

# Predicting metawebs: graph embeddings can help alleviate spatial data deficiencies

Tanya Strydom<sup>1,2,‡</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>‡</sup> These authors contributed equally to the work

## Correspondance to:

Timothée Poisot — [timothee.poisot@umontreal.ca](mailto:timothee.poisot@umontreal.ca)

1. Metawebs, i.e. networks of potential interactions within a species pool, are a powerful abstraction to understand how large-scales species interaction networks are structured.
2. Because metawebs are typically expressed at large spatial and taxonomic scales, assembling them is a tedious and costly process; predictive methods can help circumvent the limitations in data deficiencies, by providing 'draft' metawebs.
3. One way to improve the predictive ability is to maximize the information used for prediction, by using graph embeddings rather than the list of species interactions. Graph embedding is an emerging field in machine learning that holds great potential for ecological problems.
4. In this perspective, we outline how the challenges associated with inferring metawebs line-up with the advantages of graph embeddings; furthermore, because metawebs are inherently spatial objects, we discuss how the choice of the species pool has consequences on the reconstructed network, but also embeds hypotheses about which human-made boundaries are ecologically meaningful.

1 Having a general solution for inferring *potential* interactions (despite the unavailability of interaction data)  
2 could be the catalyst for significant breakthroughs in our ability to start thinking about species interaction  
3 networks over large spatial scales. In a recent overview of the field of ecological network prediction,  
4 Strydom et al. (2021) identified two challenges of interest to the prediction of interactions at large scales.  
5 First, there is a relative scarcity of relevant data in most places globally – paradoxically, this restricts our  
6 ability to infer interactions to locations where inference is perhaps the least required; second, accurate  
7 predictions often demand accurate predictors, and the lack of methods that can leverage small amount of  
8 data is a serious impediment to our predictive ability globally.

9 Following the definition of Dunne (2006), a metaweb is a network analogue to the regional species pool;  
10 specifically, it is an inventory of all *potential* interactions between species from a spatially delimited area  
11 (and so captures the  $\gamma$  diversity of interactions). The metaweb is, therefore, *not* a prediction of the food  
12 web at a specific locale within the spatial area it covers, and will have a different structure (notably by  
13 having a larger connectance; see e.g. Wood et al., 2015). These local food webs (which captures the  $\alpha$   
14 diversity of interactions) are a subset of the metaweb’s species and interactions, and have been called  
15 “metaweb realizations” (Poisot et al., 2015). Differences between local food web and their metaweb are  
16 due to chance, species abundance and co-occurrence, local environmental conditions, and local  
17 distribution of functional traits, among others.

18 Because the metaweb represents the joint effect of functional, phylogenetic, and macroecological  
19 processes (Morales-Castilla et al., 2015), it holds valuable ecological information. Specifically, it is the  
20 “upper bounds” on what the composition of the local networks can be (see e.g. McLeod et al., 2021). These  
21 local networks, in turn, can be reconstructed given appropriate knowledge of local species composition,  
22 providing information on structure of food webs at finer spatial scales. This has been done for example for  
23 tree-galler-parasitoid systems (Gravel et al., 2018), fish trophic interactions (Albouy et al., 2019), tetrapod  
24 trophic interactions (O’Connor et al., 2020), and crop-pest networks (Grünig et al., 2020). Whereas the  
25 original metaweb definition, and indeed most past uses of metawebs, was based on the presence/absence  
26 of interactions, we focus on *probabilistic* metawebs where interactions are represented as the chance of  
27 success of a Bernoulli trial (see e.g. Poisot et al., 2016); therefore, not only does our method recommend  
28 interactions that may exist, it gives each interaction a score, allowing us to properly weigh them.

## 29 **The metaweb is an inherently probabilistic object**

30 Yet, owing to the inherent plasticity of interactions, there have been documented instances of food webs  
31 undergoing rapid collapse/recovery cycles over short periods of time (Pedersen et al., 2017). The  
32 embedding of a network, in a sense, embeds its macro-evolutionary history, especially as RDPG captures  
33 ecological signal (Dalla Riva & Stouffer, 2016); at this point, it is important to recall that a metaweb is  
34 intended as a catalogue of all potential interactions, which should then be filtered (Morales-Castilla et al.,  
35 2015). In practice (and in this instance) the reconstructed metaweb will predict interactions that are  
36 plausible based on the species' evolutionary history, however some interactions would/would not be  
37 realized due to human impact.

38 Dallas et al. (2017) suggested that most links in ecological networks may be cryptic, *i.e.* uncommon or  
39 otherwise hard to observe. This argument essentially echoes Jordano (2016): the sampling of ecological  
40 interactions is difficult because it requires first the joint observation of two species, and then the  
41 observation of their interaction. In addition, it is generally expected that weak or rare links would be more  
42 common in networks (Csermely, 2004), compared to strong, persistent links; this is notably the case in  
43 food chains, wherein many weaker links are key to the stability of a system (Neutel et al., 2002). In the  
44 light of these observations, the results in fig. ?? are not particularly surprising: we expect to see a surge in  
45 these low-probability interactions under a model that has a good predictive accuracy. Because the  
46 predictions we generate are by design probabilistic, then one can weigh these rare links appropriately. In a  
47 sense, that most ecological interactions are elusive can call for a slightly different approach to sampling:  
48 once the common interactions are documented, the effort required in documenting each rare interaction  
49 may increase exponentially. Recent proposals suggest that machine learning algorithms, in these  
50 situations, can act as data generators (Hoffmann et al., 2019): in this perspective, high quality  
51 observational data can be supplemented with synthetic data coming from predictive models, which  
52 increases the volume of information available for inference. Indeed, Strydom et al. (2021) suggested that  
53 knowing the metaweb may render the prediction of local networks easier, because it fixes an “upper  
54 bound” on which interactions can exist; indeed, with a probabilistic metaweb, we can consider that the  
55 metaweb represents an aggregation of informative priors on the interactions.

## 56 Graph embedding offers promises for the inference of potential 57 interactions

58 Graph embedding is a varied family of machine learning techniques aiming to transform nodes and edges  
59 into a vector space, usually of a lower dimension, whilst maximally retaining key properties of the graph  
60 (Yan et al., 2005). Ecological networks are an interesting candidate for the widespread application of  
61 embeddings, as they tend to possess a shared structural backbone (Mora et al., 2018), which hints at  
62 structural invariants that can be revealed at lower dimensions. Indeed, previous work by Eklöf et al. (2013)  
63 suggests that food webs are inherently low-dimensional objects, and can be adequately represented with  
64 less than ten dimensions.

65 The popularity of graph embedding techniques in machine learning is rather intuitive: while graphs are  
66 discrete objects, machine learning techniques tend to handle continuous data better. Therefore, bringing a  
67 discrete graph into a continuous vector space opens up a broader variety of predictive algorithms.

Method	Embedding approach	Reference	Ecological application
RDPG	graphs through SVD	Young & Scheinerman (2007)	Wardeh et al. (2021)
tSNE	nodes through statistical divergence	Hinton & Roweis (2002)	
DeepWalk	graph walk	Perozzi et al. (2014)	
FastEmbed	graph through PCA/SVD analogue	Ramasamy & Madhoo (2015)	
LINE	nodes through statistical divergence	Tang et al. (2015)	
SDNE	nodes through auto-encoding	D. Wang et al. (2016)	
node2vec	node embedding	Grover & Leskovec (2016)	
graph2vec	sub-graph embedding	Narayanan et al. (2017)	
HARP	nodes through a meta-strategy	Chen et al. (2017)	
Joint methods	multiple graphs	S. Wang et al. (2021)	

## The metaweb embeds hypotheses about which spatial boundaries are meaningful

As Herbert (1965) rightfully pointed out, “[y]ou can’t draw neat lines around planet-wide problems”; in this regard, our approach (and indeed, any inference of a metaweb at large scales) must contend with several interesting and interwoven families of problems. The first is the 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 to make a reliable inference decreases; this would likely be indicated by large confidence intervals during ancestral character estimation, but the lack of well documented metawebs is currently preventing the development of more concrete guidelines. The question of phylogenetic relatedness and dispersal is notably true if the metaweb is assembled in an area with mostly endemic species, and as with every predictive algorithm, there is room for the application of our best ecological judgement. Conversely, the metaweb should be reliably filled, which assumes that the  $S^2$  interactions in a pool of  $S$  species have been examined, either through literature surveys or expert elicitation. Supp. Mat. 1 provides some guidance as to the type of sampling effort that should be prioritized. While RDPG was able to maintain very high predictive power when interactions were missing, the addition of false positive interactions was immediately detected; this suggests that it may be appropriate to err on the side of “too many” interactions when constructing the initial metaweb to be transferred. The second series of problems are related to determining which area should be used to infer the new metaweb in, as this determines the species pool that must be used.

In our application, we focused on the mammals of Canada. The upside of this approach is that information at the country level is likely to be required by policy makers and stakeholders for their biodiversity assessment, as each country tends to set goals at the national level (Buxton et al., 2021) for which quantitative instruments are designed (Turak et al., 2017), with specific strategies often enacted at smaller scales (Ray et al., 2021). And yet, we do not really have a satisfying answer to the question of “where does a food web stop?”; the current most satisfying solutions involve examining the spatial consistency of network area relationships (see e.g. Galiana et al., 2018, 2019, 2021; Fortin2021NetEco?), which is of course impossible in the absence of enough information about the network itself. This suggests that an *a posteriori* refinement of the results may be required, based on a downscaling of the metaweb. The final family of problems relates less to the availability of data or quantitative tools, and

97 more to the praxis of spatial ecology. Operating under the context of national divisions, in large parts of  
98 the world, reflects nothing more than the legacy of settler colonialism. Indeed, the use of ecological data is  
99 not an apolitical act (Nost & Goldstein, 2021), as data infrastructures tend to be designed to answer  
100 questions within national boundaries, and their use both draws upon and reinforces territorial statecraft;  
101 as per Machen & Nost (2021), this is particularly true when the output of “algorithmic thinking” (e.g.  
102 relying on machine learning to generate knowledge) can be re-used for governance (e.g. enacting  
103 conservation decisions at the national scale). We therefore recognize that methods such as we propose  
104 operate under the framework that contributed to the ongoing biodiversity crisis (Adam, 2014), reinforced  
105 environmental injustice (Choudry, 2013; Domínguez & Luoma, 2020), and on Turtle Island especially,  
106 should be replaced by Indigenous principles of land management (Eichhorn et al., 2019; No’kmaq et al.,  
107 2021). As we see AI/ML being increasingly mobilized to generate knowledge that is lacking for  
108 conservation decisions (e.g. Lamba et al., 2019; Mosebo Fernandes et al., 2020), our discussion of these  
109 tools need to go beyond the technical, and into the governance consequences they can have.

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

## 123 **References**

124 Adam, R. (2014). *Elephant treaties: The Colonial legacy of the biodiversity crisis*. UPNE.

125 Albouy, C., Archambault, P., Appeltans, W., Araújo, M. B., Beauchesne, D., Cazelles, K., Cirtwill, A. R.,  
 126 Fortin, M.-J., Galiana, N., Leroux, S. J., Pellissier, L., Poisot, T., Stouffer, D. B., Wood, S. A., & Gravel, D.  
 127 (2019). The marine fish food web is globally connected. *Nature Ecology & Evolution*, 3(8, 8),  
 128 1153–1161. <https://doi.org/10.1038/s41559-019-0950-y>

129 Buxton, R. T., Bennett, J. R., Reid, A. J., Shulman, C., Cooke, S. J., Francis, C. M., Nyboer, E. A., Pritchard,  
 130 G., Binley, A. D., Avery-Gomm, S., Ban, N. C., Beazley, K. F., Bennett, E., Blight, L. K., Bortolotti, L. E.,  
 131 Camfield, A. F., Gadallah, F., Jacob, A. L., Naujokaitis-Lewis, I., ... Smith, P. A. (2021). Key  
 132 information needs to move from knowledge to action for biodiversity conservation in Canada.  
 133 *Biological Conservation*, 256, 108983. <https://doi.org/10.1016/j.biocon.2021.108983>

134 Chen, H., Perozzi, B., Hu, Y., & Skiena, S. (2017, November 16). *HARP: Hierarchical Representation*  
 135 *Learning for Networks*. <http://arxiv.org/abs/1706.07845>

136 Choudry, A. (2013). Saving biodiversity, for whom and for what? Conservation NGOs, complicity,  
 137 colonialism and conquest in an era of capitalist globalization. In *NGOization: Complicity,*  
 138 *contradictions and prospects* (pp. 24–44). Bloomsbury Publishing.

139 Csermely, P. (2004). Strong links are important, but weak links stabilize them. *Trends in Biochemical*  
 140 *Sciences*, 29(7), 331–334. <https://doi.org/10.1016/j.tibs.2004.05.004>

141 Dalla Riva, G. V., & Stouffer, D. B. (2016). Exploring the evolutionary signature of food webs' backbones  
 142 using functional traits. *Oikos*, 125(4), 446–456. <https://doi.org/10.1111/oik.02305>

143 Dallas, T., Park, A. W., & Drake, J. M. (2017). Predicting cryptic links in host-parasite networks. *PLOS*  
 144 *Computational Biology*, 13(5), e1005557. <https://doi.org/10.1371/journal.pcbi.1005557>

145 Domínguez, L., & Luoma, C. (2020). Decolonising Conservation Policy: How Colonial Land and  
 146 Conservation Ideologies Persist and Perpetuate Indigenous Injustices at the Expense of the  
 147 Environment. *Land*, 9(3, 3), 65. <https://doi.org/10.3390/land9030065>

148 Dunne, J. A. (2006). The Network Structure of Food Webs. In J. A. Dunne & M. Pascual (Eds.), *Ecological*  
 149 *networks: Linking structure and dynamics* (pp. 27–86). Oxford University Press.

150 Eichhorn, M. P., Baker, K., & Griffiths, M. (2019). Steps towards decolonising biogeography. *Frontiers of*  
 151 *Biogeography*, 12(1), 1–7. <https://doi.org/10.21425/F5FBG44795>

152 Eklöf, A., Jacob, U., Kopp, J., Bosch, J., Castro-Urgal, R., Chacoff, N. P., Dalsgaard, B., de Sassi, C., Galetti,



153 M., Guimarães, P. R., Lomáscolo, S. B., Martín González, A. M., Pizo, M. A., Rader, R., Rodrigo, A.,  
 154 Tylianakis, J. M., Vázquez, D. P., & Allesina, S. (2013). The dimensionality of ecological networks.  
 155 *Ecology Letters*, 16(5), 577–583. <https://doi.org/10.1111/ele.12081>

156 Galiana, N., Barros, C., Braga, J., Ficetola, G. F., Maiorano, L., Thuiller, W., Montoya, J. M., & Lurgi, M.  
 157 (2021). The spatial scaling of food web structure across European biogeographical regions. *Ecography*,  
 158 *n/a(n/a)*. <https://doi.org/10.1111/ecog.05229>

159 Galiana, N., Hawkins, B. A., & Montoya, J. M. (2019). The geographical variation of network structure is  
 160 scale dependent: Understanding the biotic specialization of host–parasitoid networks. *Ecography*,  
 161 42(6), 1175–1187. <https://doi.org/10.1111/ecog.03684>

162 Galiana, N., Lurgi, M., Claramunt-López, B., Fortin, M.-J., Leroux, S., Cazelles, K., Gravel, D., & Montoya,  
 163 J. M. (2018). The spatial scaling of species interaction networks. *Nature Ecology & Evolution*, 2(5),  
 164 782–790. <https://doi.org/10.1038/s41559-018-0517-3>

165 Gravel, D., Baiser, B., Dunne, J. A., Kopelke, J.-P., Martinez, N. D., Nyman, T., Poisot, T., Stouffer, D. B.,  
 166 Tylianakis, J. M., Wood, S. A., & Roslin, T. (2018). Bringing Elton and Grinnell together: A quantitative  
 167 framework to represent the biogeography of ecological interaction networks. *Ecography*, 0(0).  
 168 <https://doi.org/10.1111/ecog.04006>

169 Grover, A., & Leskovec, J. (2016). Node2vec: Scalable Feature Learning for Networks. *Proceedings of the*  
 170 *22nd ACM SIGKDD International Conference on Knowledge Discovery and Data Mining*, 855–864.  
 171 <https://doi.org/10.1145/2939672.2939754>

172 Grünig, M., Mazzi, D., Calanca, P., Karger, D. N., & Pellissier, L. (2020). Crop and forest pest metawebs  
 173 shift towards increased linkage and suitability overlap under climate change. *Communications Biology*,  
 174 3(1, 1), 1–10. <https://doi.org/10.1038/s42003-020-0962-9>

175 Herbert, F. (1965). *Dune* (1st ed.). Chilton Book Company.

176 Hinton, G., & Roweis, S. T. (2002). Stochastic neighbor embedding. *NIPS*, 15, 833–840.

177 Hoffmann, J., Bar-Sinai, Y., Lee, L. M., Andrejevic, J., Mishra, S., Rubinstein, S. M., & Rycroft, C. H. (2019).  
 178 Machine learning in a data-limited regime: Augmenting experiments with synthetic data uncovers  
 179 order in crumpled sheets. *Science Advances*, 5(4), eaau6792.  
 180 <https://doi.org/10.1126/sciadv.aau6792>

181 Jordano, P. (2016). Sampling networks of ecological interactions. *Functional Ecology*, 30(12), 1883–1893.  
 182 <https://doi.org/10.1111/1365-2435.12763>

183 Lamba, A., Cassey, P., Segaran, R. R., & Koh, L. P. (2019). Deep learning for environmental conservation.  
 184 *Current Biology*, 29(19), R977–R982. <https://doi.org/10.1016/j.cub.2019.08.016>

185 Machen, R., & Nost, E. (2021). Thinking algorithmically: The making of hegemonic knowledge in climate  
 186 governance. *Transactions of the Institute of British Geographers*, 46(3), 555–569.  
 187 <https://doi.org/10.1111/tran.12441>

188 McLeod, A., Leroux, S. J., Gravel, D., Chu, C., Cirtwill, A. R., Fortin, M.-J., Galiana, N., Poisot, T., & Wood,  
 189 S. A. (2021). Sampling and asymptotic network properties of spatial multi-trophic networks. *Oikos*,  
 190 *n/a*(n/a). <https://doi.org/10.1111/oik.08650>

191 Mora, B. B., Gravel, D., Gilarranz, L. J., Poisot, T., & Stouffer, D. B. (2018). Identifying a common backbone  
 192 of interactions underlying food webs from different ecosystems. *Nature Communications*, 9(1), 2603.  
 193 <https://doi.org/10.1038/s41467-018-05056-0>

194 Morales-Castilla, I., Matias, M. G., Gravel, D., & Araújo, M. B. (2015). Inferring biotic interactions from  
 195 proxies. *Trends in Ecology & Evolution*, 30(6), 347–356.  
 196 <https://doi.org/10.1016/j.tree.2015.03.014>

197 Mosebo Fernandes, A. C., Quintero Gonzalez, R., Lenihan-Clarke, M. A., Leslie Trotter, E. F., & Jokar  
 198 Arsanjani, J. (2020). Machine Learning for Conservation Planning in a Changing Climate.  
 199 *Sustainability*, 12(18, 18), 7657. <https://doi.org/10.3390/su12187657>

200 Narayanan, A., Chandramohan, M., Venkatesan, R., Chen, L., Liu, Y., & Jaiswal, S. (2017, July 17).  
 201 *Graph2vec: Learning Distributed Representations of Graphs*. <http://arxiv.org/abs/1707.05005>

202 Neutel, A.-M., Heesterbeek, J. A. P., & de Ruiter, P. C. (2002). Stability in Real Food Webs: Weak Links in  
 203 Long Loops. *Science*, 296(5570), 1120–1123. <https://doi.org/10.1126/science.1068326>

204 No'kmaq, M., Marshall, A., Beazley, K. F., Hum, J., Joudry, shalan, Papadopoulos, A., Pictou, S., Rabesca,  
 205 J., Young, L., & Zurba, M. (2021). “Awakening the sleeping giant”: Re-Indigenization principles for  
 206 transforming biodiversity conservation in Canada and beyond. *FACETS*, 6(1), 839–869.

207 Nost, E., & Goldstein, J. E. (2021). A political ecology of data. *Environment and Planning E: Nature and*  
 208 *Space*, 25148486211043503. <https://doi.org/10.1177/25148486211043503>

209 O'Connor, L. M. J., Pollock, L. J., Braga, J., Ficetola, G. F., Maiorano, L., Martinez-Almoyna, C.,  
 210 Montemaggiori, A., Ohlmann, M., & Thuiller, W. (2020). Unveiling the food webs of tetrapods across  
 211 Europe through the prism of the Eltonian niche. *Journal of Biogeography*, 47(1), 181–192.  
 212 <https://doi.org/10.1111/jbi.13773>

213 Pedersen, E. J., Thompson, P. L., Ball, R. A., Fortin, M.-J., Gouhier, T. C., Link, H., Moritz, C., Nenzen, H.,  
 214 Stanley, R. R. E., Taranu, Z. E., Gonzalez, A., Guichard, F., & Pepin, P. (2017). Signatures of the  
 215 collapse and incipient recovery of an overexploited marine ecosystem. *Royal Society Open Science*, 4(7),  
 216 170215. <https://doi.org/10.1098/rsos.170215>

217 Perozzi, B., Al-Rfou, R., & Skiena, S. (2014). DeepWalk: Online learning of social representations.  
 218 *Proceedings of the 20th ACM SIGKDD International Conference on Knowledge Discovery and Data*  
 219 *Mining*, 701–710. <https://doi.org/10.1145/2623330.2623732>

220 Poisot, T., Cirtwill, A. R., Cazelles, K., Gravel, D., Fortin, M.-J., & Stouffer, D. B. (2016). The structure of  
 221 probabilistic networks. *Methods in Ecology and Evolution*, 7(3), 303–312.  
 222 <https://doi.org/10.1111/2041-210X.12468>

223 Poisot, T., Stouffer, D. B., & Gravel, D. (2015). Beyond species: Why ecological interaction networks vary  
 224 through space and time. *Oikos*, 124(3), 243–251. <https://doi.org/10.1111/oik.01719>

225 Ramasamy, D., & Madhoo, U. (2015). Compressive spectral embedding: Sidestepping the SVD. In C.  
 226 Cortes, N. Lawrence, D. Lee, M. Sugiyama, & R. Garnett (Eds.), *Advances in neural information*  
 227 *processing systems* (Vol. 28). Curran Associates, Inc. <https://proceedings.neurips.cc/paper/2015/file/4f6ffe13a5d75b2d6a3923922b3922e5-Paper.pdf>

229 Ray, J. C., Grimm, J., & Olive, A. (2021). The biodiversity crisis in Canada: Failures and challenges of  
 230 federal and sub-national strategic and legal frameworks. *FACETS*, 6, 1044–1068.  
 231 <https://doi.org/10.1139/facets-2020-0075>

232 Strydom, T., Catchen, M. D., Banville, F., Caron, D., Dansereau, G., Desjardins-Proulx, P., Forero-Muñoz,  
 233 N. R., Higino, G., Mercier, B., Gonzalez, A., Gravel, D., Pollock, L., & Poisot, T. (2021). A roadmap  
 234 towards predicting species interaction networks (across space and time). *Philosophical Transactions of*  
 235 *the Royal Society B: Biological Sciences*, 376(1837), 20210063.  
 236 <https://doi.org/10.1098/rstb.2021.0063>

237 Tang, J., Qu, M., Wang, M., Zhang, M., Yan, J., & Mei, Q. (2015). LINE: Large-scale Information Network

238 Embedding. *Proceedings of the 24th International Conference on World Wide Web*, 1067–1077.  
 239 <https://doi.org/10.1145/2736277.2741093>

240 Turak, E., Brazill-Boast, J., Cooney, T., Drielsma, M., DelaCruz, J., Dunkerley, G., Fernandez, M., Ferrier,  
 241 S., Gill, M., Jones, H., Koen, T., Leys, J., McGeoch, M., Mihoub, J.-B., Scanes, P., Schmeller, D., &  
 242 Williams, K. (2017). Using the essential biodiversity variables framework to measure biodiversity  
 243 change at national scale. *Biological Conservation*, 213, 264–271.  
 244 <https://doi.org/10.1016/j.biocon.2016.08.019>

245 Wang, D., Cui, P., & Zhu, W. (2016). Structural Deep Network Embedding. *Proceedings of the 22nd ACM*  
 246 *SIGKDD International Conference on Knowledge Discovery and Data Mining*, 1225–1234.  
 247 <https://doi.org/10.1145/2939672.2939753>

248 Wang, S., Arroyo, J., Vogelstein, J. T., & Priebe, C. E. (2021). Joint Embedding of Graphs. *IEEE*  
 249 *Transactions on Pattern Analysis and Machine Intelligence*, 43(4), 1324–1336.  
 250 <https://doi.org/10.1109/TPAMI.2019.2948619>

251 Wardeh, M., Baylis, M., & Blagrove, M. S. C. (2021). Predicting mammalian hosts in which novel  
 252 coronaviruses can be generated. *Nature Communications*, 12(1, 1), 780.  
 253 <https://doi.org/10.1038/s41467-021-21034-5>

254 Wood, S. A., Russell, R., Hanson, D., Williams, R. J., & Dunne, J. A. (2015). Effects of spatial scale of  
 255 sampling on food web structure. *Ecology and Evolution*, 5(17), 3769–3782.  
 256 <https://doi.org/10.1002/ece3.1640>

257 Yan, S., Xu, D., Zhang, B., & Zhang, H.-J. (2005). Graph embedding: A general framework for  
 258 dimensionality reduction. *2005 IEEE Computer Society Conference on Computer Vision and Pattern*  
 259 *Recognition (CVPR'05)*, 2, 830–837 vol. 2. <https://doi.org/10.1109/CVPR.2005.170>

260 Young, S. J., & Scheinerman, E. R. (2007). Random Dot Product Graph Models for Social Networks. In A.  
 261 Bonato & F. R. K. Chung (Eds.), *Algorithms and Models for the Web-Graph* (pp. 138–149). Springer.  
 262 [https://doi.org/10.1007/978-3-540-77004-6\\_11](https://doi.org/10.1007/978-3-540-77004-6_11)