

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

Tanya Strydom<sup>1,2,‡</sup>, Salomé Bouskila<sup>1,‡</sup>, Francis Banville<sup>1,2,3</sup>, Ceres Barros<sup>4</sup>, Dominique Caron<sup>2,5</sup>, Maxwell J Farrell<sup>6</sup>, Marie-Josée Fortin<sup>6</sup>, Victoria Hemming<sup>7</sup>, Benjamin Mercier<sup>2,3</sup>, Laura J. Pollock<sup>2,5</sup>, Rogini Runghen<sup>8</sup>, Giulio V. Dalla Riva<sup>9</sup>, Timothée Poisot<sup>1,2,‡</sup>

<sup>1</sup> Département de Sciences Biologiques, Université de Montréal, Montréal, Canada; <sup>2</sup> Quebec Centre for Biodiversity Science, Montréal, Canada; <sup>3</sup> Département de Biologie, Université de Sherbrooke, Sherbrooke, Canada; <sup>4</sup> Department of Forest Resources Management, University of British Columbia, Vancouver, B.C., Canada; <sup>5</sup> Department of Biology, McGill University, Montréal, Canada; <sup>6</sup> Department of Ecology & Evolutionary Biology, University of Toronto, Toronto, Canada; <sup>7</sup> Department of Forest and Conservation Sciences, University of British Columbia, Vancouver, Canada; <sup>8</sup> Centre for Integrative Ecology, School of Biological Sciences, University of Canterbury, Canterbury, New Zealand; <sup>9</sup> School of Mathematics and Statistics, University of Canterbury, Canterbury, New Zealand

‡ Equal contributions

## Correspondance to:

Timothée Poisot — timothee.poisot@umontreal.ca

**Keywords:**  
ecological networks  
network embedding  
transfer learning  
network macroecology

, (networks of potential interactions within a species pool) are a powerful abstraction to understand how large-scale species interaction networks are structured. 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. 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. 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 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 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  $\gamma$  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  $\alpha$  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. 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 lack of co-occurrence cannot be used to rule out lack of a feasible interaction. 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 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.

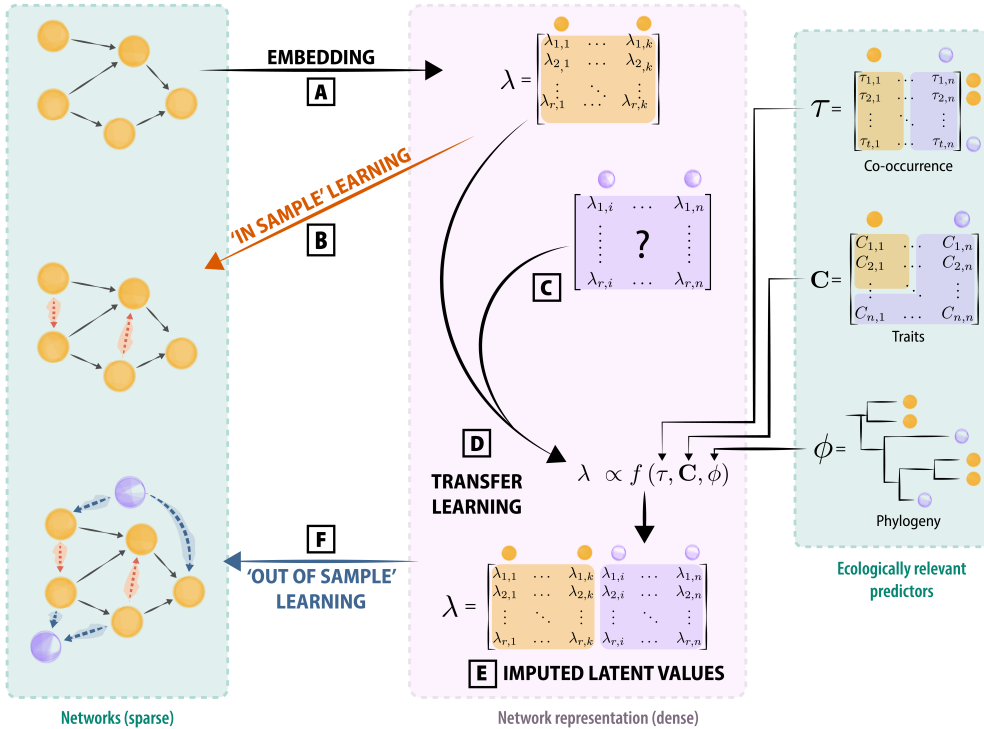
1

## A metaweb is an inherently probabilistic object

Treating interactions as probabilistic (as opposed to binary) events is a more nuanced and realistic way to represent them. Dallas et al. (2017) suggested that most links in ecological networks are cryptic, *i.e.* uncommon or hard to observe. This argument echoes Jordano (2016): sampling ecological interactions is difficult because it requires first the joint observation of two species, and then the observation of their interaction. In addition, it is generally expected weak or rare links to be more prevalent in networks than common or strong links (Csermely, 2004), compared to strong, persistent links; this is notably the case in food chains, wherein many weaker links are key to the stability of a system (Neutel et al., 2002). In the light of these observations, we expect to see an over-representation of low-probability (rare) interactions under a model that accurately predicts interaction probabilities.

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). 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 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 inter-



**Figure 1** The embedding process (A) can help to identify links (interactions) that may have been missed within the current sample (community, B), while transfer learning (D) allows for predicting links (interactions) for species external to the original sample as well as within sample links (F). Transfer learning allows for the prediction links (interactions) when novel species (C) are included in the sample by learning using other relevant predictors (e.g. traits) in conjunction with the known interactions to infer latent values (E). Within this context the predicted networks as well as the ecological predictors used (green boxes) are products that can be quantified through field measurements, whereas the embedded as well as imputed matrices are representative of **TK**

actions 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).

## 2 **Graph embedding offers promises for the inference of potential interactions**

Graph (or Network) embedding (fig. ??) 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. Branon 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. ??, 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. ?. 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** 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. <sup>a</sup>: application is concerned with *statistical* interactions, which are not necessarily direct biotic interactions; <sup>b</sup>: 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)	Gibb et al. (2021); Cieslak et al. (2020) <sup>a</sup>
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) <sup>b</sup>
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)

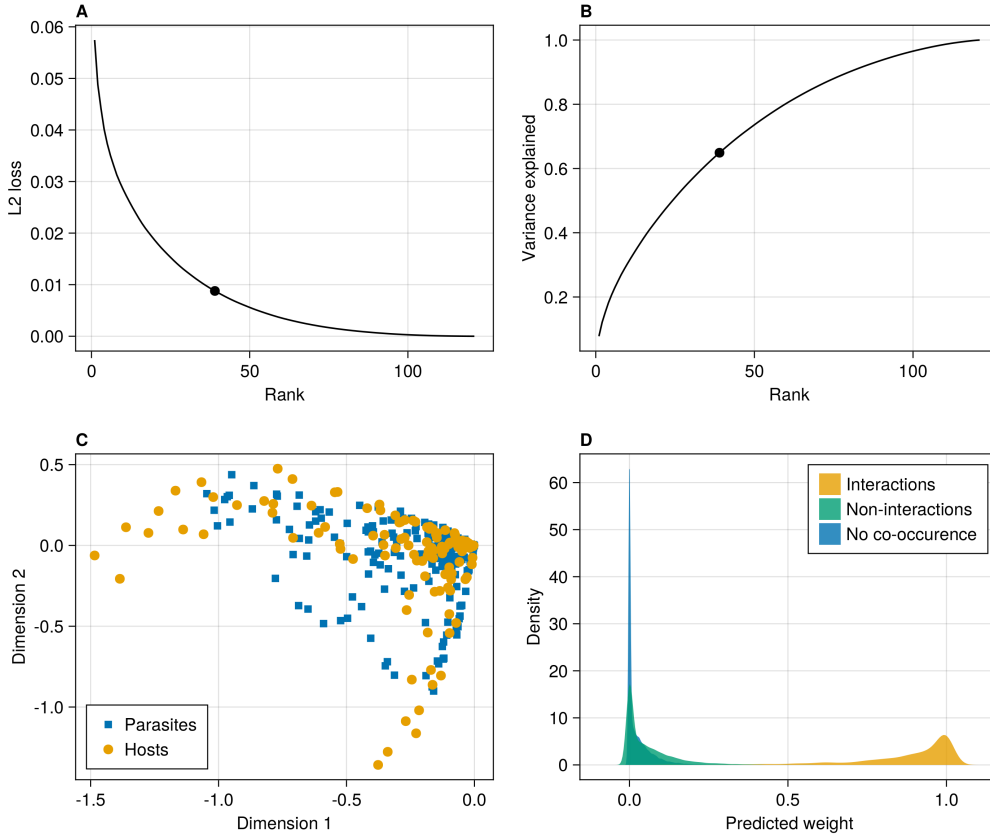
Method	Object	Technique	Reference	Application
GraphKKE	graph	stochastic differential equation	Melnyk et al. (2020)	Melnyk et al. (2020) <sup>a</sup>
FastEmbed	graph	eigen decomposition	Ramasamy & Madhow (2015)	
PCA	graph	eigen decomposition	S & Surendran (2013)	Strydom, Catchen, et al. (2021)
Joint methods	multiple graphs	multiple strategies	S. Wang et al. (2021)	

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. ?? 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 (Dalla Riva & 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; Gravel et al., 2013). 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 reconstructed 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.



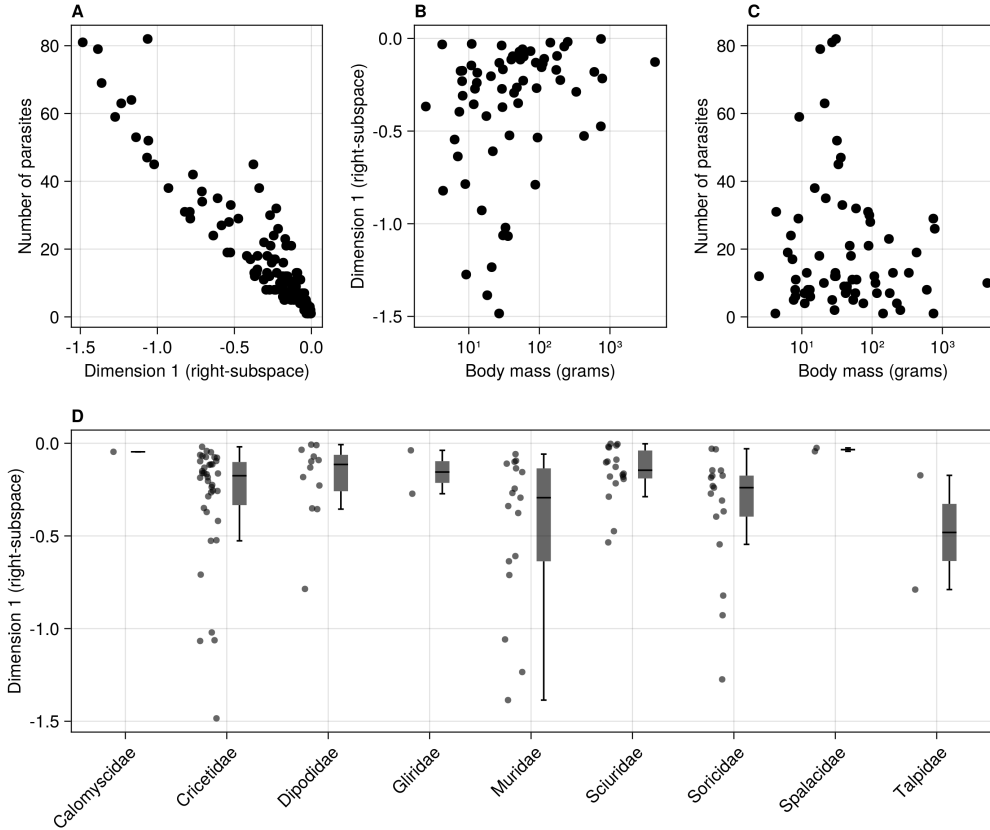
**Figure 2** Validation of an embedding for a host-parasite metaweb, using Random Dot Product Graphs. **A**, decrease in approximation error as the number of dimensions in the subspaces increases. **B**, increase in cumulative variance explained as the number of ranks considered increases; in **A** and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

3

## 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., 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).

In fig. ??, 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,



**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.

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 25) as a function of whether the interactions are observed, not-observed, or unknown due to lack of co-occurrence. 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 RDGP are not bound to the unit interval, we performed a clamping of the weights to the unit space, showing a one-inflation in documented interaction, and a zero-inflation in other species pairs. This last figure crosses from the 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.

The results of fig. ?? show that we can extract an embedding of the metaweb that captures enough variance to be relevant; specifically, this is true both of  $L_2$  loss (indicating that RDGP is able to capture pairwise processes) and the cumulative variance explained (indicating that RDGP is able to capture network-level structure). Therefore, in fig. ??, 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 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 addressed 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. Recent results by (Martins2022GloReg?) suggest 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.

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. These considerations are even more urgent in the specific context of biodiversity data, as long-term colonial legacies still shape taxonomic composition to this day (Lenzner2022NatAli?; Raja2022ColSha?), and



where much shorter-term changes in taxonomic and genetic richness emerged as a consequence of environmental racism. (**Schmidt2022SysRac?**).

Predictive approaches, 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). 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.

**Acknowledgements:** We acknowledge that this study was conducted on land within the traditional unceded territory of the Saint Lawrence Iroquoian, Anishinabewaki, Mohawk, Huron-Wendat, and Omàmiwininiwak nations. TP, TS, DC, and LP received funding from the Canadian Institute for Ecology & Evolution. FB is funded by the Institute for Data Valorization (IVADO). TS, SB, and TP are funded by a donation from the Courtois Foundation. CB was awarded a Mitacs Elevate Fellowship no. IT12391, in partnership with fRI Research, and also acknowledges funding from Alberta Innovates and the Forest Resources Improvement Association of Alberta. M-JF acknowledges funding from NSERC Discovery Grant and NSERC CRC. RR is funded by New Zealand's Biological Heritage Ngā Kōiora Tuku Iho National Science Challenge, administered by New Zealand Ministry of Business, Innovation, and Employment. BM is funded by the NSERC Alexander Graham Bell Canada Graduate Scholarship and the FRQNT master's scholarship. LP acknowledges funding from NSERC Discovery Grant (NSERC RGPIN-2019-05771). TP acknowledges financial support from the Fondation Courtois, and NSERC through the Discovery Grants and Discovery Accelerator Supplement programs. MJF is supported by an NSERC PDF and an RBC Post-Doctoral Fellowship.

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

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

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

---

## References

- Adam, R. (2014). *Elephant treaties: The Colonial legacy of the biodiversity crisis*. UPNE.
- Albouy, C., Archambault, P., Appeltans, W., Araújo, M. B., Beauchesne, D., Cazelles, K., Cirtwill, A. R., Fortin, M.-J., Galiana, N., Leroux, S. J., Pellissier, L., Poisot, T., Stouffer, D. B., Wood, S. A., & Gravel, D. (2019). The marine fish food web is globally connected. *Nature Ecology & Evolution*, 3(8), 1153–1161. <https://doi.org/10.1038/s41559-019-0950-y>
- Anowar, F., Sadaoui, S., & Selim, B. (2021). Conceptual and empirical comparison of dimensionality reduction algorithms (PCA, KPCA, LDA, MDS, SVD, LLE, ISOMAP, LE, ICA, t-SNE). *Computer Science Review*, 40, 100378. <https://doi.org/10.1016/j.cosrev.2021.100378>
- Arsov, N., & Mirceva, G. (2019). *Network Embedding: An Overview*. <http://arxiv.org/abs/1911.11726>
- Athreya, A., Fishkind, D. E., Levin, K., Lyzinski, V., Park, Y., Qin, Y., Sussman, D. L., Tang, M., Vogelstein, J. T., & Priebe, C. E. (2017). *Statistical inference on random dot product graphs: A survey* (No. arXiv:1709.05454). arXiv. <http://arxiv.org/abs/1709.05454>
- Bartomeus, I. (2013). Understanding linkage rules in plant-pollinator networks by using hierarchical models that incorporate pollinator detectability and plant traits. *PloS One*, 8(7), e69200. <http://journals.plos.org/plosone/article?id=10.1371/journal.pone.0069200>

- Bartomeus, I., Gravel, D., Tylianakis, J. M., Aizen, M. A., Dickie, I. A., & Bernard-Verdier, M. (2016). A common framework for identifying linkage rules across different types of interactions. *Functional Ecology*, 30(12), 1894–1903. <http://onlinelibrary.wiley.com/doi/10.1111/1365-2435.12666/full>
- Bezanson, J., Edelman, A., Karpinski, S., & Shah, V. (2017). Julia: A Fresh Approach to Numerical Computing. *SIAM Review*, 59(1), 65–98. <https://doi.org/10.1137/141000671>
- Blanchet, F. G., Cazelles, K., & Gravel, D. (2020). Co-occurrence is not evidence of ecological interactions. *Ecology Letters*.
- Bohan, D. A., Vacher, C., Tamaddoni-Nezhad, A., Raybould, A., Dumbrell, A. J., & Woodward, G. (2017). Next-Generation Global Biomonitoring: Large-scale, Automated Reconstruction of Ecological Networks. *Trends in Ecology & Evolution*. <https://doi.org/10.1016/j.tree.2017.03.001>
- Botella, C., Dray, S., Matias, C., Miele, V., & Thuiller, W. (2022). An appraisal of graph embeddings for comparing trophic network architectures. *Methods in Ecology and Evolution*, 13(1), 203–216. <https://doi.org/10.1111/2041-210X.13738>
- Braga, J., Pollock, L. J., Barros, C., Galiana, N., Montoya, J. M., Gravel, D., Maiorano, L., Montemaggiore, A., Ficetola, G. F., Dray, S., & Thuiller, W. (2019). Spatial analyses of multi-trophic terrestrial vertebrate assemblages in Europe. *Global Ecology and Biogeography*, 28(11), 1636–1648. <https://doi.org/10.1111/geb.12981>
- Bramon Mora, B., Gravel, D., Gilarranz, L. J., Poisot, T., & Stouffer, D. B. (2018). Identifying a common backbone of interactions underlying food webs from different ecosystems. *Nature Communications*, 9(1), 2603. <https://doi.org/10.1038/s41467-018-05056-0>
- Buxton, R. T., Bennett, J. R., Reid, A. J., Shulman, C., Cooke, S. J., Francis, C. M., Nyboer, E. A., Pritchard, G., Binley, A. D., Avery-Gomm, S., Ban, N. C., Beazley, K. F., Bennett, E., Blight, L. K., Bortolotti, L. E., Camfield, A. F., Gadallah, F., Jacob, A. L., Naujokaitis-Lewis, I., ... Smith, P. A. (2021). Key information needs to move from knowledge to action for biodiversity conservation in Canada. *Biological Conservation*, 256, 108983. <https://doi.org/10.1016/j.biocon.2021.108983>
- Cazelles, K., Araújo, M. B., Mouquet, N., & Gravel, D. (2016). A theory for species co-occurrence in interaction networks. *Theoretical Ecology*, 9(1), 39–48. <https://doi.org/10.1007/s12080-015-0281-9>
- Chami, I., Abu-El-Haija, S., Perozzi, B., Ré, C., & Murphy, K. (2022). Machine Learning on Graphs: A Model and Comprehensive Taxonomy. *Journal of Machine Learning Research*, 23(89), 1–64. <http://jmlr.org/papers/v23/20-852.html>
- Chen, D., Xue, Y., Fink, D., Chen, S., & Gomes, C. P. (2017). *Deep Multi-species Embedding*. 3639–3646. <https://www.ijcai.org/proceedings/2017/509>
- Chen, H., Perozzi, B., Hu, Y., & Skiena, S. (2017). *HARP: Hierarchical Representation Learning for Networks*. <http://arxiv.org/abs/1706.07845>
- Choudry, A. (2013). Saving biodiversity, for whom and for what? Conservation NGOs, complicity, colonialism and conquest in an era of capitalist globalization. In *NGOization: Complicity, contradictions and prospects* (pp. 24–44). Bloomsbury Publishing.
- Cieslak, M. C., Castelfranco, A. M., Roncalli, V., Lenz, P. H., & Hartline, D. K. (2020). T-Distributed Stochastic Neighbor Embedding (t-SNE): A tool for eco-physiological transcriptomic analysis. *Marine Genomics*, 51, 100723. <https://doi.org/10.1016/j.margen.2019.100723>
- Csermely, P. (2004). Strong links are important, but weak links stabilize them. *Trends in Biochemical Sciences*, 29(7), 331–334. <https://doi.org/10.1016/j.tibs.2004.05.004>
- Dalla Riva, G. V., & Stouffer, D. B. (2016). Exploring the evolutionary signature of food webs' backbones using functional traits. *Oikos*, 125(4), 446–456. <https://doi.org/10.1111/oik.02305>
- Dallas, T., Park, A. W., & Drake, J. M. (2017). Predicting cryptic links in host-parasite networks. *PLOS Computational Biology*, 13(5), e1005557. <https://doi.org/10.1371/journal.pcbi.1005557>
- Danisch, S., & Krumbiegel, J. (2021). Makie.jl: Flexible high-performance data visualization for Julia. *Journal of Open Source Software*, 6(65), 3349. <https://doi.org/10.21105/joss.03349>
- Domínguez, L., & Luoma, C. (2020). Decolonising Conservation Policy: How Colonial Land and Conservation Ideologies Persist and Perpetuate Indigenous Injustices at the Expense of the Environment. *Land*, 9(3, 3), 65. <https://doi.org/10.3390/land9030065>

- Dunne, J. A. (2006). The Network Structure of Food Webs. In J. A. Dunne & M. Pascual (Eds.), *Ecological networks: Linking structure and dynamics* (pp. 27–86). Oxford University Press.
- Eero, M., Dierking, J., Humborg, C., Undeman, E., MacKenzie, B. R., Ojaveer, H., Salo, T., & Köster, F. W. (2021). Use of food web knowledge in environmental conservation and management of living resources in the Baltic Sea. *ICES Journal of Marine Science*, 78(8), 2645–2663. <https://doi.org/10.1093/icesjms/fsab145>
- Eichhorn, M. P., Baker, K., & Griffiths, M. (2019). Steps towards decolonising biogeography. *Frontiers of Biogeography*, 12(1), 1–7. <https://doi.org/10.21425/F5FBG44795>
- Eklöf, A., Jacob, U., Kopp, J., Bosch, J., Castro-Urgal, R., Chacoff, N. P., Dalsgaard, B., de Sassi, C., Galetti, M., Guimarães, P. R., Lomáscolo, S. B., Martín González, A. M., Pizo, M. A., Rader, R., Rodrigo, A., Tylianakis, J. M., Vázquez, D. P., & Allesina, S. (2013). The dimensionality of ecological networks. *Ecology Letters*, 16(5), 577–583. <https://doi.org/10.1111/ele.12081>
- Fortin, M.-J., Dale, M. R. T., & Brimacombe, C. (2021). Network ecology in dynamic landscapes. *Proceedings of the Royal Society B: Biological Sciences*, 288(1949), rspb.2020.1889, 20201889. <https://doi.org/10.1098/rspb.2020.1889>
- Fricke, E. C., Ordóñez, A., Rogers, H. S., & Svenning, J.-C. (2022). The effects of defaunation on plants' capacity to track climate change. *Science*. <https://www.science.org/doi/abs/10.1126/science.abk3510>
- Galiana, N., Barros, C., Braga, J., Ficetola, G. F., Maiorano, L., Thuiller, W., Montoya, J. M., & Lurgi, M. (2021). The spatial scaling of food web structure across European biogeographical regions. *Ecography*, n/a(n/a). <https://doi.org/10.1111/ecog.05229>
- Galiana, N., Hawkins, B. A., & Montoya, J. M. (2019). The geographical variation of network structure is scale dependent: Understanding the biotic specialization of host–parasitoid networks. *Ecography*, 42(6), 1175–1187. <https://doi.org/10.1111/ecog.03684>
- Galiana, N., Lurgi, M., Bastazini, V. A. G., Bosch, J., Cagnolo, L., Cazelles, K., Claramunt-López, B., Emer, C., Fortin, M.-J., Grass, I., Hernández-Castellano, C., Jauker, F., Leroux, S. J., McCann, K., McLeod, A. M., Montoya, D., Mulder, C., Osorio-Canadas, S., Reverté, S., ... Montoya, J. M. (2022). Ecological network complexity scales with area. *Nature Ecology & Evolution*, 1–8. <https://doi.org/10.1038/s41559-021-01644-4>
- Galiana, N., Lurgi, M., Claramunt-López, B., Fortin, M.-J., Leroux, S., Cazelles, K., Gravel, D., & Montoya, J. M. (2018). The spatial scaling of species interaction networks. *Nature Ecology & Evolution*, 2(5), 782–790. <https://doi.org/10.1038/s41559-018-0517-3>
- Gaucher, S., Klopp, O., & Robin, G. (2021). Outlier detection in networks with missing links. *Computational Statistics & Data Analysis*, 164, 107308. <https://doi.org/10.1016/j.csda.2021.107308>
- Gibb, R., Albery, G. F., Becker, D. J., Brierley, L., Connor, R., Dallas, T. A., Eskew, E. A., Farrell, M. J., Rasmussen, A. L., Ryan, S. J., Sweeny, A., Carlson, C. J., & Poisot, T. (2021). Data Proliferation, Reconciliation, and Synthesis in Viral Ecology. *BioScience*, 71(11), 1148–1156. <https://doi.org/10.1093/biosci/biab080>
- Goodfellow, I., Bengio, Y., & Courville, A. (2016). *Deep learning*. MIT Press.
- Goyal, P., & Ferrara, E. (2018). Graph embedding techniques, applications, and performance: A survey. *Knowledge-Based Systems*, 151, 78–94. <https://doi.org/10.1016/j.knosys.2018.03.022>
- Gravel, D., Baiser, B., Dunne, J. A., Kopelke, J.-P., Martinez, N. D., Nyman, T., Poisot, T., Stouffer, D. B., Tylianakis, J. M., Wood, S. A., & Roslin, T. (2018). Bringing Elton and Grinnell together: A quantitative framework to represent the biogeography of ecological interaction networks. *Ecography*, 0(0). <https://doi.org/10.1111/ecog.04006>
- Gravel, D., Poisot, T., Albouy, C., Velez, L., & Mouillot, D. (2013). Inferring food web structure from predator-prey body size relationships. *Methods in Ecology and Evolution*, 4(11), 1083–1090. <https://doi.org/10.1111/2041-210X.12103>
- Green, B., & Chen, Y. (2019). Disparate Interactions: An Algorithm-in-the-Loop Analysis of Fairness in Risk Assessments. *Proceedings of the Conference on Fairness, Accountability, and Transparency*, 90–99. <https://doi.org/10.1145/3287560.3287563>

- Grover, A., & Leskovec, J. (2016). Node2vec: Scalable Feature Learning for Networks. *Proceedings of the 22nd ACM SIGKDD International Conference on Knowledge Discovery and Data Mining*, 855–864. <https://doi.org/10.1145/2939672.2939754>
- Grünig, M., Mazzi, D., Calanca, P., Karger, D. N., & Pellissier, L. (2020). Crop and forest pest metawebs shift towards increased linkage and suitability overlap under climate change. *Communications Biology*, 3(1, 1), 1–10. <https://doi.org/10.1038/s42003-020-0962-9>
- Gupta, A., Matta, P., & Pant, B. (2021). Graph neural network: Current state of Art, challenges and applications. *Materials Today: Proceedings*, 46, 10927–10932. <https://doi.org/10.1016/j.matpr.2021.01.950>
- Hadfield, J. D., Krasnov, B. R., Poulin, R., & Nakagawa, S. (2014). A Tale of Two Phylogenies: Comparative Analyses of Ecological Interactions. *The American Naturalist*, 183(2), 174–187. <https://doi.org/10.1086/674445>
- Herbert, F. (1965). *Dune* (1st ed.). Chilton Book Company.
- Hinton, G., & Roweis, S. T. (2002). Stochastic neighbor embedding. *NIPS*, 15, 833–840.
- Hoffmann, J., Bar-Sinai, Y., Lee, L. M., Andrejevic, J., Mishra, S., Rubinstein, S. M., & Rycroft, C. H. (2019). Machine learning in a data-limited regime: Augmenting experiments with synthetic data uncovers order in crumpled sheets. *Science Advances*, 5(4), eaau6792. <https://doi.org/10.1126/sciadv.aau6792>
- Hortal, J., de Bello, F., Diniz-Filho, J. A. F., Lewinsohn, T. M., Lobo, J. M., & Ladle, R. J. (2015). Seven Shortfalls that Beset Large-Scale Knowledge of Biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, 46(1), 523–549. <https://doi.org/10.1146/annurev-ecolsys-112414-054400>
- Jones, K. E., Bielby, J., Cardillo, M., Fritz, S. A., O'Dell, J., Orme, C. D. L., Safi, K., Sechrest, W., Boakes, E. H., Carbone, C., Connolly, C., Cutts, M. J., Foster, J. K., Grenyer, R., Habib, M., Plaster, C. A., Price, S. A., Rigby, E. A., Rist, J., ... Purvis, A. (2009). PanTHERIA: A species-level database of life history, ecology, and geography of extant and recently extinct mammals: Ecological Archives E090-184. *Ecology*, 90(9), 2648–2648. <https://doi.org/10.1890/08-1494.1>
- Jordano, P. (2016). Sampling networks of ecological interactions. *Functional Ecology*, 30(12), 1883–1893. <https://doi.org/10.1111/1365-2435.12763>
- Lamba, A., Cassey, P., Segaran, R. R., & Koh, L. P. (2019). Deep learning for environmental conservation. *Current Biology*, 29(19), R977–R982. <https://doi.org/10.1016/j.cub.2019.08.016>
- Maaten, L. van der. (2009). Learning a Parametric Embedding by Preserving Local Structure. *Proceedings of the Twelfth International Conference on Artificial Intelligence and Statistics*, 384–391. <https://proceedings.mlr.press/v5/maaten09a.html>
- Machen, R., & Nost, E. (2021). Thinking algorithmically: The making of hegemonic knowledge in climate governance. *Transactions of the Institute of British Geographers*, 46(3), 555–569. <https://doi.org/10.1111/tran.12441>
- Malaterre, C., Dussault, A. C., Mermans, E., Barker, G., Beisner, B. E., Bouchard, F., Desjardins, E., Handa, I. T., Kembel, S. W., Lajoie, G., Maris, V., Munson, A. D., Odenbaugh, J., Poisot, T., Shapiro, B. J., & Suttle, C. A. (2019). Functional Diversity: An Epistemic Roadmap. *BioScience*, 69(10), 800–811. <https://doi.org/10.1093/biosci/biz089>
- McLeod, A., Leroux, S. J., Gravel, D., Chu, C., Cirtwill, A. R., Fortin, M.-J., Galiana, N., Poisot, T., & Wood, S. A. (2021). Sampling and asymptotic network properties of spatial multi-trophic networks. *Oikos*, n/a(n/a). <https://doi.org/10.1111/oik.08650>
- Melnyk, K., Klus, S., Montavon, G., & Conrad, T. O. F. (2020). GraphKKE: Graph Kernel Koopman embedding for human microbiome analysis. *Applied Network Science*, 5(1), 96. <https://doi.org/10.1007/s41109-020-00339-2>
- Morales-Castilla, I., Matias, M. G., Gravel, D., & Araújo, M. B. (2015). Inferring biotic interactions from proxies. *Trends in Ecology & Evolution*, 30(6), 347–356. <https://doi.org/10.1016/j.tree.2015.03.014>
- Morand, S., & Poulin, R. (1998). Density, body mass and parasite species richness of terrestrial mammals. *Evolutionary Ecology*, 12(6), 717–727. <https://doi.org/10.1023/A:1006537600093>

- Mosebo Fernandes, A. C., Quintero Gonzalez, R., Lenihan-Clarke, M. A., Leslie Trotter, E. F., & Jokar Arsanjani, J. (2020). Machine Learning for Conservation Planning in a Changing Climate. *Sustainability*, 12(18, 18), 7657. <https://doi.org/10.3390/su12187657>
- Murphy, K. P. (2022). *Probabilistic machine learning: An introduction*. MIT Press. [probml.ai](https://probml.ai)
- Naman, S. M., White, S. M., Bellmore, J. R., McHugh, P. A., Kaylor, M. J., Baxter, C. V., Danehy, R. J., Naiman, R. J., & Puls, A. L. (2022). Food web perspectives and methods for riverine fish conservation. *WIREs Water*, n/a(n/a), e1590. <https://doi.org/10.1002/wat2.1590>
- Narayanan, A., Chandramohan, M., Venkatesan, R., Chen, L., Liu, Y., & Jaiswal, S. (2017). *Graph2vec: Learning Distributed Representations of Graphs*. <http://arxiv.org/abs/1707.05005>
- Neutel, A.-M., Heesterbeek, J. A. P., & de Ruiter, P. C. (2002). Stability in Real Food Webs: Weak Links in Long Loops. *Science*, 296(5570), 1120–1123. <https://doi.org/10.1126/science.1068326>
- No'mkmaq, M., Marshall, A., Beazley, K. F., Hum, J., Joudry, shalan, Papadopoulos, A., Pictou, S., Rabesca, J., Young, L., & Zurba, M. (2021). “Awakening the sleeping giant”: Re-Indigenization principles for transforming biodiversity conservation in Canada and beyond. *FACETS*, 6(1), 839–869.
- Nost, E., & Goldstein, J. E. (2021). A political ecology of data. *Environment and Planning E: Nature and Space*, 25148486211043503. <https://doi.org/10.1177/25148486211043503>
- O'Connor, L. M. J., Pollock, L. J., Braga, J., Ficetola, G. F., Maiorano, L., Martinez-Almoyna, C., Montemaggiore, A., Ohlmann, M., & Thuiller, W. (2020). Unveiling the food webs of tetrapods across Europe through the prism of the Eltonian niche. *Journal of Biogeography*, 47(1), 181–192. <https://doi.org/10.1111/jbi.13773>
- Pedersen, E. J., Thompson, P. L., Ball, R. A., Fortin, M.-J., Gouhier, T. C., Link, H., Moritz, C., Nenzen, H., Stanley, R. R. E., Taranu, Z. E., Gonzalez, A., Guichard, F., & Pepin, P. (2017). Signatures of the collapse and incipient recovery of an overexploited marine ecosystem. *Royal Society Open Science*, 4(7), 170215. <https://doi.org/10.1098/rsos.170215>
- Perozzi, B., Al-Rfou, R., & Skiena, S. (2014). DeepWalk: Online learning of social representations. *Proceedings of the 20th ACM SIGKDD International Conference on Knowledge Discovery and Data Mining*, 701–710. <https://doi.org/10.1145/2623330.2623732>
- Pichler, M., Boreux, V., Klein, A.-M., Schleuning, M., & Hartig, F. (2020). Machine learning algorithms to infer trait-matching and predict species interactions in ecological networks. *Methods in Ecology and Evolution*, 11(2), 281–293. <https://doi.org/10.1111/2041-210X.13329>
- Poisot, T., Belisle, Z., Hoebeke, L., Stock, M., & Szefer, P. (2019). EcologicalNetworks.jl - analysing ecological networks. *Ecography*. <https://doi.org/10.1111/ecog.04310>
- Poisot, T., Cirtwill, A. R., Cazelles, K., Gravel, D., Fortin, M.-J., & Stouffer, D. B. (2016). The structure of probabilistic networks. *Methods in Ecology and Evolution*, 7(3), 303–312. <https://doi.org/10.1111/2041-210X.12468>
- Poisot, T., Ouellet, M.-A., Mollentze, N., Farrell, M. J., Becker, D. J., Albery, G. F., Gibb, R. J., Seifert, S. N., & Carlson, C. J. (2021). *Imputing the mammalian virome with linear filtering and singular value decomposition*. <http://arxiv.org/abs/2105.14973>
- Poisot, T., Stouffer, D. B., & Gravel, D. (2015). Beyond species: Why ecological interaction networks vary through space and time. *Oikos*, 124(3), 243–251. <https://doi.org/10.1111/oik.01719>
- Ramasamy, D., & Madhow, U. (2015). Compressive spectral embedding: Sidestepping the SVD. In C. Cortes, N. Lawrence, D. Lee, M. Sugiyama, & R. Garnett (Eds.), *Advances in neural information processing systems* (Vol. 28). Curran Associates, Inc. <https://proceedings.neurips.cc/paper/2015/file/4f6ffe13a5d75b2d6a3923922b3922e5-Paper.pdf>
- Ray, J. C., Grimm, J., & Olive, A. (2021). The biodiversity crisis in Canada: Failures and challenges of federal and sub-national strategic and legal frameworks. *FACETS*, 6, 1044–1068. <https://doi.org/10.1139/facets-2020-0075>
- Runghen, R., Stouffer, D. B., & Dalla Riva, G. V. (2021). *Exploiting node metadata to predict interactions in large networks using graph embedding and neural networks*. <https://doi.org/10.1101/2021.06.10.447991>



- S, N. S., & Surendran, S. (2013). Graph Embedding and Dimensionality Reduction - A Survey. *International Journal of Computer Science & Engineering Technology*, 4(1). <https://www.semanticscholar.org/paper/Graph-Embedding-and-Dimensionality-Reduction-A-Surendran/3f413d591e4b2b876e033eeb9390e232ad4826ca>
- Saravia, L. A., Marina, T. I., Kristensen, N. P., De Troch, M., & Momo, F. R. (2021). Ecological network assembly: How the regional metaweb influences local food webs. *Journal of Animal Ecology*, n/a(n/a). <https://doi.org/10.1111/1365-2656.13652>
- Stevenson, M. T., & Doleac, J. L. (2021). *Algorithmic Risk Assessment in the Hands of Humans* (SSRN Scholarly Paper No. 3489440). <https://doi.org/10.2139/ssrn.3489440>
- Stier, A. C., Samhouri, J. F., Gray, S., Martone, R. G., Mach, M. E., Halpern, B. S., Kappel, C. V., Scarborough, C., & Levin, P. S. (2017). Integrating Expert Perceptions into Food Web Conservation and Management. *Conservation Letters*, 10(1), 67–76. <https://doi.org/10.1111/conl.12245>
- Stouffer, D. B., Camacho, J., Jiang, W., & Nunes Amaral, L. A. (2007). Evidence for the existence of a robust pattern of prey selection in food webs. *Proceedings of the Royal Society B: Biological Sciences*, 274(1621), 1931–1940. <https://doi.org/10.1098/rspb.2007.0571>
- Stouffer, D. B., Sales-Pardo, M., Sirer, M. I., & Bascompte, J. (2012). Evolutionary Conservation of Species' Roles in Food Webs. *Science*, 335(6075), 1489–1492. <https://doi.org/10.1126/science.1216556>
- Strydom, T., Bouskila, S., Banville, F., Barros, C., Caron, D., Farrell, M. J., Fortin, M.-J., Hemming, V., Mercier, B., Pollock, L. J., Runghen, R., Dalla Riva, G. V., & Poisot, T. (2022). Food web reconstruction through phylogenetic transfer of low-rank network representation. *Methods in Ecology and Evolution*, n/a(n/a). <https://doi.org/10.1111/2041-210X.13835>
- Strydom, T., Catchen, M. D., Banville, F., Caron, D., Dansereau, G., Desjardins-Proulx, P., Forero-Muñoz, N. R., Higino, G., Mercier, B., Gonzalez, A., Gravel, D., Pollock, L., & Poisot, T. (2021). A roadmap towards predicting species interaction networks (across space and time). *Philosophical Transactions of the Royal Society B: Biological Sciences*, 376(1837), 20210063. <https://doi.org/10.1098/rstb.2021.0063>
- Strydom, T., Dalla Riva, G. V., & Poisot, T. (2021). SVD Entropy Reveals the High Complexity of Ecological Networks. *Frontiers in Ecology and Evolution*, 9. <https://doi.org/10.3389/fevo.2021.623141>
- Tang, J., Qu, M., Wang, M., Zhang, M., Yan, J., & Mei, Q. (2015). LINE: Large-scale Information Network Embedding. *Proceedings of the 24th International Conference on World Wide Web*, 1067–1077. <https://doi.org/10.1145/2736277.2741093>
- Thurman, L. L., Barner, A. K., Garcia, T. S., & Chestnut, T. (2019). Testing the link between species interactions and co-occurrence in a trophic network. *Ecography*, 0. <https://doi.org/10.1111/ecog.04360>
- Torres, L., Chan, K. S., & Eliassi-Rad, T. (2020). GLEE: Geometric Laplacian Eigenmap Embedding. *Journal of Complex Networks*, 8(2), cnaa007. <https://doi.org/10.1093/comnet/cnaa007>
- Turak, E., Brazill-Boast, J., Cooney, T., Drielsma, M., Delacruz, J., Dunkerley, G., Fernandez, M., Ferrier, S., Gill, M., Jones, H., Koen, T., Leys, J., McGeoch, M., Mihoub, J.-B., Scanes, P., Schmeller, D., & Williams, K. (2017). Using the essential biodiversity variables framework to measure biodiversity change at national scale. *Biological Conservation*, 213, 264–271. <https://doi.org/10.1016/j.biocon.2016.08.019>
- Wang, D., Cui, P., & Zhu, W. (2016). Structural Deep Network Embedding. *Proceedings of the 22nd ACM SIGKDD International Conference on Knowledge Discovery and Data Mining*, 1225–1234. <https://doi.org/10.1145/2939672.2939753>
- Wang, S., Arroyo, J., Vogelstein, J. T., & Priebe, C. E. (2021). Joint Embedding of Graphs. *IEEE Transactions on Pattern Analysis and Machine Intelligence*, 43(4), 1324–1336. <https://doi.org/10.1109/TPAMI.2019.2948619>
- Wardeh, M., Baylis, M., & Blagrove, M. S. C. (2021). Predicting mammalian hosts in which novel coronaviruses can be generated. *Nature Communications*, 12(1, 1), 780. <https://doi.org/10.1038/s41467-021-21034-5>
- Weiskopf, S. R., Harmáčková, Z. V., Johnson, C. G., Londoño-Murcia, M. C., Miller, B. W., Myers, B. J. E., Pereira, L., Arce-Plata, M. I., Blanchard, J. L., Ferrier, S., Fulton, E. A., Harfoot, M., Isbell, F.,

- Johnson, J. A., Mori, A. S., Weng, E., & Rosa, I. M. D. (2022). Increasing the uptake of ecological model results in policy decisions to improve biodiversity outcomes. *Environmental Modelling & Software*, 149, 105318. <https://doi.org/10.1016/j.envsoft.2022.105318>
- Wood, S. A., Russell, R., Hanson, D., Williams, R. J., & Dunne, J. A. (2015). Effects of spatial scale of sampling on food web structure. *Ecology and Evolution*, 5(17), 3769–3782. <https://doi.org/10.1002/ece3.1640>
- Wu, D., Palmer, D. R., & Deford, D. R. (2021). *Maximum a Posteriori Inference of Random Dot Product Graphs via Conic Programming* (No. arXiv:2101.02180). arXiv. <http://arxiv.org/abs/2101.02180>
- Xu, M. (2021). Understanding Graph Embedding Methods and Their Applications. *SIAM Review*, 63(4), 825–853. <https://doi.org/10.1137/20M1386062>
- Yan, S., Xu, D., Zhang, B., & Zhang, H.-J. (2005). Graph embedding: A general framework for dimensionality reduction. *2005 IEEE Computer Society Conference on Computer Vision and Pattern Recognition (CVPR'05)*, 2, 830–837 vol. 2. <https://doi.org/10.1109/CVPR.2005.170>
- Young, S. J., & Scheinerman, E. R. (2007). Random Dot Product Graph Models for Social Networks. In A. Bonato & F. R. K. Chung (Eds.), *Algorithms and Models for the Web-Graph* (pp. 138–149). Springer. [https://doi.org/10.1007/978-3-540-77004-6\\_11](https://doi.org/10.1007/978-3-540-77004-6_11)
- Zhou, J., Cui, G., Hu, S., Zhang, Z., Yang, C., Liu, Z., Wang, L., Li, C., & Sun, M. (2020). Graph neural networks: A review of methods and applications. *AI Open*, 1, 57–81. <https://doi.org/10.1016/j.aiopen.2021.01.001>