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

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Last revision: *June 18, 2022*

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.

Being able to infer *potential* interactions could be the catalyst for significant breakthroughs 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 predictions often demand accurate predictors, and the lack of methods that can leverage small amount of *accurate* data is a serious impediment to our global 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 their 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 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 is the "upper bounds" on what the composition of the local networks, given the 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 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 (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 use of metawebs introduces important questions for the field of network ecology.

The metaweb is an inherently probabilistic object

Treating interactions probabilistic (as opposed to binary) is a more nuanced and realistic way to represent interactions. Dallas et al. (2017) suggested that most links in ecological networks are cryptic, *i.e.* 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 that weak or rare links to be more prevalent in networks than common or rare 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 interactions under a model that accurately predicts interaction probabilities. Yet the original metaweb definition, and indeed most past uses of metawebs, was based on the 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 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). These considerations emphasize why metaweb predictions should focus on quantitative (preferentially probabilistic) predictions; this should constrain the suite of appropriate models.

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

then filtered (Morales-Castilla et al., 2015). 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. Recent proposals suggest that machine learning algorithms, in these situations, can act as data generators (Hoffmann et al., 2019): high quality observational data can generate the core rules underpinning the network structure, and be supplemented with synthetic data coming from predictive models, increasing the volume of information available for inference. 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 interactions, elusive information with the 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 embedding (fig. 1) is a varied family of machine learning techniques aiming to transform nodes and edges into a vector space (Arsov & Mirceva, 2019), usually of a lower dimension, whilst maximally retaining key properties of the graph (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 (Bramon Mora et al., 2018), which hints at structural invariants that can be revealed at lower dimensions. 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 the choice of embedding algorithm matters for the results (Goyal & Ferrara, 2018). In tbl. 1, we present a selection of common graph embedding methods, alongside examples of their use to predict species interactions.

[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, 2020) 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 nodes metadata. This example has many parallels in ecology (see fig. 2), in which node metadata can be given by phylogeny or 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 (RDPG; see Dalla Riva & Stouffer, 2016).

[Figure 2 about here.]

The metaweb embeds 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.

The first 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, or by non-overlapping trait distributions in the known and unknown species. Alternatively a metaweb is too large (taxonomically), then the resulting embeddings would have interactions relative to taxonomic groups that not present in the new location, 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 dispersal is notably true if the metaweb is assembled in an area with mostly endemic species (*e.g.* a system that has undergone recent radiation and 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.

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 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 final family of problems relates less to ecological concepts and more 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 not only drive a disparity in available ecological data, but can entrench said biases with the machine learning models that make predictions with them. Indeed, the use of ecological data is not an apolitical act (Nost & Goldstein, 2021), as data infrastructures tend to be designed to answer questions within national boundaries, and their use 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). We therefore recognize that predictive approaches deployed at the continental scale, no matter their intent, originate in the framework that contributed to the ongoing biodiversity crisis (Adam, 2014), reinforced environmental injustice (Choudry, 2013; Domínguez & Luoma, 2020), and *e.g.* as on Turtle Island, should be replaced by Indigenous principles of land management (Eichhorn et al., 2019; No'kmaq et al., 2021). 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 into the governance consequences they can have.

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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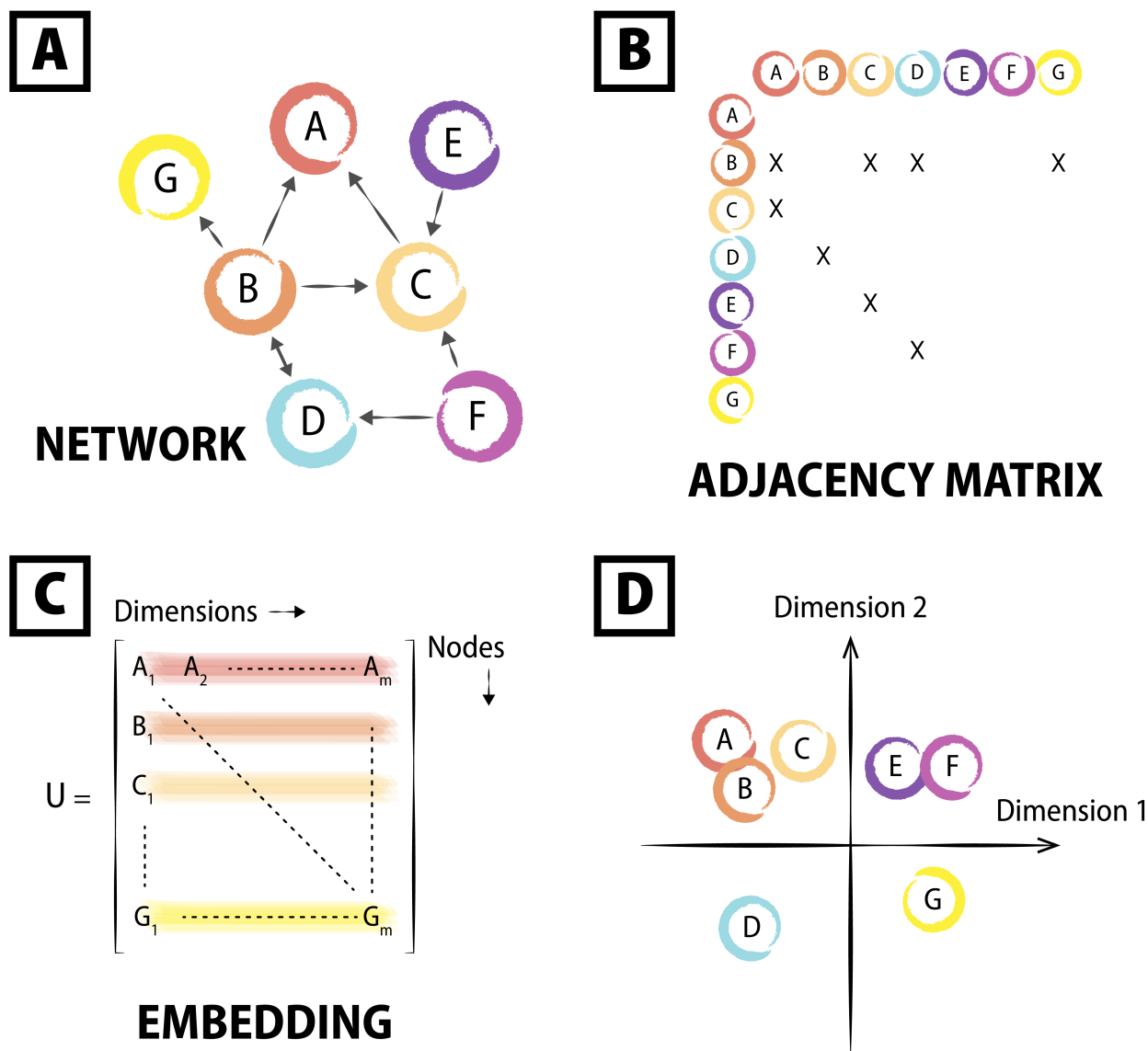https://doi.org/10.1007/978-3-540-77004-6_11

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.
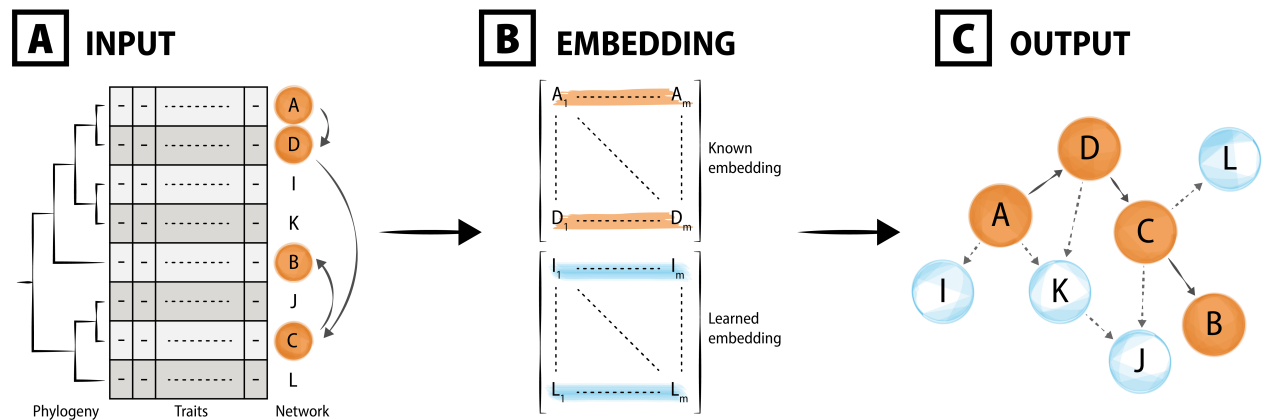
Figure 2: From a low-dimensional feature vector (see fig. 1), it is possible to develop predictive approaches. Nodes in an ecological network are species, for which we can leverage phylogenetic relatedness (*e.g.* Strydom, Bouskila, et al., 2021) or functional traits to fill the values of additional 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.

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)	