Graph embedding and transfer learning can help predict species interaction networks despite data limitations

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- 1. Metawebs, (networks of potential interactions within a species pool) are a powerful abstraction to understand how large-scale species interaction networks are structured.
- 2. Because metawebs are typically expressed at large spatial and taxonomic scales, assembling them is a tedious and costly process; predictive methods can help circumvent the limitations in data deficiencies, by providing 'draft' metawebs.
- 3. One way to improve our ability to predict metawebs is to maximize available information by using graph embeddings, instead of the list of species interactions. Graph embedding is an emerging field in machine learning that holds great potential for ecological problems.
- 4. In this perspective, we outline how the challenges associated with inferring metawebs line-up with the advantages of graph embeddings; as well as discuss how the choice of the species pool has consequences on the reconstructed network, but also embeds hypotheses about which human-made boundaries are ecologically meaningful.

- Being able to infer *potential* interactions could serve as a significant breakthrough in our ability to start
- thinking about species interaction networks over large spatial scales (Hortal et al., 2015). Understanding
- species interactions holds enormous potential to not only understand and more rapidly learn about
- 4 species interactions and metawebs, but also how changes in management of a single species may impact
- 5 non-target species. In a recent overview of the field of ecological network prediction, Strydom, Catchen, et
- 6 al. (2021) identified two challenges of interest to the prediction of interactions at large scales. First, there
- is a relative scarcity of relevant data in most places globally paradoxically, this restricts our ability to infer
- 8 interactions for locations where inference is perhaps the least required (and leaves us unable to make
- 9 inference in regions without interaction data); second, accurate predictors are important for accurate
- predictions, and the lack of methods that can leverage a small amount of accurate data is a serious
- impediment to our predictive ability. In most places, our most reliable biodiversity knowledge is that of a
- species pool (i.e. a set of potentially interacting species in a given area): through the analysis of databases
- like GBIF or IUCN, it is possible to construct a list of species in a region of interest; but inferring the
- potential interactions between these species is difficult.
- Following the definition of Dunne (2006), a metaweb is the ecological network analogue to the species
- pool; specifically, it inventories all potential interactions between species for a spatially delimited area (and
- 17 so captures the γ diversity of interactions). The metaweb is not a prediction of the network at a specific
- point within the spatial area it covers: it will have a different structure, notably by having a larger
- connectance (see e.g. Wood et al., 2015) and complexity (see e.g. Galiana et al., 2022), from any of these
- local networks. These local networks (which capture the α diversity of interactions) are a subset of the
- 21 metaweb's species and realized interactions, and have been called "metaweb realizations" (Poisot et al.,
- 22 2015). Differences between local networks and their metawebs are due to chance, species abundance and
- 23 co-occurrence, local environmental conditions, and local distribution of functional traits, among others.
- 24 Yet, recent results by Saravia et al. (2021) strongly suggest that the local (metaweb) realizations only
- 25 respond weakly to local conditions: instead, they reflect constraints inherited by the structure of their
- metaweb. This establishes the metaweb structure as the core goal of predictive network ecology, as it is a
- 27 required information to accurately produce downscaled, local predictions.
- 28 Because the metaweb represents the joint effect of functional, phylogenetic, and macroecological
- 29 processes (Morales-Castilla et al., 2015), it holds valuable ecological information. Specifically, it represents
- the "upper bounds" on what the composition of the local networks, given a local species pool, can be (see

- e.g. McLeod et al., 2021); this information can help evaluate the ability of ecological assemblages to
- withstand the effects of, for example, climate change (Fricke et al., 2022). These local networks may be
- 33 reconstructed given an appropriate knowledge of local species composition and provide information on
- the structure of food webs at finer spatial scales. This has been done for example for tree-galler-parasitoid
- systems (Gravel et al., 2018), fish trophic interactions (Albouy et al., 2019), tetrapod trophic interactions
- 36 (Braga et al., 2019; O'Connor et al., 2020), and crop-pest networks (Grünig et al., 2020). In this
- contribution, we highlight the power in viewing (and constructing) metawebs as probabilistic objects in
- the context of rare interactions, discuss how a family of machine learning tools (graph embeddings and
- transfer learning) can be used to overcome data limitations to metaweb inference, and highlight how the
- 40 use of metawebs introduces important questions for the field of network ecology.

41 A metaweb is an inherently probabilistic object

- Treating interactions as probabilistic (as opposed to binary) events is a more nuanced and realistic way to
- represent them. Dallas et al. (2017) suggested that most links in ecological networks are cryptic, i.e.
- 44 uncommon or hard to observe. This argument echoes Jordano (2016): sampling ecological interactions is
- difficult because it requires first the joint observation of two species, and then the observation of their
- interaction. In addition, it is generally expected weak or rare links to be more prevalent in networks than
- common or strong links (Csermely, 2004), compared to strong, persistent links; this is notably the case in
- food chains, wherein many weaker links are key to the stability of a system (Neutel et al., 2002). In the
- light of these observations, we expect to see an over-representation of low-probability (rare) interactions
- under a model that accurately predicts interaction probabilities.
- 51 Yet the original metaweb definition, and indeed most past uses of metawebs, was based on the
- 52 presence/absence of interactions. Moving towards *probabilistic* metawebs, by representing interactions as
- Bernoulli events (see e.g. Poisot et al., 2016), offers the opportunity to weigh these rare interactions
- 54 appropriately. The inherent plasticity of interactions is important to capture: there have been documented
- instances of food webs undergoing rapid collapse/recovery cycles over short periods of time (e.g. Pedersen
- et al., 2017). Furthermore, because the structure of the metaweb cannot be known in advance, it is
- 57 important to rely on predictive tools that do not assume a specific network topology for link prediction
- Gaucher et al., 2021), but are able to work on generalizations of the network. These considerations

emphasize why metaweb predictions should focus on quantitative (preferentially probabilistic) predictions, and this should constrain the suite of appropriate models used to predict them. 60 It is important to recall that a metaweb is intended as a catalogue of all potential (feasible) interactions, which is then filtered for a given application (Morales-Castilla et al., 2015). It is therefore important to separate the interactions that happen "almost surely" (repeated observational data), "almost never" (repeated lack of evidence or evidence that the link is forbidden through e.g. trait mis-match), and interactions with a probability that lays somewhere in between. In a sense, that most ecological interactions are elusive can call for a slightly different approach to sampling: once the common interactions are documented, the effort required in documenting each rare interaction will increase exponentially (Jordano, 2016). Recent proposals in other fields emphasize the idea that machine learning algorithms can also act as data generators (Hoffmann et al., 2019): high quality observational data can be 69 used to infer core rules underpinning network structure, and be supplemented with synthetic data coming 70 from predictive models trained on them, thereby increasing the volume of information available for 71 analysis. Indeed, Strydom, Catchen, et al. (2021) suggested that knowing the metaweb may render the prediction of local networks easier, because it fixes an "upper bound" on which interactions can exist. In this context, a probabilistic metaweb represents an aggregation of informative priors on the biological feasibility of interactions, which is usually hard to obtain yet has possibly the most potential to boost our predictive ability (Bartomeus et al., 2016).

[Figure 1 about here.]

Graph embedding offers promises for the inference of potential interactions

77

Graph (or Network) embedding (fig. 1) is a family of machine learning techniques, whose main task is to
learn a mapping function from a discrete graph to a continuous domain (Arsov & Mirceva, 2019; Chami et
al., 2022). Their main goal is to learn a low dimensional vector representations for the nodes of the graph
(embeddings), such that key properties of the graph (e.g. local or global structures) are retained in the
embedding space (Yan et al., 2005). Ecological networks are an interesting candidate for the widespread
application of embeddings, as they tend to possess a shared structural backbone (see *e.g.* Bramon Mora et

al., 2018 for food webs), which hints at structural invariants in empirical data; assuming that these structural invariants are indeed widespread, they would dominate the structure of networks, and therefore 87 be adequately captured by the first (lower) dimensions of an embedding, without the need to measure derived aspects of their structure (e.g. motifs, paths, modularity, ...). Indeed, food webs are inherently low-dimensional objects, and can be adequately represented with less than ten dimensions (Braga et al., 2019; Eklöf et al., 2013). Simulation results by Botella et al. (2022) 91 suggest that there is no best method to identify architectural similarities between networks, and that multiple approaches need to be tested and compared to the network descriptor of interest. This matches 93 previous, more general results on graph embedding, which suggest that different embedding algorithms yield different network embeddings (Goyal & Ferrara, 2018), calling for a careful selection of the problem-specific approach to use. In tbl. 1, we present a selection of common graph and node embedding methods, alongside examples of their use to predict species interactions; most of these methods rely either 97 on linear algebra, or on pseudo-random walks on graphs. One prominent family of approaches we do not discuss in the present manuscript is Graph Neural Networks (GNN; Zhou et al., 2020). GNN are, in a sense, a method to embed a graph into a dense 100 subspace, but belong to the family of deep learning methods, which has its own set of practices (see e.g. Goodfellow et al., 2016). An important issue with methods based on deep learning is that, because their 102 parameter space is immense, the sample size of the data fed into them must be similarly large (typically 103 thousands of instances). This is a requirement for the model to converge correctly during training, but this 104 assumption is unlikely to be met given the size of datasets currently available for metawebs (or single time/location species interaction networks). This data volume requirement is mostly absent from the 106 techniques we list below. Furthermore, GNN still have some challenges related to their shallow structure, 107 and concerns related to scalability (see Gupta et al., 2021 for a review), which are mostly absent from the methods listed in tbl. 1. Assuming that the uptake of next-generation biomonitoring techniques does 109 indeed deliver larger datasets on species interactions (Bohan et al., 2017), there is a potential for GNN to 110 become an applicable embedding/predictive technique in the coming years. 111

[Table 1 about here.]

The popularity of graph embedding techniques in machine learning is more than the search for structural invariants: graphs are discrete objects, and machine learning techniques tend to handle continuous data

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better. Bringing a sparse graph into a continuous, dense vector space (Xu, 2020) opens up a broader variety of predictive algorithms, notably of the sort that are able to predict events as probabilities (Murphy, 2022). 116 Furthermore, the projection of the graph itself is a representation that can be learned; Runghen et al. 117 (2021), for example, used a neural network to learn the embedding of a network in which not all interactions were known, based on the nodes' metadata. This example has many parallels in ecology (see 119 fig. 1 C), in which node metadata can be represented by phylogeny, abundance, or functional traits. Using 120 phylogeny as a source of information assumes (or strives to capture) the action of evolutionary processes 121 on network structure, which at least for food webs have been well documented TK REF; similarly, the use 122 of functional traits assumes that interactions can be infered from the knowledge of trait-matching rules, 123 which is similarly well supported in the empirical literature **TK REF**. Relating this information to an 124 embedding rather than a list of networks measures would allow to capture their effect on the more fundamental aspects of network structure; conversely, the absence of a phylogenetic or functional signal 126 may suggest that evolutionary/trait processes are not strong drivers of network structure, therefore 127 opening a new way to perform hypothesis testing. Rather than directly predicting biological rules (see e.g. Pichler et al., 2020 for an overview), which may be 129 confounded by the sparse nature of graph data, learning embeddings works in the low-dimensional space 130 that maximizes information about the network structure. This approach is further justified by the 131 observation, for example, that the macro-evolutionary history of a network is adequately represented by 132 some graph embeddings (Random dot product graphs (RDPG); see Dalla Riva & Stouffer, 2016). In a 133 recent publication, Strydom et al. (2022) have used an embedding (based on RDPG) to project a metaweb of trophic interactions between European mammals, and transferred this information to mammals of 135 Canada, using the phylogenetic distance between related clades to infer the values in the latent sub-space 136 into which the European metaweb was projected. By performing the RDPG step on re-constructed values, this approach yields a probabilistic trophic metaweb for mammals of Canada based on knowledge of 138 European species, despite a limited ($\approx 5\%$) taxonomic overlap. 139 Graph embeddings can serve as a dimensionality reduction method. For example, RDPG (Strydom et al., 140 2022) and t-SVD (truncated Singular Value Decomposition; Poisot et al., 2021) typically embed networks 141 using fewer dimensions than the original network (the original network has as many dimensions as species, and as many informative dimensions as trophically unique species; Strydom, Dalla Riva, et al., 2021). But this is not necessarily the case – indeed, one may perform a PCA (a special case of SVD) to

project the raw data into a subspace that improves the efficacy of t-SNE (t-distributed stochastic neighbor embedding; Maaten, 2009). There are many dimensionality reductions (Anowar et al., 2021) that can be applied to an embedded network should the need for dimensionality reduction (for example for data visualisation) arise. In brief, many graph embeddings *can* serve as dimensionality reduction steps, but not all do, neither do all dimensionality reduction methods provide adequate graph embedding capacities. In the next section (and fig. ??), we show how the amount of dimensionality reduction can affect the quality of the embedding.

An illustration of metaweb embedding

163

In this section, we illustrate the embedding of a collection of bipartite networks collected by Hadfield et al. (2014), using t-SVD and RDPG (see Strydom et al., 2022 for the full details). Briefly, an RDPG decomposes 154 a network into two subspaces (left and right), which are matrices that when multiplied give an 155 approximation of the original network. The code to reproduce this example is available as supplementary 156 material (note, for the sake of comparison, that Strydom, Catchen, et al., 2021 have an example using 157 embedding through PCA followed by prediction using a deep neural network on the same dataset). The 158 resulting (binary) metaweb \mathcal{M} has 2131 interactions between 206 parasites and 121 hosts, and its 159 adjacency matrix has full rank (i.e. it represents a space with 121 dimensions). All analyses were done 160 using Julia (Bezanson et al., 2017) version 1.7.2, Makie.jl (Danisch & Krumbiegel, 2021), and 161 EcologicalNetworks.jl (Poisot et al., 2019). 162

[Figure 2 about here.]

In fig. 2, we focus on some statistical checks of the embedding. In panel $\bf A$, we show that the averaged L_2 loss (*i.e.* the sum of squared errors) between the empirical and reconstructed metaweb decreases when the number of dimensions (rank) of the subspace increases, with an inflection at 39 dimensions (out of 120 initially) according to the finite differences method. As discussed by Runghen et al. (2021), there is often a trade-off between the number of dimensions to use (more dimensions are more computationally demanding) and the quality of the representation. In panel $\bf B$, we show the increase in cumulative variance explained at each rank, and visualize that using 39 ranks explains about 70% of the variance in the empirical metaweb. This is a different information from the L_2 loss (which is averaged across

interactions), as it works on the eigenvalues of the embedding, and therefore captures higher-level features of the network. In panel C, we show positions of hosts and parasites on the first two dimensions of the left 173 and right subspaces. Note that these values largely skew negative, because the first dimensions capture the 174 coarse structure of the network: most pairs of species do not interact, and therefore have negative values. Finally in panel **D**, we show the predicted weight (*i.e.* the result of the multiplication of the RDGP 176 subspaces at a rank of 25) as a function of whether the interactions are observed, not-observed, or 177 unknown due to lack of co-occurrence. This reveals that the observed interactions have higher predicted 178 weights, although there is some overlap; the usual approach to identify potential interactions based on this 179 information would be a thresholding analysis, which is outside the scope of this manuscript (and is done 180 in the papers cited in this illustration). Because the values returned from RDPG are not bound to the unit 181 interval, we performed a clamping of the weights to the unit space, showing a one-inflation in documented interaction, and a zero-inflation in other species pairs. This last figure crosses from the 183 statistical into the ecological, by showing that species pairs with no documented co-occurrence have 184 weights that are not distinguishable from species pairs with no documented interactions, suggesting that (as befits a host-parasite model) the ability to interact is a strong predictor of co-occurrence. 186

[Figure 3 about here.]

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As the results of fig. 2 show that we can extract an embedding of the metaweb that captures enough 188 variance to be relevant, in fig. 3, we relate the values of latent variables for hosts to different 189 ecologically-relevant data. In panel A, we show that host with a higher value on the first dimension have 190 fewer parasites. This relates to the body size of hosts in the PanTHERIA database (Jones et al., 2009), as 191 shown in panel B: interestingly, the position on the first axis is only weakly correlated to body mass of the 192 host; this matches well establihed results showing that body size/mass is not always a direct predictor of parasite richness in terrestrial mammals (Morand & Poulin, 1998), a result we observe in panel C. Finally, 194 in panel D, we can see how different taxonomic families occupy different positions on the first axis, with 195 e.g. Sciuridae being biased towards higher values. These results show how we can look for ecological informations in the output of network embeddings, which can further be refined into the selection of 197 predictors for transfer learning.

199 The metaweb embeds both ecological hypotheses and practices

The goal of metaweb inference is to provide information about the interactions between species at a large spatial scale. But as Herbert (1965) rightfully pointed out, "[y]ou can't draw neat lines around planet-wide 201 problems"; any inference of a metaweb at large scales must contend with several novel, and interwoven, 202 families of problems. In this section, we list some of the most pressing research priorities (i.e. problems that can be adressed with subsequent data analysis or simulations), as well as issues related to the 204 application of these methods at the science-policy interface. 205 The first open research problem is the taxonomic and spatial limit of the metaweb to embed and transfer. If the initial metaweb is too narrow in scope, notably from a taxonomic point of view, the chances of 207 finding another area with enough related species (through phylogenetic relatedness or similarity of 208 functional traits) to make a reliable inference decreases; this would likely be indicated by large confidence intervals during estimation of the values in the low-rank space, meaning that the representation of the 210 original graph is difficult to transfer to the new problem. Alternatively, if the initial metaweb is too large (taxonomically), then the resulting embeddings would need to represent interactions between taxonomic groups that are not present in the new location. This would lead to a much higher variance in the starting 213 dataset, and to under-dispersion in the target dataset, resulting in the potential under or over estimation of 214 the strength of new predicted interactions. The lack of well documented metawebs is currently preventing 215 the development of more concrete guidelines. The question of phylogenetic relatedness and distribution is 216 notably relevant if the metaweb is assembled in an area with mostly endemic species (e.g. a system that 217 has undergone recent radiation or that has remained in isolation for a long period of time might not have 218 an analogous system with which to draw knowledge from), and as with every predictive algorithm, there is room for the application of our best ecological judgement. Because this problem relates to distribution 220 of species in the geographic or phylogenetic space, it can certainly be approached through assessing the 221 performance of embedding transfer in simulated starting/target species pools. The second series of problems relate to determining which area should be used to infer the new metaweb 223 in, as this determines the species pool that must be used. Metawebs can be constructed by assigning 224 interactions in a list of species within geographic boundaries. The upside of this approach is that 225 information at the country level is likely to be required for biodiversity assessments, as countries set 226 conservation goals at the national level (Buxton et al., 2021), and as quantitative instruments are designed 227

to work at these scales (Turak et al., 2017); specific strategies are often enacted at smaller scales, nested within a specific country (Ray et al., 2021). But there is no guarantee that these boundaries are 229 meaningful. In fact, we do not have a satisfying answer to the question of "where does a food web stop?"; 230 the most promising 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 impossible in the absence of enough 232 information about the network itself. This suggests that inferred metawebs should be further downscaled 233 to allow for a posteriori analyses. The methodology for metaweb downscaling is currently limited, and it is 234 likely that the sustained effort to characterize the spatial dependency of food web structure will lead to 235 more prescriptive guidelines about the need for prediction downscaling. 236 The final family of problems relates less to ecological methods than to the praxis of ecological research. Operating under the context of national divisions, in large parts of the world, reflects nothing more than 238 the legacy of settler colonialism, which drives a disparity in available ecological data. Applying any 239 embedding to biased data does not debias them, but instead embeds these very same biases, propagating them to the machine learning models using embeddings to make predictions. Indeed, the use of ecological 241 data is not an apolitical act (Nost & Goldstein, 2021), as data infrastructures tend to be designed to answer 242 questions within national boundaries (therefore placing contingencies on what is available to be 243 embedded), and their use often draws upon and reinforces territorial statecraft. As per Machen & Nost 244 (2021), this is particularly true when the output of "algorithmic thinking" (e.g. relying on machine 245 learning to generate knowledge) can be re-used for governance (e.g. enacting conservation decisions at the 246 national scale). As information on species interaction networks structure is increasingly leveraged as a tool to guide conservation actions (see e.g. recent discussions for food-web based conservation; Eero et al., 248 2021; Naman et al., 2022; Stier et al., 2017), the need to appraise and correct biases that are unwittingly 249 propagated to algorithms when embedded from the original data is paramount. Predictive approaches deployed at the continental scale, no matter their intent, originate in the framework that contributed to 251 the ongoing biodiversity crisis (Adam, 2014) and reinforced environmental injustice (Choudry, 2013; 252 Domínguez & Luoma, 2020). Particularly on Turtle Island and other territories that were traditionally 253 stewarded by Indigenous people, these approaches should be replaced (or at least guided and framed) by 254 Indigenous principles of land management (Eichhorn et al., 2019; No'kmag et al., 2021), as part of an 255 "algorithm-in-the-loop" approach. Human-algorithm interactions are notoriously difficult and can yield 256 adverse effect (Green & Chen, 2019; Stevenson & Doleac, 2021), suggesting the need to systematically

- study them for the specific purpose of biodiversity governance, as well as to improve the algorithmic literacy of decision makers. As we see artificial intelligence/machine learning being increasingly 259 mobilized to generate knowledge that is lacking for conservation decisions (e.g. Lamba et al., 2019; 260 Mosebo Fernandes et al., 2020) and drive policy decisions (Weiskopf et al., 2022), our discussion of these tools need to go beyond the technical and statistical, and into the governance consequences they can have. 262 Acknowledgements: We acknowledge that this study was conducted on land within the traditional 263 unceded territory of the Saint Lawrence Iroquoian, Anishinabewaki, Mohawk, Huron-Wendat, and Omàmiwininiwak nations. TP, TS, DC, and LP received funding from the Canadian Institute for Ecology 265 & Evolution. FB is funded by the Institute for Data Valorization (IVADO). TS, SB, and TP are funded by a 266 donation from the Courtois Foundation. CB was awarded a Mitacs Elevate Fellowship no. IT12391, in partnership with fRI Research, and also acknowledges funding from Alberta Innovates and the Forest 268 Resources Improvement Association of Alberta. M-JF acknowledges funding from NSERC Discovery 269 Grant and NSERC CRC. RR is funded by New Zealand's Biological Heritage Ngā Koiora Tuku Iho 270 National Science Challenge, administered by New Zealand Ministry of Business, Innovation, and 271 Employment. BM is funded by the NSERC Alexander Graham Bell Canada Graduate Scholarship and the 272 FRQNT master's scholarship. LP acknowledges funding from NSERC Discovery Grant (NSERC 273 RGPIN-2019-05771). TP acknowledges financial support from the Fondation Courtois, and NSERC 274 through the Discovery Grants and Discovery Accelerator Supplement programs. MJF is supported by an 275 NSERC PDF and an RBC Post-Doctoral Fellowship. 276
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References

- Adam, R. (2014). Elephant treaties: The Colonial legacy of the biodiversity crisis. UPNE.
- Albouy, C., Archambault, P., Appeltans, W., Araújo, M. B., Beauchesne, D., Cazelles, K., Cirtwill, A. R.,
- Fortin, M.-J., Galiana, N., Leroux, S. J., Pellissier, L., Poisot, T., Stouffer, D. B., Wood, S. A., & Gravel, D.

```
(2019). The marine fish food web is globally connected. Nature Ecology & Evolution, 3(8, 8),
285
       1153-1161. https://doi.org/10.1038/s41559-019-0950-y
286
    Anowar, F., Sadaoui, S., & Selim, B. (2021). Conceptual and empirical comparison of dimensionality
287
       reduction algorithms (PCA, KPCA, LDA, MDS, SVD, LLE, ISOMAP, LE, ICA, t-SNE). Computer
288
       Science Review, 40, 100378. https://doi.org/10.1016/j.cosrev.2021.100378
289
    Arsov, N., & Mirceva, G. (2019). Network Embedding: An Overview. http://arxiv.org/abs/1911.11726
290
    Bartomeus, I., Gravel, D., Tylianakis, J. M., Aizen, M. A., Dickie, I. A., & Bernard-Verdier, M. (2016). A
291
       common framework for identifying linkage rules across different types of interactions. Functional
292
       Ecology, 30(12), 1894-1903.
293
       http://onlinelibrary.wiley.com/doi/10.1111/1365-2435.12666/full
294
    Bezanson, J., Edelman, A., Karpinski, S., & Shah, V. (2017). Julia: A Fresh Approach to Numerical
295
       Computing. SIAM Review, 59(1), 65–98. https://doi.org/10.1137/141000671
296
    Bohan, D. A., Vacher, C., Tamaddoni-Nezhad, A., Raybould, A., Dumbrell, A. J., & Woodward, G. (2017).
297
       Next-Generation Global Biomonitoring: Large-scale, Automated Reconstruction of Ecological
298
       Networks. Trends in Ecology & Evolution. https://doi.org/10.1016/j.tree.2017.03.001
299
    Botella, C., Dray, S., Matias, C., Miele, V., & Thuiller, W. (2022). An appraisal of graph embeddings for
300
       comparing trophic network architectures. Methods in Ecology and Evolution, 13(1), 203–216.
301
       https://doi.org/10.1111/2041-210X.13738
302
    Braga, J., Pollock, L. J., Barros, C., Galiana, N., Montoya, J. M., Gravel, D., Maiorano, L., Montemaggiori,
303
       A., Ficetola, G. F., Dray, S., & Thuiller, W. (2019). Spatial analyses of multi-trophic terrestrial vertebrate
304
       assemblages in Europe. Global Ecology and Biogeography, 28(11), 1636-1648.
305
       https://doi.org/10.1111/geb.12981
306
    Bramon Mora, B., Gravel, D., Gilarranz, L. J., Poisot, T., & Stouffer, D. B. (2018). Identifying a common
307
       backbone of interactions underlying food webs from different ecosystems. Nature Communications,
308
       9(1), 2603. https://doi.org/10.1038/s41467-018-05056-0
309
    Buxton, R. T., Bennett, J. R., Reid, A. J., Shulman, C., Cooke, S. J., Francis, C. M., Nyboer, E. A., Pritchard,
310
       G., Binley, A. D., Avery-Gomm, S., Ban, N. C., Beazley, K. F., Bennett, E., Blight, L. K., Bortolotti, L. E.,
311
```

Camfield, A. F., Gadallah, F., Jacob, A. L., Naujokaitis-Lewis, I., ... Smith, P. A. (2021). Key

312

- information needs to move from knowledge to action for biodiversity conservation in Canada.
- Biological Conservation, 256, 108983. https://doi.org/10.1016/j.biocon.2021.108983
- Chami, I., Abu-El-Haija, S., Perozzi, B., Ré, C., & Murphy, K. (2022). Machine Learning on Graphs: A
- Model and Comprehensive Taxonomy. *Journal of Machine Learning Research*, 23(89), 1–64.
- http://jmlr.org/papers/v23/20-852.html
- ³¹⁸ Chen, D., Xue, Y., Fink, D., Chen, S., & Gomes, C. P. (2017). Deep Multi-species Embedding. 3639–3646.
- https://www.ijcai.org/proceedings/2017/509
- 320 Chen, H., Perozzi, B., Hu, Y., & Skiena, S. (2017). HARP: Hierarchical Representation Learning for
- Networks. http://arxiv.org/abs/1706.07845
- 322 Choudry, A. (2013). Saving biodiversity, for whom and for what? Conservation NGOs, complicity,
- colonialism and conquest in an era of capitalist globalization. In NGOization: Complicity,
- contradictions and prospects (pp. 24–44). Bloomsbury Publishing.
- ³²⁵ Cieslak, M. C., Castelfranco, A. M., Roncalli, V., Lenz, P. H., & Hartline, D. K. (2020). T-Distributed
- Stochastic Neighbor Embedding (t-SNE): A tool for eco-physiological transcriptomic analysis. *Marine*
- 327 Genomics, 51, 100723. https://doi.org/10.1016/j.margen.2019.100723
- csermely, P. (2004). Strong links are important, but weak links stabilize them. Trends in Biochemical
- Sciences, 29(7), 331-334. https://doi.org/10.1016/j.tibs.2004.05.004
- Dalla Riva, G. V., & Stouffer, D. B. (2016). Exploring the evolutionary signature of food webs' backbones
- using functional traits. Oikos, 125(4), 446–456. https://doi.org/10.1111/oik.02305
- Dallas, T., Park, A. W., & Drake, J. M. (2017). Predicting cryptic links in host-parasite networks. PLOS
- 333 Computational Biology, 13(5), e1005557. https://doi.org/10.1371/journal.pcbi.1005557
- Danisch, S., & Krumbiegel, J. (2021). Makie.jl: Flexible high-performance data visualization for Julia.
- *Journal of Open Source Software*, 6(65), 3349. https://doi.org/10.21105/joss.03349
- Domínguez, L., & Luoma, C. (2020). Decolonising Conservation Policy: How Colonial Land and
- Conservation Ideologies Persist and Perpetuate Indigenous Injustices at the Expense of the
- Environment. Land, 9(3, 3), 65. https://doi.org/10.3390/land9030065
- Dunne, J. A. (2006). The Network Structure of Food Webs. In J. A. Dunne & M. Pascual (Eds.), *Ecological*
- networks: Linking structure and dynamics (pp. 27–86). Oxford University Press.

- Eero, M., Dierking, J., Humborg, C., Undeman, E., MacKenzie, B. R., Ojaveer, H., Salo, T., & Köster, F. W.
- (2021). Use of food web knowledge in environmental conservation and management of living
- resources in the Baltic Sea. *ICES Journal of Marine Science*, 78(8), 2645–2663.
- https://doi.org/10.1093/icesjms/fsab145
- Eichhorn, M. P., Baker, K., & Griffiths, M. (2019). Steps towards decolonising biogeography. Frontiers of
- 346 Biogeography, 12(1), 1–7. https://doi.org/10.21425/F5FBG44795
- Eklöf, A., Jacob, U., Kopp, J., Bosch, J., Castro-Urgal, R., Chacoff, N. P., Dalsgaard, B., de Sassi, C., Galetti,
- M., Guimarães, P. R., Lomáscolo, S. B., Martín González, A. M., Pizo, M. A., Rader, R., Rodrigo, A.,
- Tylianakis, J. M., Vázquez, D. P., & Allesina, S. (2013). The dimensionality of ecological networks.
- Ecology Letters, 16(5), 577–583. https://doi.org/10.1111/ele.12081
- Fortin, M.-J., Dale, M. R. T., & Brimacombe, C. (2021). Network ecology in dynamic landscapes.
- Proceedings of the Royal Society B: Biological Sciences, 288(1949), rspb.2020.1889, 20201889.
- 353 https://doi.org/10.1098/rspb.2020.1889
- Fricke, E. C., Ordonez, A., Rogers, H. S., & Svenning, J.-C. (2022). The effects of defaunation on plants'
- capacity to track climate change. *Science*.
- https://www.science.org/doi/abs/10.1126/science.abk3510
- Galiana, N., Barros, C., Braga, J., Ficetola, G. F., Maiorano, L., Thuiller, W., Montoya, J. M., & Lurgi, M.
- (2021). The spatial scaling of food web structure across European biogeographical regions. *Ecography*,
- n/a(n/a). https://doi.org/10.1111/ecog.05229
- Galiana, N., Hawkins, B. A., & Montoya, J. M. (2019). The geographical variation of network structure is
- scale dependent: Understanding the biotic specialization of host–parasitoid networks. *Ecography*,
- 362 42(6), 1175-1187. https://doi.org/10.1111/ecog.03684
- Galiana, N., Lurgi, M., Bastazini, V. A. G., Bosch, J., Cagnolo, L., Cazelles, K., Claramunt-López, B., Emer,
- C., Fortin, M.-J., Grass, I., Hernández-Castellano, C., Jauker, F., Leroux, S. J., McCann, K., McLeod, A.
- M., Montoya, D., Mulder, C., Osorio-Canadas, S., Reverté, S., ... Montoya, J. M. (2022). Ecological
- network complexity scales with area. *Nature Ecology & Evolution*, 1–8.
- 367 https://doi.org/10.1038/s41559-021-01644-4
- Galiana, N., Lurgi, M., Claramunt-López, B., Fortin, M.-J., Leroux, S., Cazelles, K., Gravel, D., & Montoya,
- J. M. (2018). The spatial scaling of species interaction networks. *Nature Ecology & Evolution*, 2(5),

```
782-790. https://doi.org/10.1038/s41559-018-0517-3
370
    Gaucher, S., Klopp, O., & Robin, G. (2021). Outlier detection in networks with missing links.
371
        Computational Statistics & Data Analysis, 164, 107308.
372
       https://doi.org/10.1016/j.csda.2021.107308
373
    Gibb, R., Albery, G. F., Becker, D. J., Brierley, L., Connor, R., Dallas, T. A., Eskew, E. A., Farrell, M. J.,
374
       Rasmussen, A. L., Ryan, S. J., Sweeny, A., Carlson, C. J., & Poisot, T. (2021). Data Proliferation,
375
       Reconciliation, and Synthesis in Viral Ecology. BioScience, 71(11), 1148–1156.
376
       https://doi.org/10.1093/biosci/biab080
377
    Goodfellow, I., Bengio, Y., & Courville, A. (2016). Deep learning. MIT Press.
378
    Goyal, P., & Ferrara, E. (2018). Graph embedding techniques, applications, and performance: A survey.
379
       Knowledge-Based Systems, 151, 78-94. https://doi.org/10.1016/j.knosys.2018.03.022
380
    Gravel, D., Baiser, B., Dunne, J. A., Kopelke, J.-P., Martinez, N. D., Nyman, T., Poisot, T., Stouffer, D. B.,
381
       Tylianakis, J. M., Wood, S. A., & Roslin, T. (2018). Bringing Elton and Grinnell together: A quantitative
382
       framework to represent the biogeography of ecological interaction networks. Ecography, O(0).
383
       https://doi.org/10.1111/ecog.04006
384
    Green, B., & Chen, Y. (2019). Disparate Interactions: An Algorithm-in-the-Loop Analysis of Fairness in
385
       Risk Assessments. Proceedings of the Conference on Fairness, Accountability, and Transparency, 90–99.
386
       https://doi.org/10.1145/3287560.3287563
387
    Grover, A., & Leskovec, J. (2016). Node2vec: Scalable Feature Learning for Networks. Proceedings of the
388
       22nd ACM SIGKDD International Conference on Knowledge Discovery and Data Mining, 855-864.
389
       https://doi.org/10.1145/2939672.2939754
390
    Grünig, M., Mazzi, D., Calanca, P., Karger, D. N., & Pellissier, L. (2020). Crop and forest pest metawebs
391
       shift towards increased linkage and suitability overlap under climate change. Communications Biology,
392
       3(1, 1), 1-10. https://doi.org/10.1038/s42003-020-0962-9
393
    Gupta, A., Matta, P., & Pant, B. (2021). Graph neural network: Current state of Art, challenges and
394
       applications. Materials Today: Proceedings, 46, 10927–10932.
395
       https://doi.org/10.1016/j.matpr.2021.01.950
396
```

Hadfield, J. D., Krasnov, B. R., Poulin, R., & Nakagawa, S. (2014). A Tale of Two Phylogenies: Comparative

- Analyses of Ecological Interactions. *The American Naturalist*, 183(2), 174–187.
- 399 https://doi.org/10.1086/674445
- Herbert, F. (1965). *Dune* (1st ed.). Chilton Book Company.
- Hinton, G., & Roweis, S. T. (2002). Stochastic neighbor embedding. NIPS, 15, 833-840.
- Hoffmann, J., Bar-Sinai, Y., Lee, L. M., Andrejevic, J., Mishra, S., Rubinstein, S. M., & Rycroft, C. H. (2019).
- Machine learning in a data-limited regime: Augmenting experiments with synthetic data uncovers
- order in crumpled sheets. *Science Advances*, *5*(4), eaau6792.
- https://doi.org/10.1126/sciadv.aau6792
- Hortal, J., de Bello, F., Diniz-Filho, J. A. F., Lewinsohn, T. M., Lobo, J. M., & Ladle, R. J. (2015). Seven
- Shortfalls that Beset Large-Scale Knowledge of Biodiversity. *Annual Review of Ecology, Evolution, and*
- Systematics, 46(1), 523-549. https://doi.org/10.1146/annurev-ecolsys-112414-054400
- Jones, K. E., Bielby, J., Cardillo, M., Fritz, S. A., O'Dell, J., Orme, C. D. L., Safi, K., Sechrest, W., Boakes, E.
- H., Carbone, C., Connolly, C., Cutts, M. J., Foster, J. K., Grenyer, R., Habib, M., Plaster, C. A., Price, S.
- A., Rigby, E. A., Rist, J., ... Purvis, A. (2009). PanTHERIA: A species-level database of life history,
- ecology, and geography of extant and recently extinct mammals: Ecological Archives E090-184.
- Ecology, 90(9), 2648-2648. https://doi.org/10.1890/08-1494.1
- Jordano, P. (2016). Sampling networks of ecological interactions. Functional Ecology, 30(12), 1883–1893.
- https://doi.org/10.1111/1365-2435.12763
- Lamba, A., Cassey, P., Segaran, R. R., & Koh, L. P. (2019). Deep learning for environmental conservation.
- 417 Current Biology, 29(19), R977-R982. https://doi.org/10.1016/j.cub.2019.08.016
- 418 Maaten, L. van der. (2009). Learning a Parametric Embedding by Preserving Local Structure. *Proceedings*
- of the Twelth International Conference on Artificial Intelligence and Statistics, 384–391.
- https://proceedings.mlr.press/v5/maaten09a.html
- Machen, R., & Nost, E. (2021). Thinking algorithmically: The making of hegemonic knowledge in climate
- governance. Transactions of the Institute of British Geographers, 46(3), 555–569.
- https://doi.org/10.1111/tran.12441
- McLeod, A., Leroux, S. J., Gravel, D., Chu, C., Cirtwill, A. R., Fortin, M.-J., Galiana, N., Poisot, T., & Wood,
- S. A. (2021). Sampling and asymptotic network properties of spatial multi-trophic networks. *Oikos*,

```
n/a(n/a). https://doi.org/10.1111/oik.08650
```

- Melnyk, K., Klus, S., Montavon, G., & Conrad, T. O. F. (2020). GraphKKE: Graph Kernel Koopman
- embedding for human microbiome analysis. Applied Network Science, 5(1), 96.
- https://doi.org/10.1007/s41109-020-00339-2
- 430 Morales-Castilla, I., Matias, M. G., Gravel, D., & Araújo, M. B. (2015). Inferring biotic interactions from
- proxies. *Trends in Ecology & Evolution*, *30*(6), 347–356.
- https://doi.org/10.1016/j.tree.2015.03.014
- 433 Morand, S., & Poulin, R. (1998). Density, body mass and parasite species richness of terrestrial mammals.
- 434 Evolutionary Ecology, 12(6), 717–727. https://doi.org/10.1023/A:1006537600093
- Mosebo Fernandes, A. C., Quintero Gonzalez, R., Lenihan-Clarke, M. A., Leslie Trotter, E. F., & Jokar
- Arsanjani, J. (2020). Machine Learning for Conservation Planning in a Changing Climate.
- Sustainability, 12(18, 18), 7657. https://doi.org/10.3390/su12187657
- Murphy, K. P. (2022). Probabilistic machine learning: An introduction. MIT Press. probml.ai
- Naman, S. M., White, S. M., Bellmore, J. R., McHugh, P. A., Kaylor, M. J., Baxter, C. V., Danehy, R. J.,
- Naiman, R. J., & Puls, A. L. (2022). Food web perspectives and methods for riverine fish conservation.
- WIREs Water, n/a(n/a), e1590. https://doi.org/10.1002/wat2.1590
- Narayanan, A., Chandramohan, M., Venkatesan, R., Chen, L., Liu, Y., & Jaiswal, S. (2017). *Graph2vec*:
- Learning Distributed Representations of Graphs. http://arxiv.org/abs/1707.05005
- Neutel, A.-M., Heesterbeek, J. A. P., & de Ruiter, P. C. (2002). Stability in Real Food Webs: Weak Links in
- Long Loops. Science, 296(5570), 1120–1123. https://doi.org/10.1126/science.1068326
- No'kmaq, M., Marshall, A., Beazley, K. F., Hum, J., joudry, shalan, Papadopoulos, A., Pictou, S., Rabesca,
- J., Young, L., & Zurba, M. (2021). "Awakening the sleeping giant": Re-Indigenization principles for
- transforming biodiversity conservation in Canada and beyond. FACETS, 6(1), 839–869.
- Nost, E., & Goldstein, J. E. (2021). A political ecology of data. Environment and Planning E: Nature and
- 450 Space, 25148486211043503. https://doi.org/10.1177/25148486211043503
- 451 O'Connor, L. M. J., Pollock, L. J., Braga, J., Ficetola, G. F., Maiorano, L., Martinez-Almoyna, C.,
- Montemaggiori, A., Ohlmann, M., & Thuiller, W. (2020). Unveiling the food webs of tetrapods across

- Europe through the prism of the Eltonian niche. *Journal of Biogeography*, 47(1), 181–192.
- https://doi.org/10.1111/jbi.13773
- Pedersen, E. J., Thompson, P. L., Ball, R. A., Fortin, M.-J., Gouhier, T. C., Link, H., Moritz, C., Nenzen, H.,
- Stanley, R. R. E., Taranu, Z. E., Gonzalez, A., Guichard, F., & Pepin, P. (2017). Signatures of the
- collapse and incipient recovery of an overexploited marine ecosystem. Royal Society Open Science, 4(7),
- 458 170215. https://doi.org/10.1098/rsos.170215
- Perozzi, B., Al-Rfou, R., & Skiena, S. (2014). DeepWalk: Online learning of social representations.
- 460 Proceedings of the 20th ACM SIGKDD International Conference on Knowledge Discovery and Data
- 461 Mining, 701-710. https://doi.org/10.1145/2623330.2623732
- Pichler, M., Boreux, V., Klein, A.-M., Schleuning, M., & Hartig, F. (2020). Machine learning algorithms to
- infer trait-matching and predict species interactions in ecological networks. *Methods in Ecology and*
- Evolution, 11(2), 281-293. https://doi.org/10.1111/2041-210X.13329
- Poisot, T., Belisle, Z., Hoebeke, L., Stock, M., & Szefer, P. (2019). EcologicalNetworks.jl analysing
- ecological networks. *Ecography*. https://doi.org/10.1111/ecog.04310
- Poisot, T., Cirtwill, A. R., Cazelles, K., Gravel, D., Fortin, M.-J., & Stouffer, D. B. (2016). The structure of
- probabilistic networks. *Methods in Ecology and Evolution*, 7(3), 303–312.
- https://doi.org/10.1111/2041-210X.12468
- Poisot, T., Ouellet, M.-A., Mollentze, N., Farrell, M. J., Becker, D. J., Albery, G. F., Gibb, R. J., Seifert, S. N.,
- & Carlson, C. J. (2021). Imputing the mammalian virome with linear filtering and singular value
- decomposition. http://arxiv.org/abs/2105.14973
- Poisot, T., Stouffer, D. B., & Gravel, D. (2015). Beyond species: Why ecological interaction networks vary
- through space and time. Oikos, 124(3), 243–251. https://doi.org/10.1111/oik.01719
- Ramasamy, D., & Madhow, U. (2015). Compressive spectral embedding: Sidestepping the SVD. In C.
- 476 Cortes, N. Lawrence, D. Lee, M. Sugiyama, & R. Garnett (Eds.), Advances in neural information
- 477 processing systems (Vol. 28). Curran Associates, Inc. https:
- //proceedings.neurips.cc/paper/2015/file/4f6ffe13a5d75b2d6a3923922b3922e5-Paper.pdf
- Ray, J. C., Grimm, J., & Olive, A. (2021). The biodiversity crisis in Canada: Failures and challenges of
- federal and sub-national strategic and legal frameworks. *FACETS*, *6*, 1044–1068.

```
https://doi.org/10.1139/facets-2020-0075
481
    Runghen, R., Stouffer, D. B., & Dalla Riva, G. V. (2021). Exploiting node metadata to predict interactions in
482
       large networks using graph embedding and neural networks.
483
       https://doi.org/10.1101/2021.06.10.447991
484
    S, N. S., & Surendran, S. (2013). Graph Embedding and Dimensionality Reduction - A Survey.
485
       International Journal of Computer Science & Engineering Technology, 4(1). https://www.
486
       semanticscholar.org/paper/Graph-Embedding-and-Dimensionality-Reduction-A-Surendran/
487
       3f413d591e4b2b876e033eeb9390e232ad4826ca
488
    Saravia, L. A., Marina, T. I., Kristensen, N. P., De Troch, M., & Momo, F. R. (2021). Ecological network
489
       assembly: How the regional metaweb influences local food webs. Journal of Animal Ecology, n/a(n/a).
490
       https://doi.org/10.1111/1365-2656.13652
491
    Stevenson, M. T., & Doleac, J. L. (2021). Algorithmic Risk Assessment in the Hands of Humans (SSRN
492
       Scholarly Paper No. 3489440). https://doi.org/10.2139/ssrn.3489440
493
    Stier, A. C., Samhouri, J. F., Gray, S., Martone, R. G., Mach, M. E., Halpern, B. S., Kappel, C. V.,
494
       Scarborough, C., & Levin, P. S. (2017). Integrating Expert Perceptions into Food Web Conservation and
495
       Management. Conservation Letters, 10(1), 67-76. https://doi.org/10.1111/conl.12245
496
    Strydom, T., Bouskila, S., Banville, F., Barros, C., Caron, D., Farrell, M. J., Fortin, M.-J., Hemming, V.,
497
       Mercier, B., Pollock, L. J., Runghen, R., Dalla Riva, G. V., & Poisot, T. (2022). Food web reconstruction
498
       through phylogenetic transfer of low-rank network representation. Methods in Ecology and Evolution,
499
       n/a(n/a). https://doi.org/10.1111/2041-210X.13835
500
    Strydom, T., Catchen, M. D., Banville, F., Caron, D., Dansereau, G., Desjardins-Proulx, P., Forero-Muñoz,
501
       N. R., Higino, G., Mercier, B., Gonzalez, A., Gravel, D., Pollock, L., & Poisot, T. (2021). A roadmap
502
       towards predicting species interaction networks (across space and time). Philosophical Transactions of
503
       the Royal Society B: Biological Sciences, 376(1837), 20210063.
504
       https://doi.org/10.1098/rstb.2021.0063
505
    Strydom, T., Dalla Riva, G. V., & Poisot, T. (2021). SVD Entropy Reveals the High Complexity of Ecological
506
       Networks. Frontiers in Ecology and Evolution, 9. https://doi.org/10.3389/fevo.2021.623141
507
```

Tang, J., Qu, M., Wang, M., Zhang, M., Yan, J., & Mei, Q. (2015). LINE: Large-scale Information Network

```
Embedding. Proceedings of the 24th International Conference on World Wide Web, 1067–1077.
509
       https://doi.org/10.1145/2736277.2741093
510
    Torres, L., Chan, K. S., & Eliassi-Rad, T. (2020). GLEE: Geometric Laplacian Eigenmap Embedding.
511
       Journal of Complex Networks, 8(2), cnaa007. https://doi.org/10.1093/comnet/cnaa007
512
    Turak, E., Brazill-Boast, J., Cooney, T., Drielsma, M., DelaCruz, J., Dunkerley, G., Fernandez, M., Ferrier,
513
       S., Gill, M., Jones, H., Koen, T., Leys, J., McGeoch, M., Mihoub, J.-B., Scanes, P., Schmeller, D., &
514
       Williams, K. (2017). Using the essential biodiversity variables framework to measure biodiversity
515
       change at national scale. Biological Conservation, 213, 264–271.
516
       https://doi.org/10.1016/j.biocon.2016.08.019
517
    Wang, D., Cui, P., & Zhu, W. (2016). Structural Deep Network Embedding. Proceedings of the 22nd ACM
518
       SIGKDD International Conference on Knowledge Discovery and Data Mining, 1225–1234.
519
       https://doi.org/10.1145/2939672.2939753
520
    Wang, S., Arroyo, J., Vogelstein, J. T., & Priebe, C. E. (2021). Joint Embedding of Graphs. IEEE
521
       Transactions on Pattern Analysis and Machine Intelligence, 43(4), 1324-1336.
522
       https://doi.org/10.1109/TPAMI.2019.2948619
523
    Wardeh, M., Baylis, M., & Blagrove, M. S. C. (2021). Predicting mammalian hosts in which novel
524
       coronaviruses can be generated. Nature Communications, 12(1, 1), 780.
525
       https://doi.org/10.1038/s41467-021-21034-5
526
    Weiskopf, S. R., Harmáčková, Z. V., Johnson, C. G., Londoño-Murcia, M. C., Miller, B. W., Myers, B. J. E.,
       Pereira, L., Arce-Plata, M. I., Blanchard, J. L., Ferrier, S., Fulton, E. A., Harfoot, M., Isbell, F., Johnson,
528
       J. A., Mori, A. S., Weng, E., & Rosa, I. M. D. (2022). Increasing the uptake of ecological model results in
529
       policy decisions to improve biodiversity outcomes. Environmental Modelling & Software, 149, 105318.
530
       https://doi.org/10.1016/j.envsoft.2022.105318
531
    Wood, S. A., Russell, R., Hanson, D., Williams, R. J., & Dunne, J. A. (2015). Effects of spatial scale of
532
       sampling on food web structure. Ecology and Evolution, 5(17), 3769–3782.
533
       https://doi.org/10.1002/ece3.1640
534
    Xu, M. (2020). Understanding graph embedding methods and their applications.
       http://arxiv.org/abs/2012.08019
536
```

- Yan, S., Xu, D., Zhang, B., & Zhang, H.-J. (2005). Graph embedding: A general framework for
 dimensionality reduction. 2005 IEEE Computer Society Conference on Computer Vision and Pattern

 Recognition (CVPR'05), 2, 830–837 vol. 2. https://doi.org/10.1109/CVPR.2005.170
- Young, S. J., & Scheinerman, E. R. (2007). Random Dot Product Graph Models for Social Networks. In A.
- Bonato & F. R. K. Chung (Eds.), *Algorithms and Models for the Web-Graph* (pp. 138–149). Springer.
- https://doi.org/10.1007/978-3-540-77004-6_11
- Zhou, J., Cui, G., Hu, S., Zhang, Z., Yang, C., Liu, Z., Wang, L., Li, C., & Sun, M. (2020). Graph neural
 networks: A review of methods and applications. *AI Open*, 1, 57–81.
- https://doi.org/10.1016/j.aiopen.2021.01.001

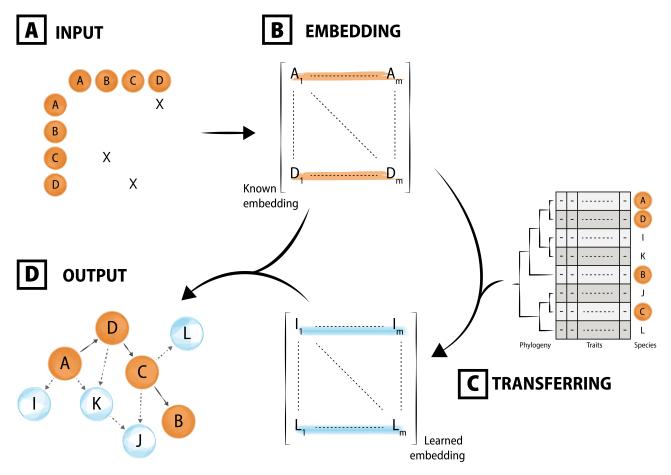


Figure 1: Overview of the embedding process. A network (**A**), represented here as its adjacency matrix, is converted into a lower-dimensional object (**B**) where nodes, subgraphs, or edges have specific values (see tbl. 1 for an overview of methods and their use for species interactions). For the purposes of prediction, this low-dimensional object encodes feature vectors for *e.g.* the nodes. Embedding also allows to visualize the structure in the data differently (see fig. ??), much like with a principal component analysis. From a low-dimensional feature vector, it is possible to develop predictive approaches. Nodes in an ecological network are usually species (**C**), for which we can leverage phylogenetic relatedness (*e.g.* Strydom et al., 2022) or functional traits to fill the values of additional species we would like to project in this space (here for nodes I, J, K, and L) from the embedding of known species (here, nodes A, B, C, and D). Because embeddings can be projected back to a graph, this allows us to reconstruct a network with these new species (**D**). This entire cycle constitutes an instance of transfer learning, where the transfered information is the representation of graph **A** through its embedding.

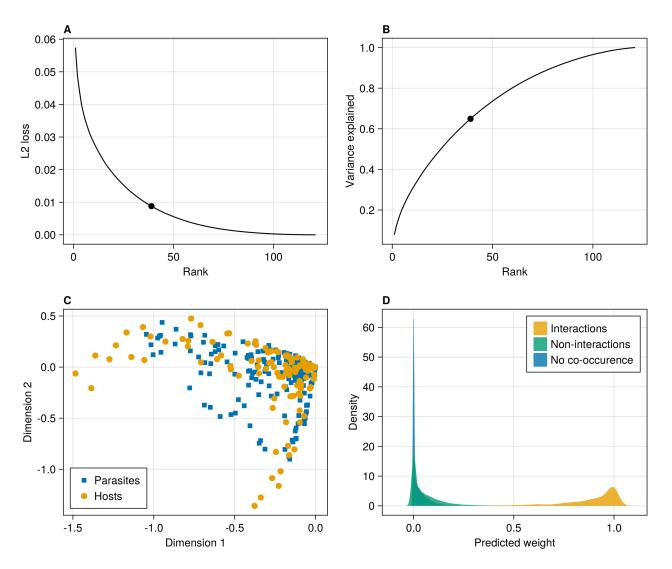


Figure 2: Validation of an embedding for a host-parasite metaweb, using Random Dot Product Graphs. **A**, decrease in approximation error as the number of dimensions in the subspaces increases. **B**, increase in cumulative variance explained as the number of ranks considered increases; in **A** and **B**, the dot represents the point of inflexion in the curve (at rank 39) estimated using the finite differences method. **C**, position of hosts and parasites in the space of latent variables on the first and second dimensions of their respective subspaces (the results have been clamped to the unit interval). **D**, predicted interaction weight from the RDPG based on the status of the species pair in the metaweb.

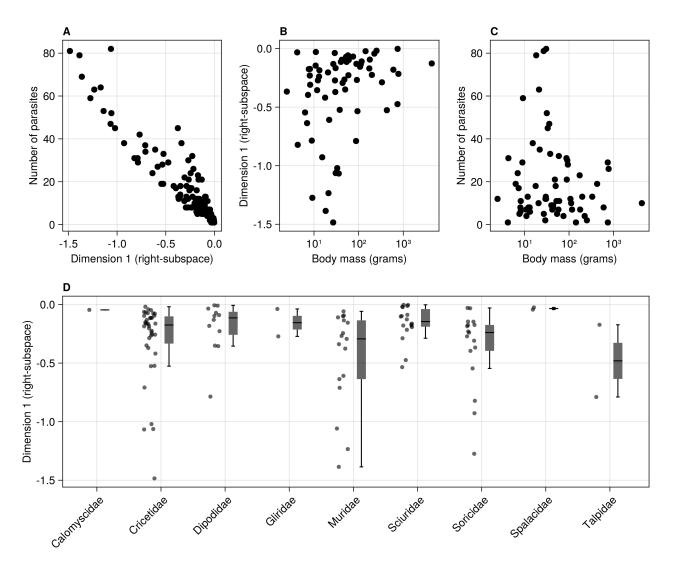


Figure 3: Ecological analysis of an embedding for a host-parasite metaweb, using Random Dot Product Graphs. **A**, relationship between the number of parasites and position along the first axis of the right-subspace for all hosts, showing that the embedding captures elements of network structure at the species scale. **B**, weak relationship between the body mass of hosts (in grams) and the position alongside the same dimension. **C**, weak relationship between bodymass of hosts and parasite richness. **D**, distribution of positions alongside the same axis for hosts grouped by taxonomic family.

Table 1: Overview of some common graph embedding approaches, by type of embedded objects, alongside examples of their use in the prediction of species interactions. These methods have not yet been routinely used to predict species interactions; most examples that we identified were either statistical associations, or analogues to joint species distribution models. ^a: statistical interactions; ^b: joint-SDM-like approach. Given the need to evaluate different methods on a problem-specific basis, the fact that a lot of methods have not been used on network problems is an opportunity for benchmarking and method development. Note that the row for PCA also applies to kernel/probabilistic PCA, which are variations on the more general method of SVD. Note further that tSNE has been included because it is frequently used to embed graphs, including of species associations/interactions, despite not being strictly speaking, a graph embedding technique (see *e.g.* Chami et al., 2022)

Method	Object	Technique	Reference	Application
tSNE	nodes	statistical divergence	Hinton &	Gibb et al. (2021); Cieslak et
			Roweis (2002)	al. (2020) ^a
LINE	nodes	stochastic gradient	Tang et al.	
		descent	(2015)	
SDNE	nodes	gradient descent	D. Wang et al.	
			(2016)	
node2vec	nodes	stochastic gradient	Grover &	
		descent	Leskovec	
			(2016)	
HARP	nodes	meta-strategy	H. Chen et al.	
			(2017)	
DMSE	joint nodes	deep neural network	D. Chen et al.	D. Chen et al. (2017) <i>b</i>
			(2017)	
graph2vec	sub-graph	skipgram network	Narayanan et	
			al. (2017)	
RDPG	graph	SVD	Young &	Poisot et al. (2021); Dalla Riva
			Scheinerman	& Stouffer (2016)
			(2007)	
GLEE	graph	Laplacian eigenmap	Torres et al.	
			(2020)	
DeepWalk	graph	stochastic gradient	Perozzi et al.	Wardeh et al. (2021)
		descent	(2014)	
GraphKKE	E graph	stochastic differential	Melnyk et al.	Melnyk et al. (2020) ^a
		equation	(2020)	
FastEmbed	graph	eigen decomposition	Ramasamy &	
			Madhow	
			(2015)	
PCA	graph	eigen decomposition	S & Surendran	Strydom, Catchen, et al.
			(2013)	(2021)
Joint	multiple	multiple strategies	S. Wang et al.	
methods	graphs		(2021)	