Graph embedding and transfer learning can help predict potential 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 a first approximation of metawebs.

3. One way to improve our ability to predict metawebs is to maximize available information by using graph embeddings, as opposed to an exhaustive list of species interactions. Graph embedding is an emerging field in machine learning that holds great potential for ecological problems.

4. Here, we outline how the challenges associated with inferring metawebs line-up with the advantages of graph embeddings; followed by a discussion as to how the choice of the species pool has consequences on the reconstructed network, specifically as to the role of human-made (or arbitrarily assigned) boundaries and how these my influence ecological hypotheses.

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The ability to infer *potential* interactions could serve as a significant breakthrough in our ability to conceptualize species interaction networks over large spatial scales (Hortal et al., 2015). Reliable inferences would not only boost our understanding of the structure of species interaction networks, but also increase the amount of information that can be used for biodiversity management. 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 – restricting the inference of interactions to locations where least required (and leaves us unable to make inference in data scarce regions); 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 where a set of potentially interacting species in a given area could occur: through the analysis of databases like the Global Biodiversity Information Facility (GBIF) or the International Union for the Conservation of Nature (IUCN), it is possible to construct a list of species for a region of interest; however inferring the potential interactions between these species still remains a challenge.

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 itself is not a prediction of local networks at specific locations 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 its 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. Specifically, although co-occurrence can be driven by interactions (Cazelles et al., 2016), co-occurrence alone is not a predictor of interactions (Blanchet et al., 2020; Thurman et al., 2019), and therefore the lack of co-occurrence cannot be used to infer the lack of a feasible interaction. Yet, recent results by Saravia et al. (2021) strongly suggested that local (metaweb) realizations only respond weakly to local conditions: instead, they reflect constraints inherited by the structure of their metaweb. This sets up the core goal of predictive network ecology as the prediction of metaweb structure, as it is required 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 *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 (J. Braga et al., 2019; O'Connor et al., 2020), and crop-pest networks (Grünig et al., 2020). In this contribution, we highlight the power of viewing (and constructing) metawebs as *probabilistic* objects in the context of low-probability 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.

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 interactions (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 interactions will be more prevalent in networks than common or strong interactions (Csermely, 2004), compared to strong, persistent interactions; this is notably the case in food chains, wherein many weaker interactions 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 (hereafter rare) interactions under a model that accurately predicts interaction probabilities. Although defining an interaction as 'rare' is perhaps not as straight forward as one may assume (rare in the context of likelihood of occurrence or the context of biologically plausible?) but for the context of the discussion in this manuscript the core idea is that construction of probabilistic networks affords us the nuance of capturing this inherit variability of interaction occurrence.

Critically, 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). Furthermore, because the structure of the metaweb cannot be known in advance, it is 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 models that are appropriate for prediction.

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 (Catchen et al., 2023). 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 relying on machine learning approaches emphasize the idea that algorithms meant to predict, through the assumption that they approximate the process generating the data, 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 of local networks (Bartomeus, 2013; Bartomeus et al., 2016). This would represent a departure from simple rules expressed at the network scale (*e.g.* Williams & Martinez, 2000) to a view of network prediction based on learning the rules that underpin interactions *and* their variability (Gupta et al., 2022).

[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 of the graph (embeddings), such that its key properties (*e.g.* local or global structures) are retained in the embedding space (Yan et al., 2005). The embedding space may, but will not necessarily, have lower dimensionality than the graph. Ecological networks are promising candidates for the routine application of embeddings, as they tend to possess a shared structural backbone (see *e.g.* Bramon Mora et al., 2018), which hints at structural invariants in empirical data. Assuming that these structural invariants are common enough, 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, …).

Graph embedding produces latent variables (but not traits)

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 interpreted 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 performance, 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 subspace 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, and illustrates how the values derived from an embedding can be used for prediction without being "traits" of the species they represent.

Ecological networks are good candidates for embedding

Food webs are inherently low-dimensional objects, and can be adequately represented with less than ten dimensions (J. Braga et al., 2019; M. P. Braga et al., 2021; Eklöf et al., 2013). Simulation results by Botella et al. (2022) suggested that there is no dominant method to identify architectural similarities between networks: multiple approaches need to be tested and compared to the network descriptor of interest on a problem-specific basis. This matches previous results on graph embedding, wherein 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 interactions or statistical associations between species. These methods rely largely on linear algebra or pseudo-random walks on graphs. All forms of embeddings presented in tbl. 1 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 (*i.e.* species interactions), while graph embeddings focus on maintaining the network structure (*i.e.* emergent properties). Nevertheless, some graph embedding techniques (like RDPG, see *e.g.* Wu et al., 2021) will provide high-quality node-level embeddings while also preserving network structure.

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)]. However, 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 visualization) 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. 1), we show how the amount of dimensionality reduction can affect the quality of the embedding.

Graph embedding has been under-used in the prediction of species interactions

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 nevertheless the potential for GNN to become an applicable embedding/predictive technique in the coming years.

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]: application is concerned with *statistical* interactions, which are not necessarilly direct biotic interactions; [b]:application is concerned with joint-SDM-like approach, which is also very close to statistical associations as opposed to direct biotic interactions. 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)	(Cieslak et al., 2020, species-environment responses [a]) (Gibb et al., 2021, host-virus network representation)
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, species-environment interactions [b])
graph2vec	sub-graph	skipgram network	Narayanan et al. (2017)	
RDPG	graph	SVD	Young & Scheinerman (2007)	(Dalla Riva & Stouffer, 2016, trophic interactions) (Poisot et al., 2021, host-virus network prediction)

Method	Object	Technique	Reference	Application
GLEE	graph	Laplacian eigenmap	Torres et al. (2020)	
DeepWalk	graph	stochastic gradient descent	Perozzi et al. (2014)	(Wardeh et al., 2021, host-virus interactions)
GraphKKE	graph	stochastic differential equation	Melnyk et al. (2020)	(Melnyk et al., 2020, microbiome species associations [a])
FastEmbed	graph	eigen decomposition	Ramasamy & Madhow (2015)	
PCA	graph	eigen decomposition	Surendran (2013)	(Strydom, Catchen, et al., 2021, host-parasite interactions)
Joint methods	multiple graphs	multiple strategies	S. Wang et al. (2021)	

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 (M. P. Braga et al., 2021; Dalla Riva & Stouffer, 2016; Eklöf & Stouffer, 2016; Stouffer et al., 2012; Stouffer et al., 2007); similarly, the use of functional traits assumes that interactions can be inferred from the knowledge of trait-matching rules, which is similarly well supported in the empirical literature (Bartomeus, 2013; Bartomeus et al.,

2016; Goebel et al., 2023; Gravel et al., 2013). Relating this information to an embedding rather than a list of network 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.

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. 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., 2021 have an example using embedding through PCA followed by prediction using a deep neural network on the same dataset). The resulting (binary) metaweb $\mathcal{M}$ has 2131 interactions between 206 parasites and 121 hosts, and its adjacency matrix has full rank (*i.e.* it represents a space with 121 dimensions). All analyses were done using Julia (Bezanson et al., 2017) version 1.7.2, *Makie.jl* (Danisch & Krumbiegel, 2021), and *EcologicalNetworks.jl* (Poisot et al., 2019).

[Figure 2 about here.]

In fig. 2, we focus on some statistical checks of the embedding. In panel **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 **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 and right subspaces. Note that these values largely skew negative, because the first dimensions capture the 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 subspaces at a rank of 39) as a function of whether the interactions are observed, not-observed, or unknown due to lack of co-occurrence in the original dataset. This reveals that the observed interactions have higher predicted weights, although there is some overlap; the usual approach to identify potential interactions based on this information would be a thresholding analysis, which is outside the scope of this manuscript (and is done in the papers cited in this illustration). Because the values returned from RDPG are not bound to the unit interval, we performed a clamping of the weights to the unit space, showing a one-inflation in documented interactions, and a zero-inflation in other species pairs. This last figure crosses from the statistical into the ecological, by showing that species pairs with no documented co-occurrence have 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.

[Figure 3 about here.]

The results of fig. 2 show that we can extract an embedding of the metaweb that captures enough variance to be relevant; specifically, this is true for both L_2 loss (indicating that RDPG is able to capture pairwise processes) and the cumulative variance explained (indicating that RDPG is able to capture network-level structure). Therefore, 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 established 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 merges ecological hypotheses and practices

Metaweb inference seeks to provide information about the interactions between species at a large spatial scale, typically a scale large enough to be considered of biogeographic relevance (indeed, many of the examples covered in the introduction span areas larger than a country, some of them global). But as Herbert (1965) rightfully pointed out, "[y]ou can't draw neat lines around planet-wide problems"; any inference of a metaweb must therefore contend with several novel, interwoven, families of problems. In this section, we outline three that we think are particularly important, and can discuss how they may addressed with subsequent data analysis or simulations, and how they emerge in the specific context of using embeddings; some of these issues are related to the application of these methods at the science-policy interface.

Identifying the properties of the network to embed

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 is because transfer requires similarity (fig. 1). A diagnostic for the lack of similar species would likely be large confidence intervals during estimation of the values in the low-rank space. In other words, 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. Llewelyn et al. (2022) provided compelling evidence for these situations by showing that, even at small spatial scales, the transfer of information about interactions becomes more challenging when areas rich with endemic species are considered. 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.

Identifying the scope of the prediction to perform

The area for which we seek to predict the metaweb should determine the species pool on which the embedding is performed. Metawebs can be constructed by assigning interactions in a list of species within specific regions. The upside of this approach is that information relevant for the construction of this dataset is likely to exist, as countries usually set conservation goals at the national level (Buxton et al., 2021), and as quantitative instruments are consequently 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). However, there is no guarantee that these arbitrary boundaries are meaningful. In fact, we do not have a satisfying answer to the question of "where does an ecological network stop?", the answer to which would dictate the spatial span to embed/predict. Recent results by Martins et al. (2022) suggested that networks are shaped within eco-regions, with abrupt structural transitions from an eco-region to the next. Should this trend hold generally, this would provide an ecologically-relevant scale at which metawebs can be downscaled and predicted. Other solutions could leverage network-area relationships to identify areas in which networks are structurally similar (see *e.g.* Fortin et al., 2021; Galiana et al., 2022, 2018). Both of these solutions require ample pre-existing information about the network in space. Nevertheless, the inclusion of species for which we have data but that are not in the right spatial extent *may* improve the performance of approaches based on embedding and transfer, *if* they increase the similarity between the target and destination network. This proposal can specifically be evaluated by adding nodes to the network to embed, and assessing the performance of predictive models (see *e.g.* Llewelyn et al., 2022).

Minding legacies shaping ecological datasets

In large parts of the world, boundaries that delineate geographic regions are merely a reflection the legacy of settler colonialism, which drives global disparity in capacity to collect and publish ecological data. Applying any embedding to biased data does not debias them, but rather embeds these biases, propagating them to the models using embeddings to make predictions. Furthermore, the use of ecological data itself is

not an apolitical act (Nost & Goldstein, 2021): data infrastructures tend to be designed to answer questions within national boundaries (therefore placing contingencies on what is available to be embedded), their use often drawing upon, and reinforcing, territorial statecraft (see *e.g.* Barrett, 2005). As per Machen & Nost (2021), these biases are particularly important to consider when knowledge generated algorithmically is used to supplement or replace human decision-making, especially for governance (*e.g.* enacting conservation decisions on the basis of model prediction). As information on networks is increasingly leveraged for conservation actions (see *e.g.* 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 immense. These considerations are even more urgent in the specific context of biodiversity data. Long-term colonial legacies still shape taxonomic composition to this day (Lenzner et al., 2022; Raja, 2022), and much shorter-term changes in taxonomic and genetic richness of wildlife emerged through environmental racism (Schmidt & Garroway, 2022). Thus, the set of species found at a specific location is not only as the result of a response to ecological processes separate from human influence, but also the result of human-environment interaction as well as the result legislative/political histories.

Conclusion: metawebs, predictions, and people

Predictive approaches in ecology, regardless of the scale at which they are deployed and the intent of their deployment, originate in the framework that contributed to the ongoing biodiversity crisis (Adam, 2014) and reinforced environmental injustice (Choudry, 2013; Domínguez & Luoma, 2020). The risk of embedding this legacy in our models is real, especially when the impact of this legacy on species pools is being increasingly documented. This problem can be addressed by re-framing the way we interact with models, especially when models are intended to support conservation actions. Particularly on territories that were traditionally stewarded by Indigenous people, we must interrogate how predictive approaches and the biases that underpin them can be put to task in accompanying Indigenous principles of land management (Eichhorn et al., 2019; No'kmaq et al., 2021). The discussion of "algorithm-in-the-loop" approaches that is now pervasive in the machine learning community provides examples of why this is important. Human-algorithm interactions are notoriously difficult and can yield adverse effects (Green & Chen, 2019; Stevenson & Doleac, 2021), suggesting the need to systematically study them for the specific purpose of, here, biodiversity governance. Improving the algorithmic literacy of decision makers is part of

the solution (*e.g.* Lamba et al., 2019; Mosebo Fernandes et al., 2020), as we can reasonably expect that model outputs will be increasingly used to drive policy decisions (Weiskopf et al., 2022). Our discussion of these approaches need to go beyond the technical and statistical, and into the governance consequences they can have. To embed data also embeds historical and contemporary biases that acted on these data, both because they shaped the ecological processes generating them, and the global processes leading to their measurement and publication. For a domain as vast as species interaction networks, these biases exist at multiple scales along the way, and a challenge for prediction is not only to develop (or adopt) new quantitative tools, but to assess the behavior of these tools in the proper context.

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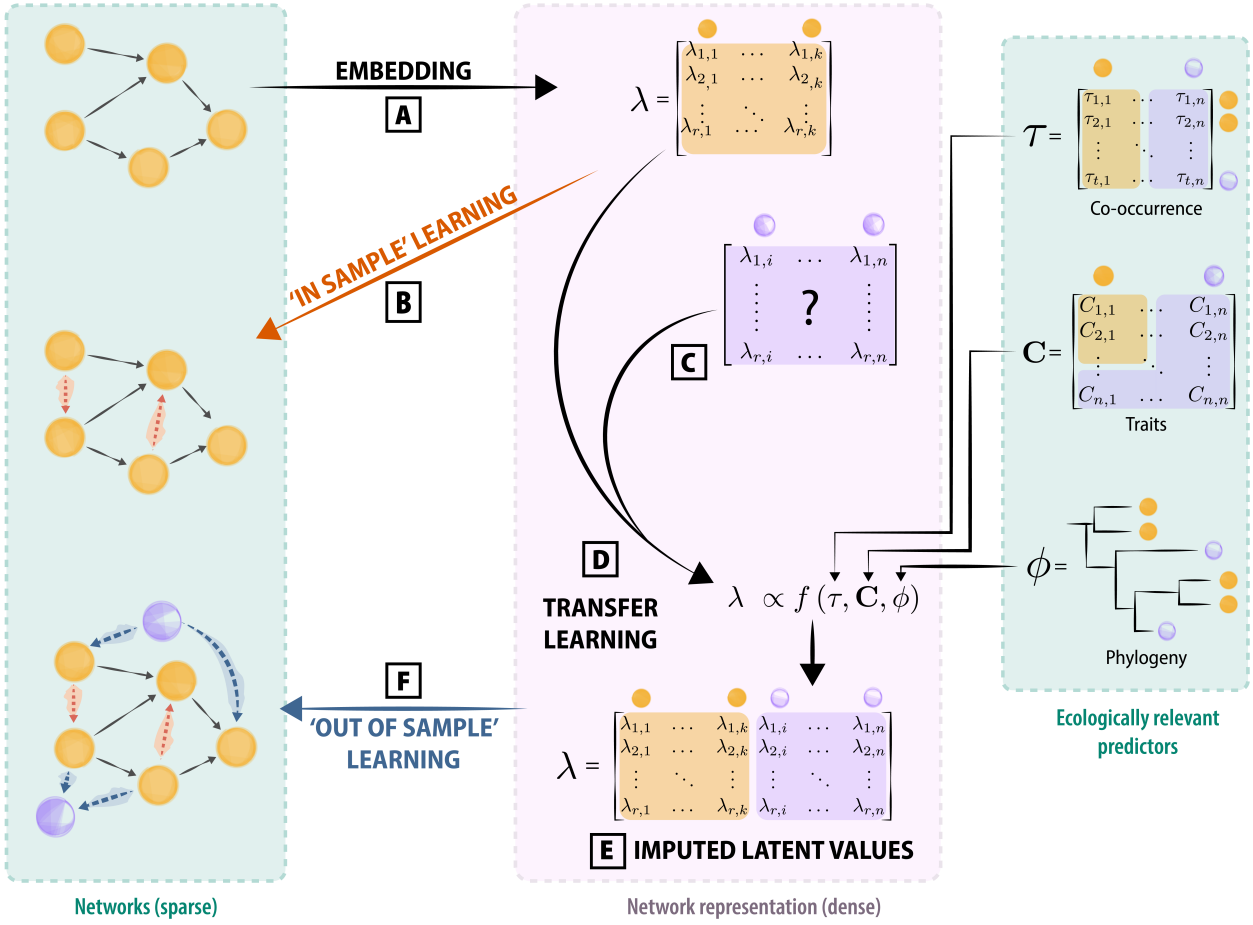

Figure 1: The embedding process (**A**) can help to identify links (interactions) that may have been missed within the original community (represented by the orange dashed arrows, **B**). Transfer learning (**D**) allows for the prediction links (interactions) even when novel species (**C**) are included alongside the original community. This is achieved by learning using other relevant predictors (*e.g.* traits) in conjunction with the known interactions to infer latent values (**E**). Ultimately this allows us to predict links (interactions) for species external from the original sample (blue dashed arrows) as well as missing within sample links (**F**). Within this context the predicted (and original) networks as well as the ecological predictors used (green boxes) are products that can be quantified through measurements in the field, whereas the embedded as well as imputed matrices (purple box) are representative of a decomposition of the interaction matrices onto the embedding space

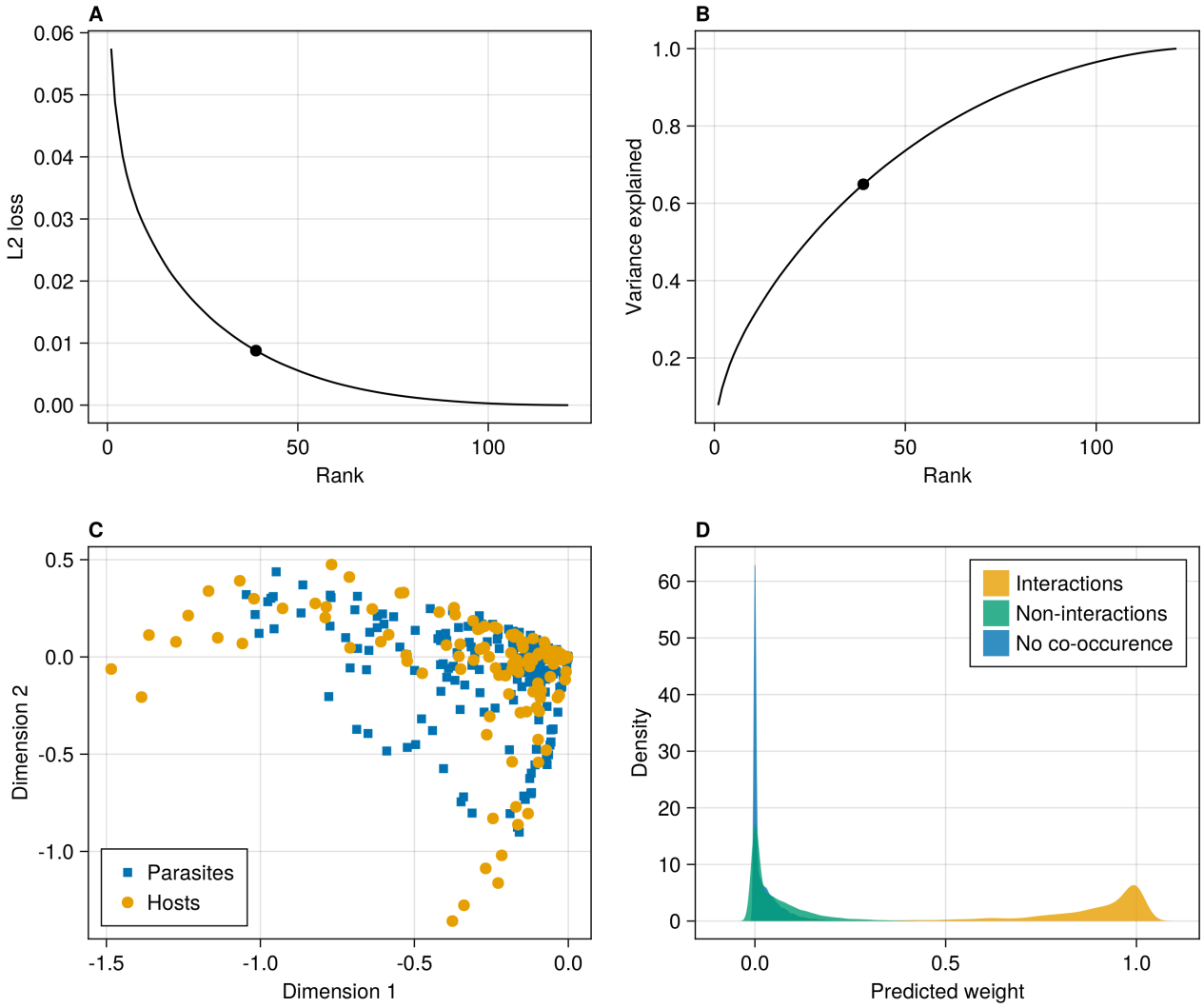

Figure 2: Validation of an embedding for a host-parasite metaweb, using Random Dot Product Graphs. **A**, decrease in approximation error as the number of dimensions in the subspaces increases. **B**, increase in cumulative variance explained as the number of ranks considered increases; in **A** and **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.

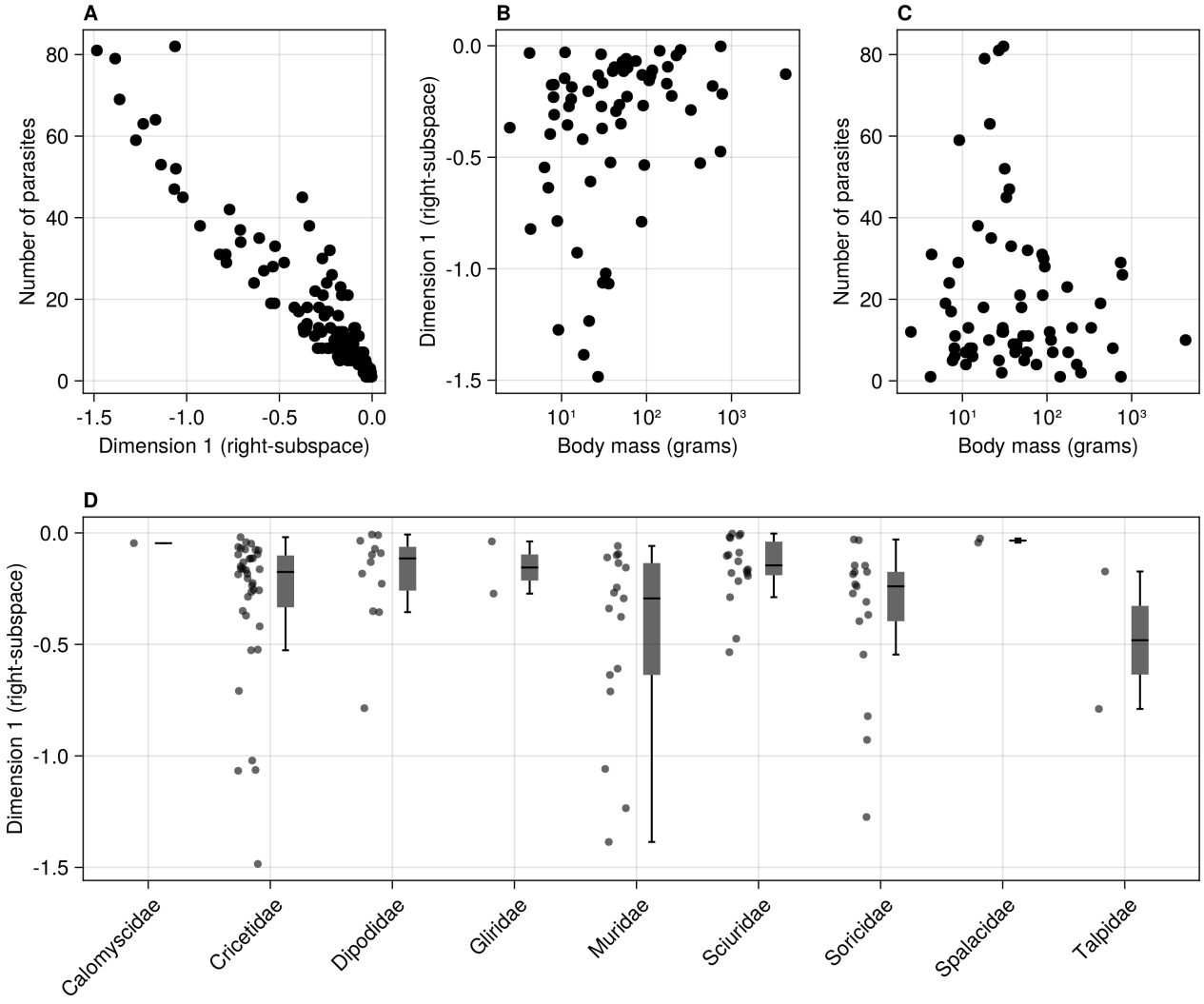

Figure 3: Ecological analysis of an embedding for a host-parasite metaweb, using Random Dot Product Graphs. **A**, relationship between the number of parasites and position along the first axis of the right-subspace for all hosts, showing that the embedding captures elements of network structure at the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