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 species interactions and metawebs, but also how changes in management of a single species may impact non-target species. In a recent overview of the field of ecological network prediction, Strydom, Catchen, et 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 interactions for locations where inference is perhaps the least required (and leaves us unable to make 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 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 metaweb's species and realized interactions, and have been called "metaweb realizations" (Poisot et al., 2015). Differences between local networks and their metawebs are due to chance, species abundance and co-occurrence, local environmental conditions, and local distribution of functional traits, among others. Yet, recent results by Saravia et al. (2021) strongly suggest that the local (metaweb) realizations only 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 required information to accurately produce downscaled, local predictions.

Because the metaweb represents the joint effect of functional, phylogenetic, and macroecological 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

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.

A 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 weak or rare links to be more prevalent in networks than

47 common or strong links (Csermely, 2004), compared to strong, persistent links; this is notably the case in

48 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 (rare) interactions

50 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

53 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

55 instances of food webs undergoing rapid collapse/recovery cycles over short periods of time (*e.g.* Pedersen

56 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

58 (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.

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 used to infer core rules underpinning network structure, and be supplemented with synthetic data coming from predictive models trained on them, thereby increasing the volume of information available for 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

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 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) 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 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 on linear algebra, or on pseudo-random walks on graphs. All forms of embeddings presented in the table share the common property of summarizing their objects into (sets of) dense feature vectors, that capture the overall network structure, pairwise information on nodes, and emergent aspects of the network, in a compressed way (*i.e.* with some information loss, as we later discuss in the illustration). Node embeddings tend to focus on maintaining pairwise relationships, while graph embeddings focus on maintaining the network structure. Nevertheless, some graph embedding techniques (like RDPG, see *e.g.* Wu et al., 2021) will provide usable node-level embeddings.

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 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 parameter space is immense, the sample size of the data fed into them must be similarly large (typically thousands of instances). This is a requirement for the model to converge correctly during training, but this 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 techniques we list below. Furthermore, GNN still have some challenges related to their shallow structure, 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

indeed deliver larger datasets on species interactions (Bohan et al., 2017), there is a potential for GNN to become an applicable embedding/predictive technique in the coming years.

[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 better. Bringing a sparse graph into a continuous, dense vector space (Xu, 2021) opens up a broader variety of predictive algorithms, notably of the sort that are able to predict events as probabilities (Murphy, 2022). Furthermore, the projection of the graph itself is a representation that can be learned; Runghen et al. (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 fig. 1 **C**), in which node metadata can be represented by phylogeny, abundance, or functional traits. Using phylogeny as a source of information assumes (or strives to capture) the action of evolutionary processes on network structure, which at least for food webs have been well documented **TK REF**; similarly, the use of functional traits assumes that interactions can be infered from the knowledge of trait-matching rules, which is similarly well supported in the empirical literature **TK REF**. Relating this information to an 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 may suggest that evolutionary/trait processes are not strong drivers of network structure, therefore opening a new way to perform hypothesis testing.

Before moving further, it is important to clarify the epistemic status of node values derived from embeddings: specifically, they are *not* functional traits, and therefore should not be discussed in terms of effects or responses. As per the framework of Malaterre et al. (2019), these values neither derive from, nor result in, changes in organismal fitness, and should therefore not be used to quantify *e.g.* functional diversity. This holds true even when there are correlations between latent values and functional traits: although these enable an ecological discussion of how traits condition the structure of the network, the existence of a statistical relationship does not elevate the latent values to the status of functional traits.

Rather than directly predicting biological rules (see *e.g.* Pichler et al., 2020 for an overview), which may be confounded by the sparse nature of graph data, learning embeddings works in the low-dimensional space that maximizes information about the network structure. This approach is further justified by the

observation, for example, that the macro-evolutionary history of a network is adequately represented by some graph embeddings (Random dot product graphs (RDPG); see Dalla Riva & Stouffer, 2016). In a 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 Canada, using the phylogenetic distance between related clades to infer the values in the latent sub-space 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 European species, despite a limited ($\approx$ 5%) taxonomic overlap.

Graph embeddings *can* serve as a dimensionality reduction method. For example, RDPG (Strydom et al., 2022) and t-SVD (truncated Singular Value Decomposition; Poisot et al., 2021) typically embed networks 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

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 a network into two subspaces (left and right), which are matrices that when multiplied give an approximation of the original network. RDPG has the particularly desirable properties of being a graph embedding technique that produces relevant node-level feature vectors, and provides good approximations of graphs with varied structures (Athreya et al., 2017). The code to reproduce this example is available as supplementary material (note, for the sake of comparison, that Strydom, Catchen, et al.,

173 2021 have an example using embedding through PCA followed by prediction using a deep neural network

174 on the same dataset). The resulting (binary) metaweb $\mathcal{M}$ has 2131 interactions between 206 parasites and

175 121 hosts, and its adjacency matrix has full rank (*i.e.* it represents a space with 121 dimensions). All

176 analyses were done using Julia (Bezanson et al., 2017) version 1.7.2, *Makie.jl* (Danisch & Krumbiegel,

177 2021), and *EcologicalNetworks.jl* (Poisot et al., 2019).

178   [Figure 2 about here.]

179 In fig. 2, we focus on some statistical checks of the embedding. In panel **A**, we show that the averaged L_2

180 loss (*i.e.* the sum of squared errors) between the empirical and reconstructed metaweb decreases when the

181 number of dimensions (rank) of the subspace increases, with an inflection at 39 dimensions (out of 120

182 initially) according to the finite differences method. As discussed by Runghen et al. (2021), there is often a

183 trade-off between the number of dimensions to use (more dimensions are more computationally

184 demanding) and the quality of the representation. In panel **B**, we show the increase in cumulative

185 variance explained at each rank, and visualize that using 39 ranks explains about 70% of the variance in

186 the empirical metaweb. This is a different information from the L_2 loss (which is averaged across

187 interactions), as it works on the eigenvalues of the embedding, and therefore captures higher-level features

188 of the network. In panel **C**, we show positions of hosts and parasites on the first two dimensions of the left

189 and right subspaces. Note that these values largely skew negative, because the first dimensions capture the

190 coarse structure of the network: most pairs of species do not interact, and therefore have negative values.

191 Finally in panel **D**, we show the predicted weight (*i.e.* the result of the multiplication of the RDGP

192 subspaces at a rank of 25) as a function of whether the interactions are observed, not-observed, or

193 unknown due to lack of co-occurrence. This reveals that the observed interactions have higher predicted

194 weights, although there is some overlap; the usual approach to identify potential interactions based on this

195 information would be a thresholding analysis, which is outside the scope of this manuscript (and is done

196 in the papers cited in this illustration). Because the values returned from RDPG are not bound to the unit

197 interval, we performed a clamping of the weights to the unit space, showing a one-inflation in

198 documented interaction, and a zero-inflation in other species pairs. This last figure crosses from the

199 statistical into the ecological, by showing that species pairs with no documented co-occurrence have

200 weights that are not distinguishable from species pairs with no documented interactions, suggesting that

201 (as befits a host-parasite model) the ability to interact is a strong predictor of co-occurrence.

As the results of fig. 2 show that we can extract an embedding of the metaweb that captures enough variance to be relevant, in fig. 3, we relate the values of latent variables for hosts to different ecologically-relevant data. In panel **A**, we show that host with a higher value on the first dimension have fewer parasites. This relates to the body size of hosts in the *PanTHERIA* database (Jones et al., 2009), as shown in panel **B**: interestingly, the position on the first axis is only weakly correlated to body mass of the 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, in panel **D**, we can see how different taxonomic families occupy different positions on the first axis, with *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 predictors for transfer learning.

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 problems"; any inference of a metaweb at large scales must contend with several novel, and interwoven, 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 application of these methods at the science-policy interface.

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 finding another area with enough related species (through phylogenetic relatedness or similarity of 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 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

dataset, and to under-dispersion in the target dataset, resulting in the potential under or over estimation of the strength of new predicted interactions. The lack of well documented metawebs is currently preventing the development of more concrete guidelines. The question of phylogenetic relatedness and distribution is notably relevant if the metaweb is assembled in an area with mostly endemic species (*e.g.* a system that has undergone recent radiation or that has remained in isolation for a long period of time might not have 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 of species in the geographic or phylogenetic space, it can certainly be approached through assessing the 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 in, as this determines the species pool that must be used. Metawebs can be constructed by assigning interactions in a list of species within geographic boundaries. The upside of this approach is that information at the country level is likely to be required for biodiversity assessments, as countries set conservation goals at the national level (Buxton et al., 2021), and as quantitative instruments are designed 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 meaningful. In fact, we do not have a satisfying answer to the question of "where does a food web stop?"; 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 information about the network itself. This suggests that inferred metawebs should be further downscaled to allow for *a posteriori* analyses. The methodology for metaweb downscaling is currently limited, and it is likely that the sustained effort to characterize the spatial dependency of food web structure will lead to more prescriptive guidelines about the need for prediction downscaling.

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 the legacy of settler colonialism, which drives a disparity in available ecological data. Applying any 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 data is not an apolitical act (Nost & Goldstein, 2021), as data infrastructures tend to be designed to answer questions within national boundaries (therefore placing contingencies on what is available to be

embedded), and their use often 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). 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., 2021; Naman et al., 2022; Stier et al., 2017), the need to appraise and correct biases that are unwittingly 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 the ongoing biodiversity crisis (Adam, 2014) and reinforced environmental injustice (Choudry, 2013; Domínguez & Luoma, 2020). Particularly on Turtle Island and other territories that were traditionally stewarded by Indigenous people, these approaches should be replaced (or at least guided and framed) by Indigenous principles of land management (Eichhorn et al., 2019; No'kmaq et al., 2021), as part of an "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.

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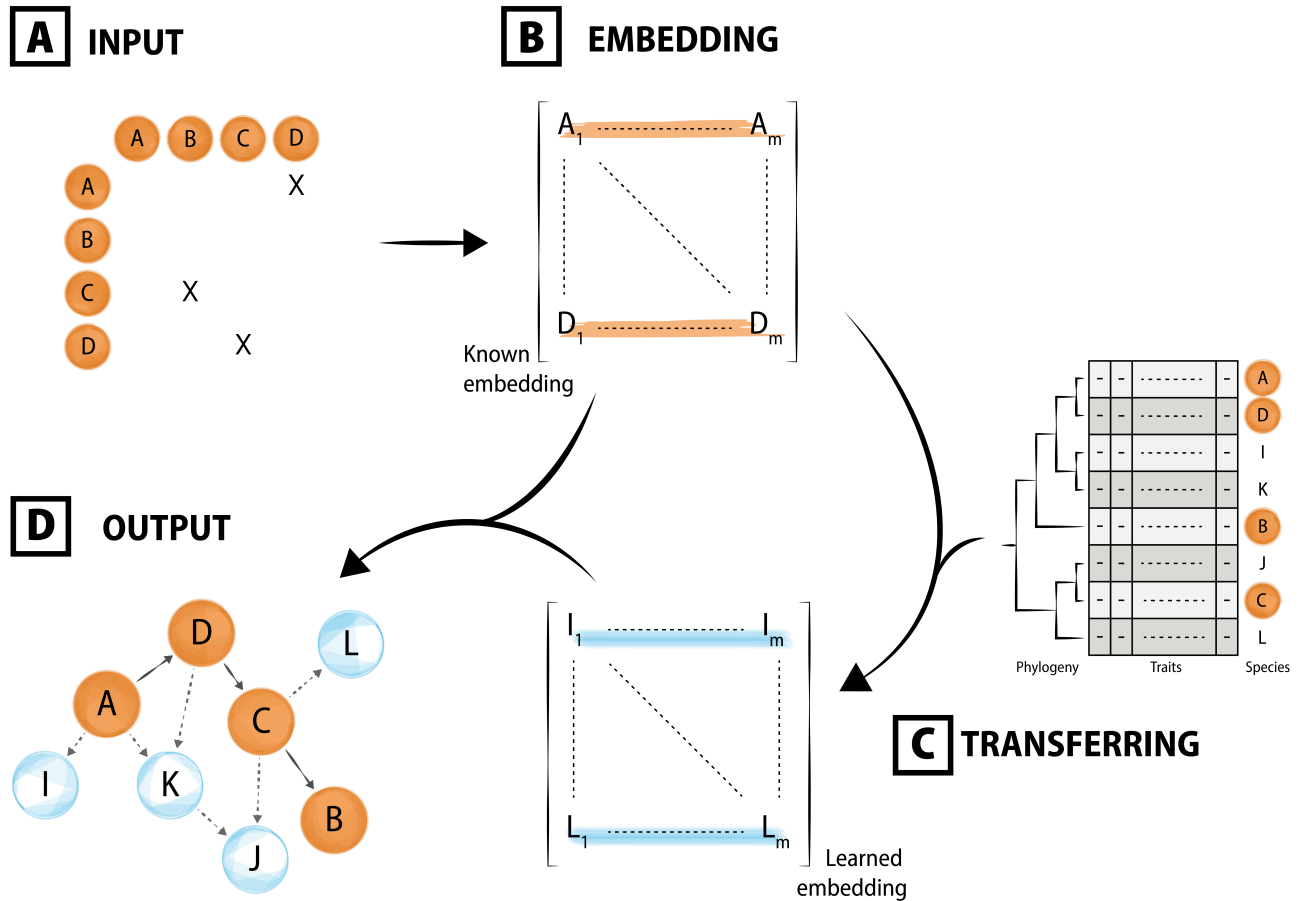569   https://doi.org/10.1016/j.aiopen.2021.01.001

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.
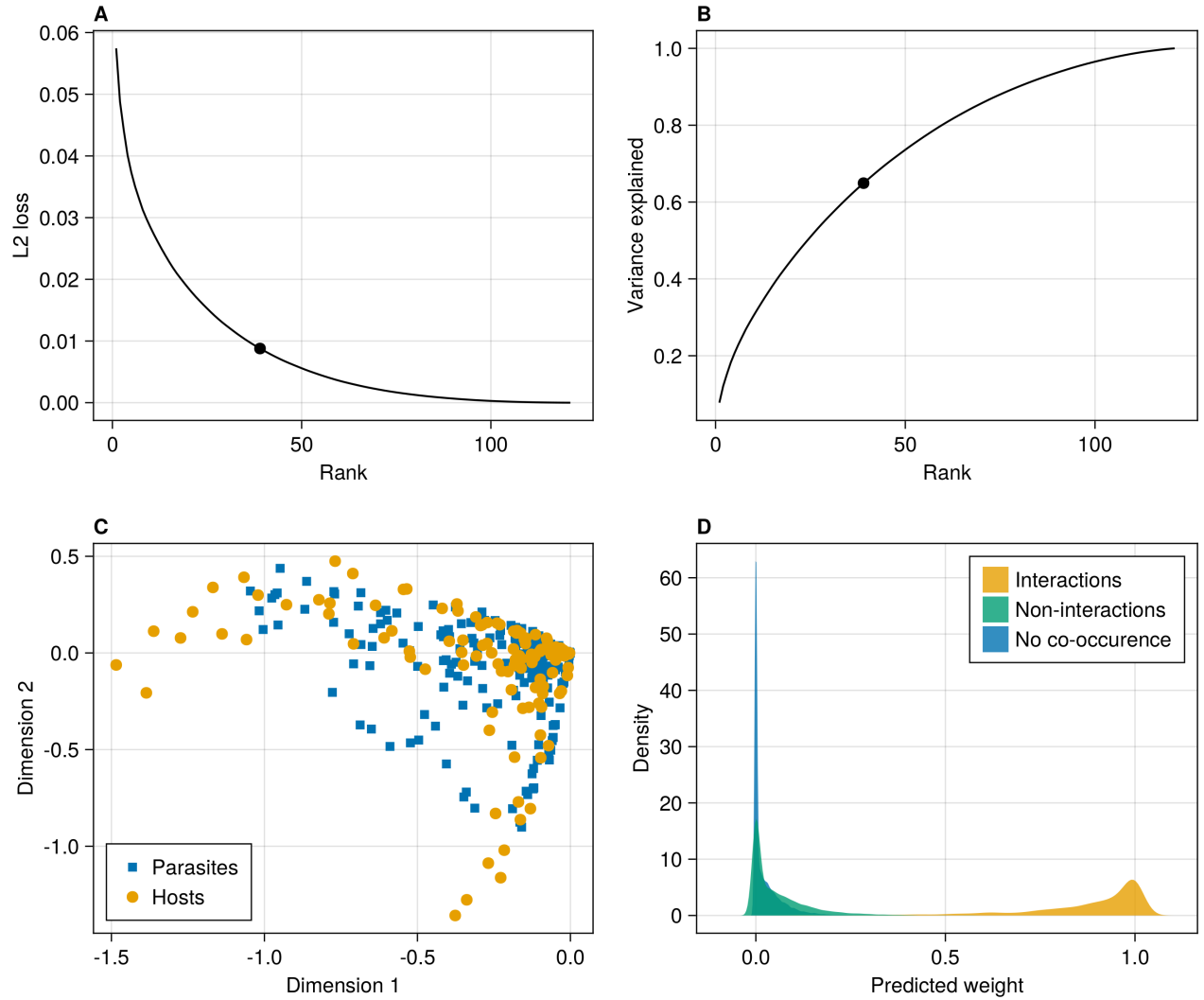
Figure 2: Validation of an embedding for a host-parasite metaweb, using Random Dot Product Graphs. **A**, decrease in approximation error as the number of dimensions in the subspaces increases. **B**, increase in cumulative variance explained as the number of ranks considered increases; in **A** and **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.
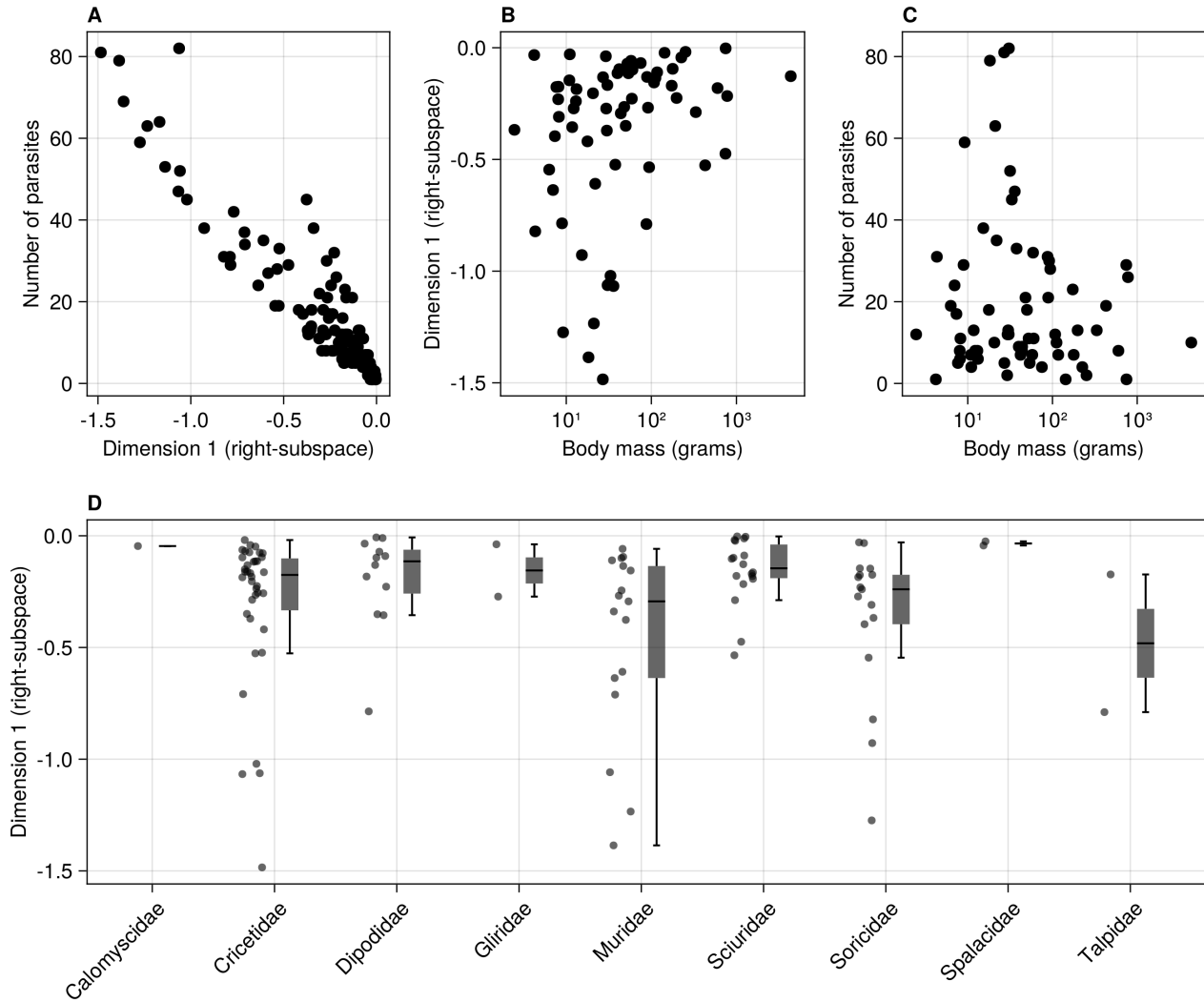
Figure 3: Ecological analysis of an embedding for a host-parasite metaweb, using Random Dot Product Graphs. **A**, relationship between the number of parasites and position along the first axis of the right-subspace for all hosts, showing that the embedding captures elements of network structure at the 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 & Roweis (2002)	Gibb et al. (2021); Cieslak et al. (2020) [a]
LINE	nodes	stochastic gradient descent	Tang et al. (2015)	
SDNE	nodes	gradient descent	D. Wang et al. (2016)	
node2vec	nodes	stochastic gradient descent	Grover & Leskovec (2016)	
HARP	nodes	meta-strategy	H. Chen et al. (2017)	
DMSE	joint nodes	deep neural network	D. Chen et al. (2017)	D. Chen et al. (2017) [b]
graph2vec	sub-graph	skipgram network	Narayanan et al. (2017)	
RDPG	graph	SVD	Young & Scheinerman (2007)	Poisot et al. (2021); Dalla Riva & Stouffer (2016)
GLEE	graph	Laplacian eigenmap	Torres et al. (2020)	
DeepWalk	graph	stochastic gradient descent	Perozzi et al. (2014)	Wardeh et al. (2021)
GraphKKE	graph	stochastic differential equation	Melnyk et al. (2020)	Melnyk et al. (2020) [a]
FastEmbed	graph	eigen decomposition	Ramasamy & Madhow (2015)	
PCA	graph	eigen decomposition	S & Surendran (2013)	Strydom, Catchen, et al. (2021)
Joint methods	multiple graphs	multiple strategies	S. Wang et al. (2021)	