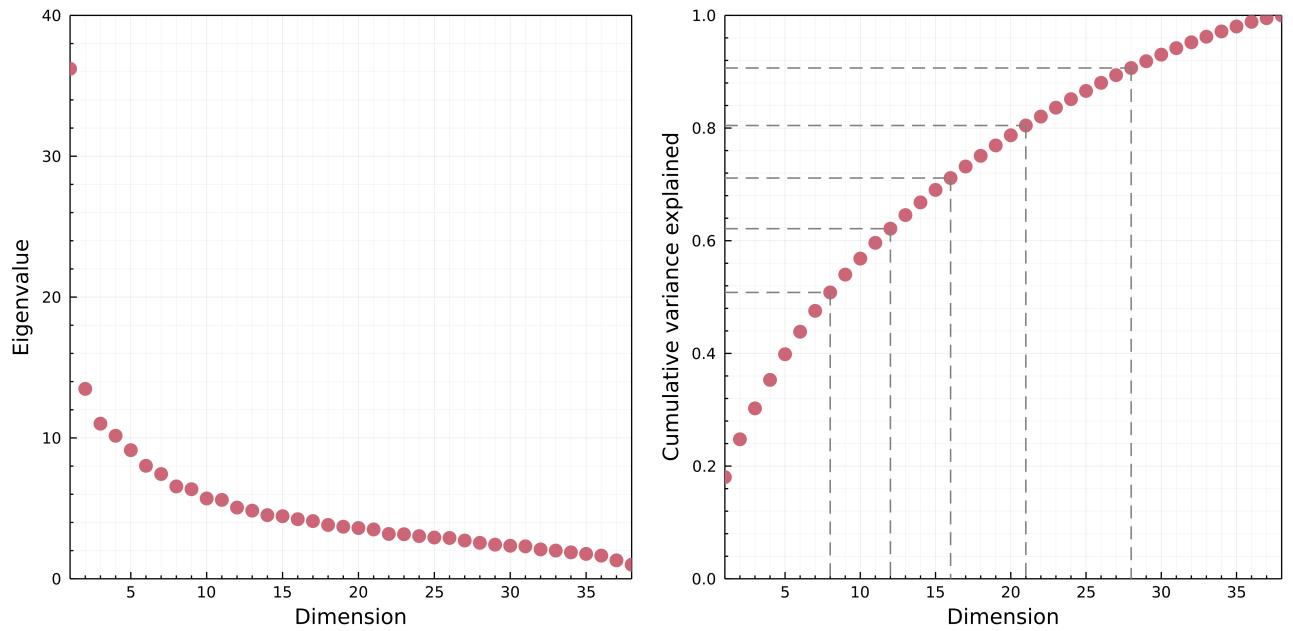


Figure 2: Left: representation of the scree plot of the singular values from the t-SVD on the European metaweb. The scree plot shows no obvious drop in the singular values that may be leveraged to automatically detect a minimal dimension for embedding, after e.g. Zhu & Ghodsi (2006). Right: cumulative fraction of variance explained by each dimension up to the rank of the European metaweb. The grey lines represent cutoffs at 50, 60, ..., 90% of variance explained. For the rest of the analysis, we reverted to an arbitrary threshold of 60% of variance explained, which represented a good tradeoff between accuracy and reduced number of features.

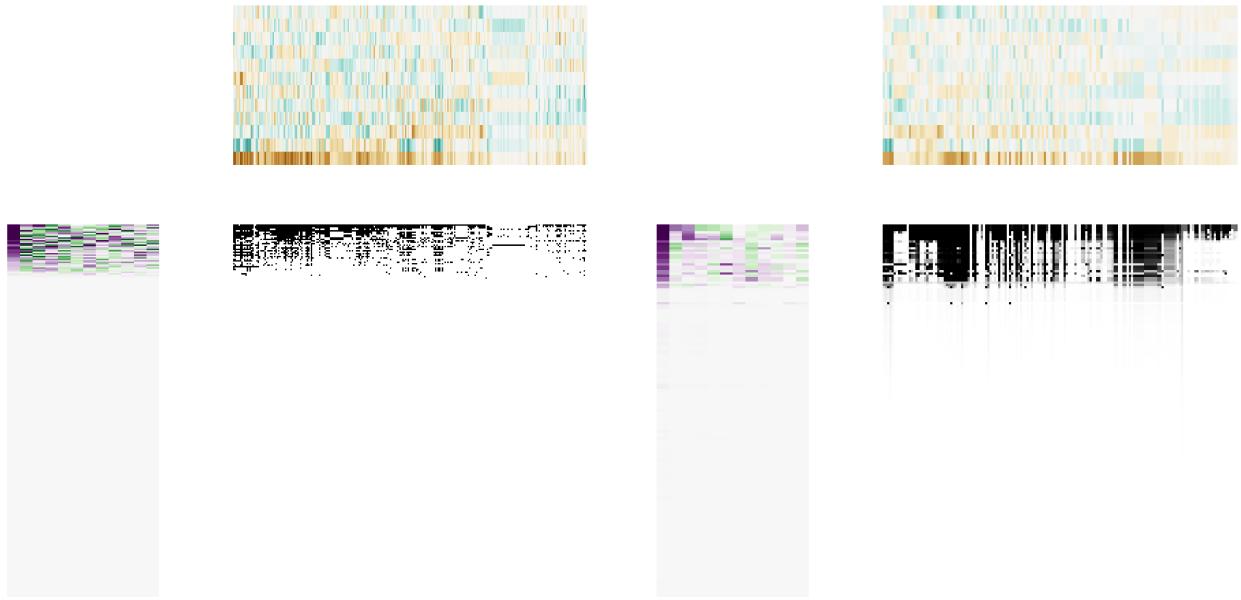


Figure 3: Visual representation of the left (green/purple) and right (green/brown) subspaces, alongside the adjacency matrix of the food web they encode (greyscale). The European metaweb is on the left, and the imputed Canadian metaweb (before data inflation) on the right. This figure illustrates how much structure the left subspace captures. As we show in fig. 6, the species with a value of 0 in the left subspace are species without any prey.

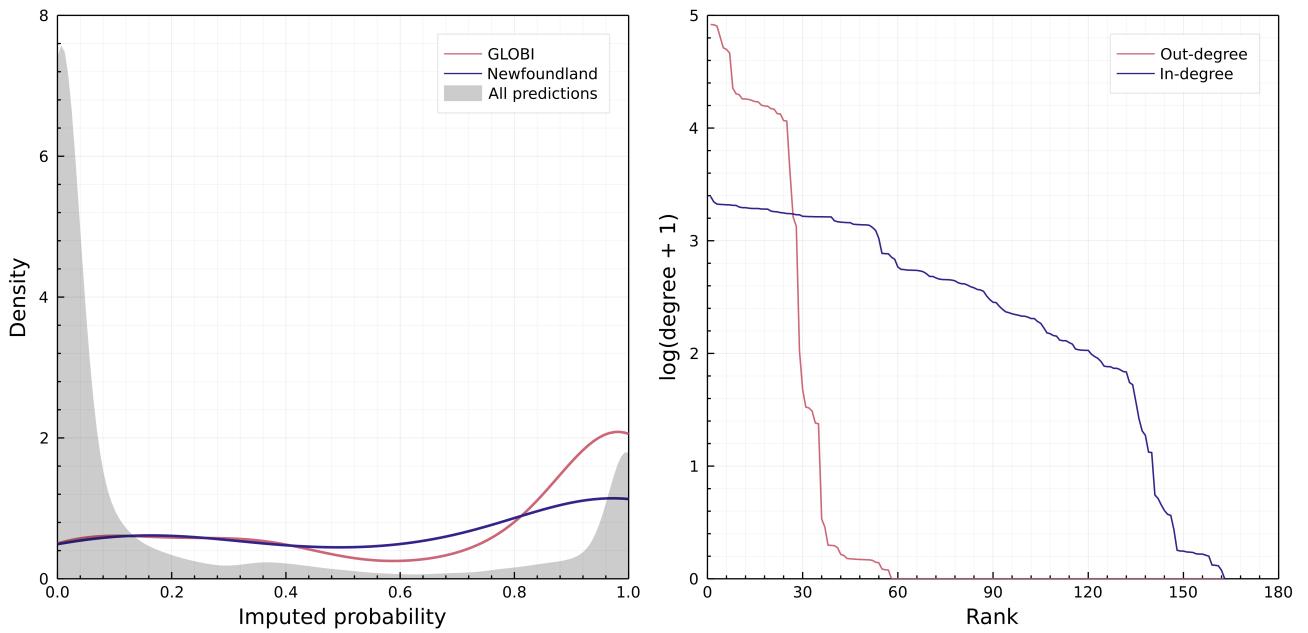


Figure 4: Left, comparison of the probabilities of interactions assigned by the model to all interactions (grey curve), the subset of interactions found in GLOBI (red), and in the Strong & Leroux (2014) Newfoundland dataset (blue). The model recovers more interactions with a low probability compared to data mining, which can suggest that collected datasets are biased towards more common or easy to identify interactions. Right, distribution of the in-degree and out-degree of the mammals from Canada in the reconstructed metaweb. This figure describes a flat, relatively short food web, in which there are few predators but a large number of preys.

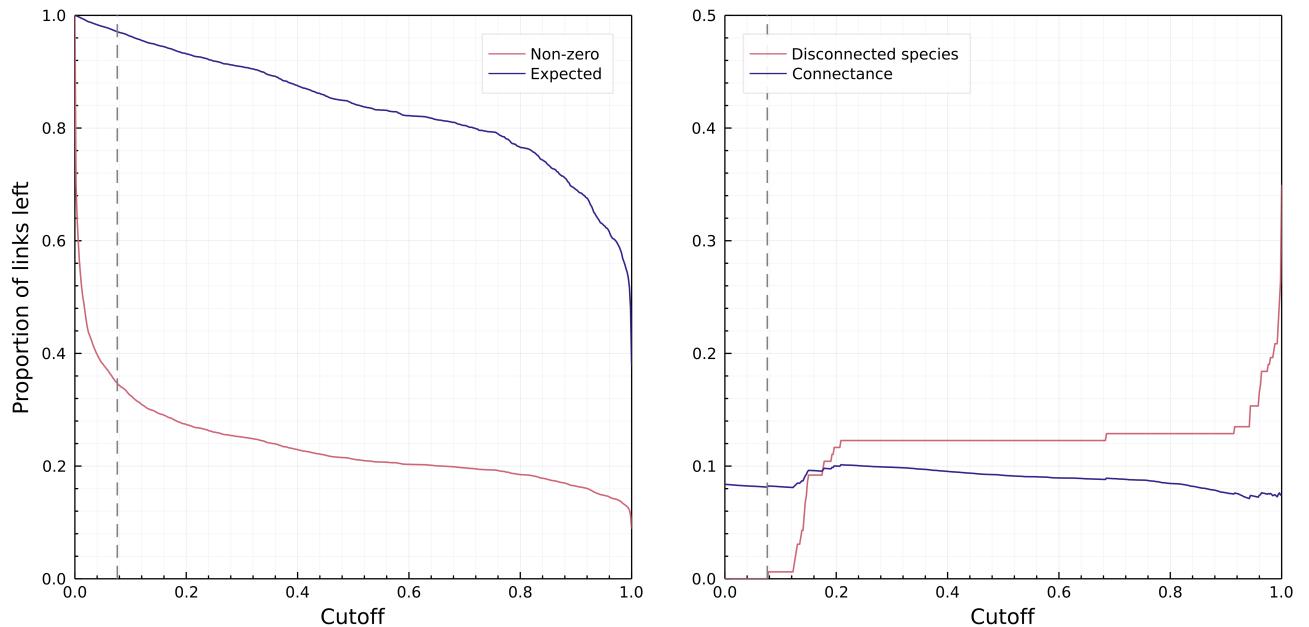


Figure 5: Left: effect of varying the cutoff for probabilities to be considered non-zero on the number of unique links and on \hat{L} , the probabilistic estimate of the number of links assuming that all interactions are independent. Right: effect of varying the cutoff on the number of disconnected species, and on network connectance. In both panels, the grey line indicates the cutoff $P(i \rightarrow j) \approx 0.08$ that resulted in the first species losing all of its interactions.

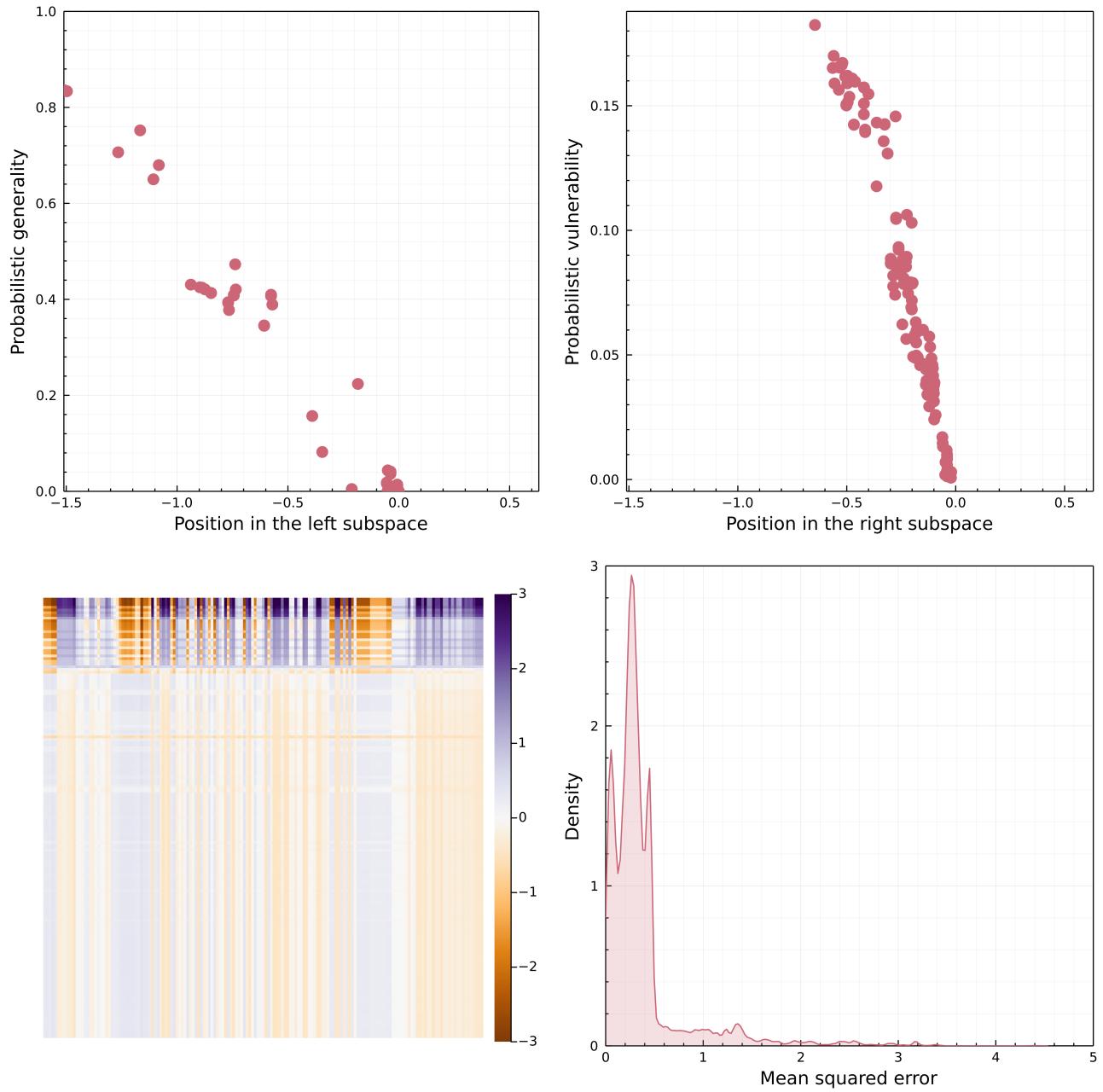


Figure 6: Top: biological significance of the first dimension. Left: there is a linear relationship between the values on the first dimension of the left subspace and the generality, *i.e.* the relative number of preys, *sensu* Schoener (1989). Species with a value of 0 in this subspace are at the bottom-most trophic level. Right: there is, similarly, a linear relationship between the position of a species on the first dimension of the right subspace and its vulnerability, *i.e.* the relative number of predators. Taken together, these two figures show that the first-order representation of this network would capture its degree distribution. Bottom: topological consequences of the first dimension. Left: differences in the z-score of the actual configuration model for the reconstructed network, and the prediction based only on the first dimension. Right: distribution of the differences in the left panel.