

The prediction of species interaction networks is facilitated by graph embedding and transfer learning despite data limitations

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1. Metawebs, i.e. networks of potential interactions within a species pool, are a powerful abstraction to understand how large-scales 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 the predictive ability is to maximize the information used for prediction, by using graph embeddings rather than 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; furthermore, because metawebs are inherently spatial objects, we 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.

1 Being able to infer *potential* interactions could be the catalyst for significant breakthroughs in our ability
2 to start thinking about species interaction networks over large spatial scales (Hortal et al., 2015).
3 Understanding species interactions holds enormous potential to not only understand and more rapidly
4 learn about species interactions and metawebs, but also how changes in management of a single species
5 may impact non-target species. In a recent overview of the field of ecological network prediction, Strydom,
6 Catchen, et al. (2021) identified two challenges of interest to the prediction of interactions at large scales.
7 First, there is a relative scarcity of relevant data in most places globally – paradoxically, this restricts our
8 ability to infer interactions for locations where inference is perhaps the least required (and leaves us
9 unable to make inference in regions without interaction data); second, accurate predictions often demand
10 accurate predictors, and the lack of methods that can leverage small amount of *accurate* data is a serious
11 impediment to our global predictive ability. In most places, our most reliable biodiversity knowledge is
12 that of a species pool (*i.e.* a set of potentially interacting species in a given area): through the analysis of
13 databases like GBIF or IUCN, it is possible to construct a list of species in a region of interest; but inferring
14 the potential interactions between these species is difficult.

15 Following the definition of Dunne (2006), a metaweb is the ecological network analogue to the species
16 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
18 point within the spatial area it covers: it will have a different structure, notably by having a larger
19 connectance (see *e.g.* Wood et al., 2015) and complexity (see *e.g.* Galiana et al., 2022), from any of these
20 local networks. These local networks (which capture the α diversity of interactions) are a subset of the
21 metaweb's species and their interactions, and have been called “metaweb realizations” (Poisot et al., 2015).
22 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 realizations only respond weakly
25 to local conditions: instead, they reflect constraints inherited by the structure of their metaweb. This
26 establishes the metaweb structure as the core goal of predictive network ecology, as it is a required
27 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 is the
30 “upper bounds” on what the composition of the local networks, given the local species pool, can be (see

31 e.g. McLeod et al., 2021); this information can help evaluate the ability of ecological assemblages to
32 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
34 the structure of food webs at finer spatial scales. This has been done for example for tree-galler-parasitoid
35 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
37 contribution, we highlight the power in viewing (and constructing) metawebs as *probabilistic* objects in
38 the context of rare interactions, discuss how a family of machine learning tools (graph embeddings and
39 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 **The metaweb is an inherently probabilistic object**

42 Treating interactions as probabilistic (as opposed to binary) events is a more nuanced and realistic way to
43 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
45 difficult because it requires first the joint observation of two species, and then the observation of their
46 interaction. In addition, it is generally expected that weak or rare links to be more prevalent in networks
47 than common or rare links (Csermely, 2004), compared to strong, persistent links; this is notably the case
48 in food chains, wherein many weaker links are key to the stability of a system (Neutel et al., 2002). In the
49 light of these observations, we expect to see an over-representation of low-probability interactions under a
50 model that accurately predicts interaction probabilities. Yet the original metaweb definition, and indeed
51 most past uses of metawebs, was based on the presence/absence of interactions. Moving towards
52 *probabilistic* metawebs, by representing interactions as Bernoulli events (see e.g. Poisot et al., 2016), offers
53 the opportunity to weigh these rare interactions appropriately. The inherent plasticity of interactions is
54 important to capture: there have been documented instances of food webs undergoing rapid
55 collapse/recovery cycles over short periods of time (e.g. Pedersen et al., 2017). These considerations
56 emphasize why metaweb predictions should focus on quantitative (preferentially probabilistic)
57 predictions; this should constrain the suite of appropriate models.

58 Yet it is important to recall that a metaweb is intended as a catalogue of all potential interactions, which is

59 then filtered (Morales-Castilla et al., 2015). In a sense, that most ecological interactions are elusive can call
60 for a slightly different approach to sampling: once the common interactions are documented, the effort
61 required in documenting each rare interaction will increase exponentially. Recent proposals suggest that
62 machine learning algorithms, in these situations, can act as data generators (Hoffmann et al., 2019): high
63 quality observational data can generate the core rules underpinning the network structure, and be
64 supplemented with synthetic data coming from predictive models, increasing the volume of information
65 available for inference. Indeed, Strydom, Catchen, et al. (2021) suggested that knowing the metaweb may
66 render the prediction of local networks easier, because it fixes an “upper bound” on which interactions
67 can exist. In this context a probabilistic metaweb represents an aggregation of informative priors on the
68 interactions, elusive information with the potential to boost our predictive ability (Bartomeus et al., 2016).

69 [Figure 1 about here.]

70 **Graph embedding offers promises for the inference of potential** 71 **interactions**

72 Graph embedding (fig. 1) is a varied family of machine learning techniques aiming to transform nodes and
73 edges into a vector space (Arsov & Mirceva, 2019), usually of a lower dimension, whilst maximally
74 retaining key properties of the graph (Yan et al., 2005). Ecological networks are an interesting candidate
75 for the widespread application of embeddings, as they tend to possess a shared structural backbone
76 (Bramon Mora et al., 2018), which hints at structural invariants that can be revealed at lower dimensions.
77 Indeed, food webs are inherently low-dimensional objects, and can be adequately represented with less
78 than ten dimensions (Braga et al., 2019; Eklöf et al., 2013). Simulation results by Botella et al. (2022)
79 suggest that there is no best method to identify architectural similarities between networks, and that
80 multiple approaches need to be tested and compared to the network descriptor of interest. This matches
81 previous, more general results on graph embedding, which suggest that the choice of embedding
82 algorithm matters for the results (Goyal & Ferrara, 2018). In tbl. 1, we present a selection of common
83 graph embedding methods, alongside examples of their use to predict species interactions; most of these
84 methods rely either on linear algebra, or on pseudo-random walks on graphs.

85 One prominent family of approaches we do not discuss in the present manuscript is Graph Neural

86 Networks (GNN; Zhou et al., 2020); GNN are, in a sense, a method to embed a graph into a dense
87 subspace, but belong to the family of deep learning methods, which has its own set of practices (see *e.g.*
88 Goodfellow et al., 2016). An important issue with methods based on deep learning is that because their
89 parameter space is immense, the sample size of the data fed into them must be similarly large (typically
90 thousands of instances). This is a requirement for the model to converge correctly during training, but this
91 assumption is unlikely to be met given the size of datasets about currently available metawebs (or single
92 time/location species interaction networks). This data volume requirement is mostly absent from the
93 techniques we list below. Furthermore, GNN still have some challenges related to their shallow structure,
94 and concerns related to scalability (see Gupta et al., 2021 for a review), which are mostly absent from the
95 methods listed in [tbl. 1](#). Assuming that the uptake of next-generation biomonitoring techniques does
96 indeed deliver larger datasets on species interactions (Bohan et al., 2017), there is a potential for GNN to
97 become an applicable embedding/predictive technique in the coming years.

98 [Table 1 about here.]

99 The popularity of graph embedding techniques in machine learning is more than the search for structural
100 invariants: graphs are discrete objects, and machine learning techniques tend to handle continuous data
101 better. Bringing a sparse graph into a continuous, dense vector space (Xu, 2020) opens up a broader variety
102 of predictive algorithms, notably of the sort that are able to predict events as probabilities (Murphy, 2022).
103 Furthermore, the projection of the graph itself is a representation that can be learned; Runghen et al.
104 (2021), for example, used a neural network to learn the embedding of a network in which not all
105 interactions were known, based on nodes metadata. This example has many parallels in ecology (see
106 [fig. ??](#)), in which node metadata can be given by phylogeny or functional traits. Rather than directly
107 predicting biological rules (see *e.g.* Pichler et al., 2020 for an overview), which may be confounded by the
108 sparse nature of graph data, learning embeddings works in the low-dimensional space that maximizes
109 information about the network structure. This approach is further justified by the observation, for
110 example, that the macro-evolutionary history of a network is adequately represented by some graph
111 embeddings (RDPG; see Dalla Riva & Stouffer, 2016). In a recent publication, Strydom, Bouskila, et al.
112 (2021) have used an embedding (based on RDPG) to project a metaweb of trophic interactions between
113 European mammals, and transferred this information to mammals of Canada by using the phylogenetic
114 distance between related clades to infer the values in the latent sub-space into which the metaweb was

115 projected. By performing the RDPG step on re-constructed value, this approach yields a probabilistic
116 trophic metaweb for mammals of Canada based on knowledge of European species, despite a limited (\approx
117 5%) taxonomic overlap.

118 Graph embeddings *can* serve as a dimensionality reduction method. For example, RDPG (Strydom,
119 Bouskila, et al., 2021) and t-SVD (Poisot et al., 2021) typically embed networks using fewer dimensions
120 than the original network (the original network has as many dimensions as species, and as many
121 informative dimensions as trophically unique species; Strydom, Dalla Riva, et al., 2021). But this is not
122 necessarily the case – indeed, one may perform a PCA (a special case of SVD) to project the raw data into
123 a subspace that improves the efficacy of t-SNE (Maaten, 2009). There are many dimensionality reductions
124 (Anowar et al., 2021) that can be applied to an embedded network should the need for dimensionality
125 reduction (for example for data visualisation) arise. In brief, many graph embeddings *can* serve as
126 dimensionality reduction steps, but not all do, neither do all dimensionality reduction methods provide
127 adequate graph embedding capacities.

128 **An illustration of metaweb embedding**

129 In this section, we illustrate the embedding of a collection of bipartite networks collected by **REF**, using
130 truncated Singular Value Decomposition (t-SVD). The code to reproduce this example (as a Jupyter
131 notebook) is available as supplementary material. The resulting (binary) metaweb \mathcal{M} has 2131 interactions
132 between 206 parasites and 121 hosts (the same metaweb was used for the illustration of interaction
133 inference through deep learning in Strydom, Catchen, et al., 2021), and its adjacency matrix has full rank
134 (*i.e.* it represents a space with 121 dimensions). All analyses were done using Julia (Bezanson et al., 2017)
135 version 1.7.2, *Makie.jl* (Danisch & Krumbiegel, 2021), and *EcologicalNetworks.jl* (Poisot et al., 2019).
136 [fig. 2](#)

137 [Figure 2 about here.]

138 **The metaweb embeds both ecological hypotheses and practices**

139 The goal of metaweb inference is to provide information about the interactions between species at a large
140 spatial scale. But as Herbert (1965) rightfully pointed out, “[y]ou can’t draw neat lines around planet-wide
141 problems”; any inference of a metaweb at large scales must contend with several novel, and interwoven,
142 families of problems. In this section, we list some of the most pressing research priorities (*i.e.* problems
143 that can be addressed with subsequent data analysis or simulations), as well as issues related to the
144 application of these methods at the science-policy interface.

145 The first open research problem is the taxonomic and spatial limit of the metaweb to embed and transfer.
146 If the initial metaweb is too narrow in scope, notably from a taxonomic point of view, the chances of
147 finding another area with enough related species (through phylogenetic relatedness or similarity of
148 functional traits) to make a reliable inference decreases; this would likely be indicated by large confidence
149 intervals during estimation of the values in the low-rank space, meaning that the representation of the
150 original graph is difficult to transfer to the new problem. In addition, other problems can arise due to
151 non-overlapping trait distributions in the known and unknown species. Alternatively a metaweb is too
152 large (taxonomically), then the resulting embeddings would need to represent interactions between
153 taxonomic groups that are not present in the new location. This would lead to a much higher variance in
154 the starting dataset, and to under-dispersal in the target dataset, resulting in the potential under or over
155 estimation of the strength of new predicted interactions. The lack of well documented metawebs is
156 currently preventing the development of more concrete guidelines. The question of phylogenetic
157 relatedness and dispersal is notably true if the metaweb is assembled in an area with mostly endemic
158 species (*e.g.* a system that has undergone recent radiation and might not have an analogous system with
159 which to draw knowledge from), and as with every predictive algorithm, there is room for the application
160 of our best ecological judgement. Because this problem relates to dispersal of species in the geographic or
161 phylogenetic space, it can certainly be approached through assessing the performance of embedding
162 transfer in simulated starting/target species pools.

163 The second series of problems relate to determining which area should be used to infer the new metaweb
164 in, as this determines the species pool that must be used. Metawebs can be constructed by assigning
165 interactions in a list of species within geographic boundaries. The upside of this approach is that
166 information at the country level is likely to be required for biodiversity assessments, as countries set goals

167 at the national level (Buxton et al., 2021), and as quantitative instruments are designed to work at these
168 scales (Turak et al., 2017); specific strategies are often enacted at smaller scales, nested within a specific
169 country (Ray et al., 2021). But there is no guarantee that these boundaries are meaningful. In fact, we do
170 not have a satisfying answer to the question of “where does a food web stop?”; the most promising
171 solutions involve examining the spatial consistency of network area relationships (Fortin et al., 2021; see
172 e.g. Galiana et al., 2018, 2019, 2021), which is impossible in the absence of enough information about the
173 network itself. This suggests that inferred metawebs should be further downscaled to allow for *a posteriori*
174 analyses. The methodology for metaweb downscaling is currently limited, and it is likely that the
175 sustained effort to characterize the spatial dependency of food web structure will lead to more prescriptive
176 guidelines about the need for prediction downscaling.

177 The final family of problems relates less to ecological methods than to the praxis of ecological research.
178 Operating under the context of national divisions, in large parts of the world, reflects nothing more than
179 the legacy of settler colonialism, which drives a disparity in available ecological data. Applying any
180 embedding to biased data does not debias them, but instead embeds these very same biases, propagating
181 them to the machine learning models using embeddings to make predictions. Indeed, the use of ecological
182 data is not an apolitical act (Nost & Goldstein, 2021), as data infrastructures tend to be designed to answer
183 questions within national boundaries (therefore placing contingencies on what is available to be
184 embedded), and their use often draws upon and reinforces territorial statecraft. As per Machen & Nost
185 (2021), this is particularly true when the output of “algorithmic thinking” (e.g. relying on machine
186 learning to generate knowledge) can be re-used for governance (e.g. enacting conservation decisions at the
187 national scale). As information on species interaction networks structure is increasingly leveraged as a
188 tool to guide conservation actions (see e.g. recent discussions for food-web based conservation; Eero et al.,
189 2021; Naman et al., 2022; Stier et al., 2017), the need to appraise and correct biases that are unwittingly
190 propagated to algorithms when embedded from the original data is paramount. Predictive approaches
191 deployed at the continental scale, no matter their intent, originate in the framework that contributed to
192 the ongoing biodiversity crisis (Adam, 2014) and reinforced environmental injustice (Choudry, 2013;
193 Domínguez & Luoma, 2020). Particularly on Turtle Island and other territories that were traditionally
194 stewarded by Indigenous people, these approaches should be replaced (or at least guided and framed) by
195 Indigenous principles of land management (Eichhorn et al., 2019; No’kmaq et al., 2021), as part of an
196 “algorithm-in-the-loop” approach. Human-algorithm interactions are notoriously difficult and can yield

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 mobilized to generate knowledge that is lacking for conservation decisions (e.g. Lamba et al., 2019; 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.

Acknowledgements: We acknowledge that this study was conducted on land within the traditional 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 & Evolution. FB is funded by the Institute for Data Valorization (IVADO). TS, SB, and TP are funded by a 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 Resources Improvement Association of Alberta. M-JF acknowledges funding from NSERC Discovery Grant and NSERC CRC. RR is funded by New Zealand's Biological Heritage Ngā Koiora Tuku Iho National Science Challenge, administered by New Zealand Ministry of Business, Innovation, and Employment. BM is funded by the NSERC Alexander Graham Bell Canada Graduate Scholarship and the FRQNT master's scholarship. LP acknowledges funding from NSERC Discovery Grant (NSERC RGPIN-2019-05771). TP acknowledges financial support from NSERC through the Discovery Grants and Discovery Accelerator Supplement programs. MJF is supported by an NSERC PDF and an RBC Post-Doctoral Fellowship

Conflict of interest: The authors have no conflict interests to disclose

Authors' contributions: TS, and TP conceived the ideas discussed in the manuscript. All authors contributed to writing and editing the manuscript.

Data availability: There is no data associated with this manuscript.

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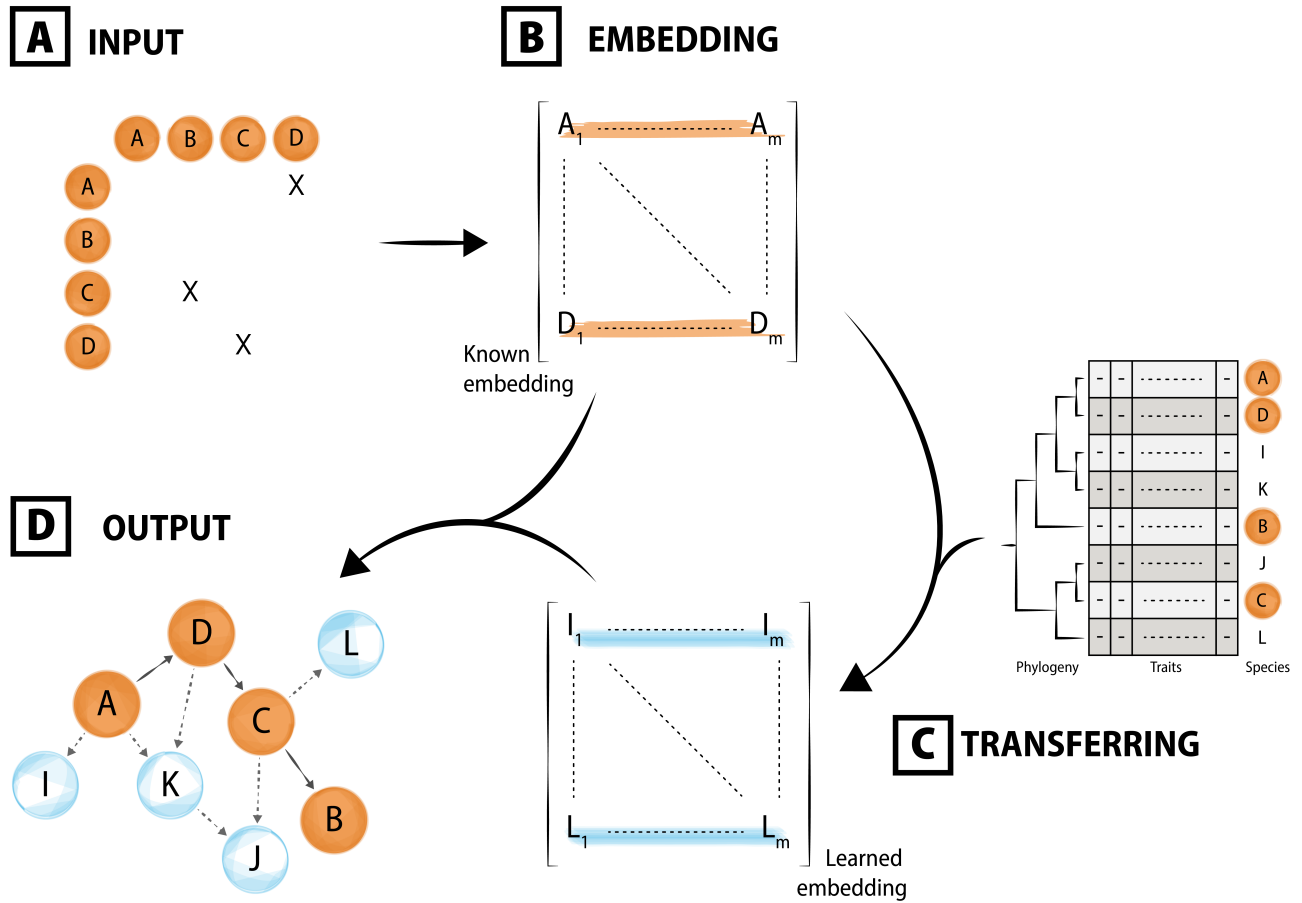


Figure 1: Overview of the embedding process. A network (A), represented as its adjacency matrix (B), is converted into a lower-dimensional object (C) where nodes, subgraphs, or edges have specific values (see tbl. 1). For the purposes of prediction, this low-dimensional object encodes feature vectors for *e.g.* the nodes. Embedding also allows to visualize the structure in the data differently (D), 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 species, for which we can leverage phylogenetic relatedness (*e.g.* Strydom, Bouskila, et al., 2021) or functional traits to fill the values of additional species we would like to project in this space (here, I, J, K, and L) from the embedding of known species (here, 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. This approach constitutes an instance of transfer learning.

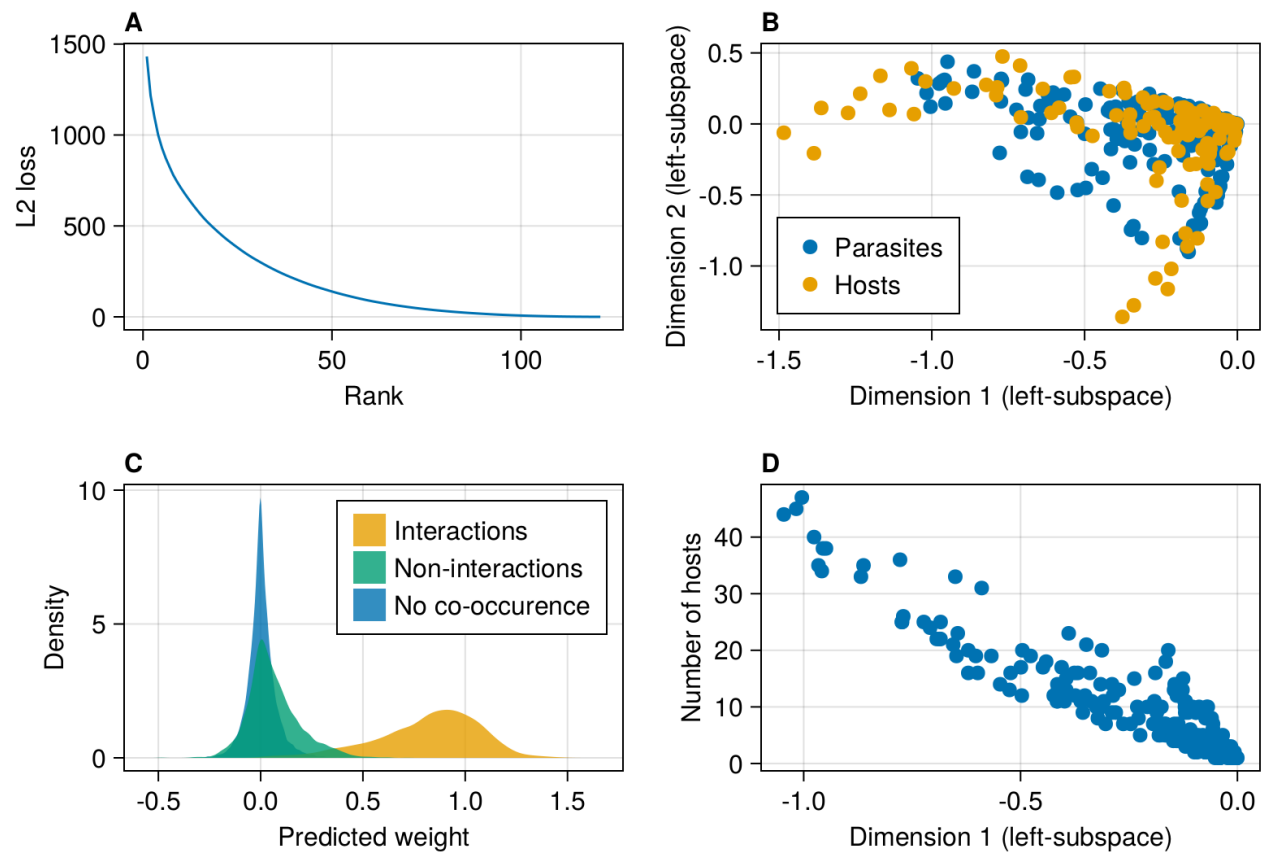


Figure 2: Need to add text here

Table 1: Overview of some common graph embedding approaches, by time of publication, 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.

Method	Embedding approach	Reference	Application in species interactions
tSNE	nodes through statistical divergence	Hinton & Roweis (2002)	Cieslak et al. (2020) ^a
RDPG	graph through SVD	Young & Scheinerman (2007)	Poisot et al. (2021); Dalla Riva & Stouffer (2016)
DeepWalk	graph walk	Perozzi et al. (2014)	Wardeh et al. (2021)
FastEmbed	graph through PCA/SVD analogue	Ramasamy & Madhow (2015)	
LINE	nodes through statistical divergence	Tang et al. (2015)	
SDNE	nodes through auto-encoding	D. Wang et al. (2016)	
node2vec	nodes embedding	Grover & Leskovec (2016)	
graph2vec	sub-graph embedding	Narayanan et al. (2017)	
DMSE	joint nodes embedding	D. Chen et al. (2017)	D. Chen et al. (2017) ^b
HARP	nodes through a meta-strategy	H. Chen et al. (2017)	
GraphKKE	graph embedding	Melnyk et al. (2020)	Melnyk et al. (2020) ^a
Joint methods	multiple graphs	S. Wang et al. (2021)	