

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

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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 the inference of potential interactions**

57 Graph embedding is a varied family of machine learning techniques aiming to transform nodes and edges  
58 into a vector space, usually of a lower dimension, whilst maximally retaining key properties of the graph.  
59 Ecological networks are an interesting candidate for the widespread application of embeddings, as they  
60 tend to possess a shared structural backbone (Mora et al., 2018), which hints at structural invariants that  
61 can be revealed at lower dimensions. Indeed, previous work by Eklöf et al. (2013) suggests that food webs  
62 are inherently low-dimensional objects, and can be adequately represented with less than ten dimensions.  
63 The popularity of graph embedding techniques in machine learning is rather intuitive: while graphs are  
64 discrete objects, machine learning techniques tend to handle continuous data better. Therefore, bringing a  
65 discrete graph into a continuous vector space opens up a broader variety of predictive algorithms.

Method	Embedded object	Reference
DeepWalk	graph walk	Perozzi et al. (2014)
node2vec	node embedding	Grover & Leskovec (2016)
graph2vec	sub-graph embedding	Narayanan et al. (2017)

66 **The metaweb embeds hypotheses about which spatial boundaries are**  
67 **meaningful**

68 As Herbert (1965) rightfully pointed out, “[y]ou can’t draw neat lines around planet-wide problems”; in  
69 this regard, our approach (and indeed, any inference of a metaweb at large scales) must contend with  
70 several interesting and interwoven families of problems. The first is the limit of the metaweb to embed  
71 and transfer. If the initial metaweb is too narrow in scope, notably from a taxonomic point of view, the  
72 chances of finding another area with enough related species to make a reliable inference decreases; this  
73 would likely be indicated by large confidence intervals during ancestral character estimation, but the lack  
74 of well documented metawebs is currently preventing the development of more concrete guidelines. The  
75 question of phylogenetic relatedness and dispersal is notably true if the metaweb is assembled in an area  
76 with mostly endemic species, and as with every predictive algorithm, there is room for the application of  
77 our best ecological judgement. Conversely, the metaweb should be reliably filled, which assumes that the

<sup>78</sup>  $S^2$  interactions in a pool of  $S$  species have been examined, either through literature surveys or expert  
<sup>79</sup> elicitation. Supp. Mat. 1 provides some guidance as to the type of sampling effort that should be  
<sup>80</sup> prioritized. While RDPG was able to maintain very high predictive power when interactions were missing,  
<sup>81</sup> the addition of false positive interactions was immediately detected; this suggests that it may be  
<sup>82</sup> appropriate to err on the side of “too many” interactions when constructing the initial metaweb to be  
<sup>83</sup> transferred. The second series of problems are related to determining which area should be used to infer  
<sup>84</sup> the new metaweb in, as this determines the species pool that must be used.

<sup>85</sup> In our application, we focused on the mammals of Canada. The upside of this approach is that  
<sup>86</sup> information at the country level is likely to be required by policy makers and stakeholders for their  
<sup>87</sup> biodiversity assessment, as each country tends to set goals at the national level (Buxton et al., 2021) for  
<sup>88</sup> which quantitative instruments are designed (Turak et al., 2017), with specific strategies often enacted at  
<sup>89</sup> smaller scales (Ray et al., 2021). And yet, we do not really have a satisfying answer to the question of  
<sup>90</sup> “where does a food web stop?”; the current most satisfying solutions involve examining the spatial  
<sup>91</sup> consistency of network area relationships (see e.g. Galiana et al., 2018, 2019, 2021; **Fortin2021NetEco?**),  
<sup>92</sup> which is of course impossible in the absence of enough information about the network itself. This  
<sup>93</sup> suggests that an *a posteriori* refinement of the results may be required, based on a downscaling of the  
<sup>94</sup> metaweb. The final family of problems relates less to the availability of data or quantitative tools, and  
<sup>95</sup> more to the praxis of spatial ecology. Operating under the context of national divisions, in large parts of  
<sup>96</sup> the world, reflects nothing more than the legacy of settler colonialism. Indeed, the use of ecological data is  
<sup>97</sup> not an apolitical act (Nost & Goldstein, 2021), as data infrastructures tend to be designed to answer  
<sup>98</sup> questions within national boundaries, and their use both draws upon and reinforces territorial statecraft;  
<sup>99</sup> as per Machen & Nost (2021), this is particularly true when the output of “algorithmic thinking” (e.g.  
<sup>100</sup> relying on machine learning to generate knowledge) can be re-used for governance (e.g. enacting  
<sup>101</sup> conservation decisions at the national scale). We therefore recognize that methods such as we propose  
<sup>102</sup> operate under the framework that contributed to the ongoing biodiversity crisis (Adam, 2014), reinforced  
<sup>103</sup> environmental injustice (Choudry, 2013; Domínguez & Luoma, 2020), and on Turtle Island especially,  
<sup>104</sup> should be replaced by Indigenous principles of land management (Eichhorn et al., 2019; No’kmaq et al.,  
<sup>105</sup> 2021). As we see AI/ML being increasingly mobilized to generate knowledge that is lacking for  
<sup>106</sup> conservation decisions (e.g. Lamba et al., 2019; Mosebo Fernandes et al., 2020), our discussion of these  
<sup>107</sup> tools need to go beyond the technical, and into the governance consequences they can have.

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## 121 References

- 122 Adam, R. (2014). *Elephant treaties: The Colonial legacy of the biodiversity crisis*. UPNE.
- 123 Albouy, C., Archambault, P., Appeltans, W., Araújo, M. B., Beauchesne, D., Cazelles, K., Cirtwill, A. R.,  
 124 Fortin, M.-J., Galiana, N., Leroux, S. J., Pellissier, L., Poisot, T., Stouffer, D. B., Wood, S. A., & Gravel, D.  
 125 (2019). The marine fish food web is globally connected. *Nature Ecology & Evolution*, 3(8, 8),  
 126 1153–1161. <https://doi.org/10.1038/s41559-019-0950-y>
- 127 Buxton, R. T., Bennett, J. R., Reid, A. J., Shulman, C., Cooke, S. J., Francis, C. M., Nyboer, E. A., Pritchard,  
 128 G., Binley, A. D., Avery-Gomm, S., Ban, N. C., Beazley, K. F., Bennett, E., Blight, L. K., Bortolotti, L. E.,  
 129 Camfield, A. F., Gadallah, F., Jacob, A. L., Naujokaitis-Lewis, I., ... Smith, P. A. (2021). Key  
 130 information needs to move from knowledge to action for biodiversity conservation in Canada.  
 131 *Biological Conservation*, 256, 108983. <https://doi.org/10.1016/j.biocon.2021.108983>
- 132 Choudry, A. (2013). Saving biodiversity, for whom and for what? Conservation NGOs, complicity,  
 133 colonialism and conquest in an era of capitalist globalization. In *NGOization: Complicity,*  
 134 *contradictions and prospects* (pp. 24–44). Bloomsbury Publishing.

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

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

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

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

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

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

148 Eklöf, A., Jacob, U., Kopp, J., Bosch, J., Castro-Urgal, R., Chacoff, N. P., Dalsgaard, B., de Sassi, C., Galetti,  
149 M., Guimarães, P. R., Lomáscolo, S. B., Martín González, A. M., Pizo, M. A., Rader, R., Rodrigo, A.,  
150 Tylianakis, J. M., Vázquez, D. P., & Allesina, S. (2013). The dimensionality of ecological networks.  
151 *Ecology Letters*, 16(5), 577–583. <https://doi.org/10.1111/ele.12081>

152 Galiana, N., Barros, C., Braga, J., Ficetola, G. F., Maiorano, L., Thuiller, W., Montoya, J. M., & Lurgi, M.  
153 (2021). The spatial scaling of food web structure across European biogeographical regions. *Ecography*,  
154 *n/a(n/a)*. <https://doi.org/10.1111/ecog.05229>

155 Galiana, N., Hawkins, B. A., & Montoya, J. M. (2019). The geographical variation of network structure is  
156 scale dependent: Understanding the biotic specialization of host–parasitoid networks. *Ecography*,  
157 42(6), 1175–1187. <https://doi.org/10.1111/ecog.03684>

158 Galiana, N., Lurgi, M., Claramunt-López, B., Fortin, M.-J., Leroux, S., Cazelles, K., Gravel, D., & Montoya,  
159 J. M. (2018). The spatial scaling of species interaction networks. *Nature Ecology & Evolution*, 2(5),  
160 782–790. <https://doi.org/10.1038/s41559-018-0517-3>

161 Gravel, D., Baiser, B., Dunne, J. A., Kopelke, J.-P., Martinez, N. D., Nyman, T., Poisot, T., Stouffer, D. B.,  
162 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>

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>

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

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>

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>

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>

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>

Mora, B. 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>

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.

191 <https://doi.org/10.1016/j.tree.2015.03.014>

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

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

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

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

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

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

208 Pedersen, E. J., Thompson, P. L., Ball, R. A., Fortin, M.-J., Gouhier, T. C., Link, H., Moritz, C., Nenzen, H.,  
 209 Stanley, R. R. E., Taranu, Z. E., Gonzalez, A., Guichard, F., & Pepin, P. (2017). Signatures of the  
 210 collapse and incipient recovery of an overexploited marine ecosystem. *Royal Society Open Science*, 4(7),  
 211 170215. <https://doi.org/10.1098/rsos.170215>

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

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

218 Poisot, T., Stouffer, D. B., & Gravel, D. (2015). Beyond species: Why ecological interaction networks vary

219 through space and time. *Oikos*, 124(3), 243–251. <https://doi.org/10.1111/oik.01719>

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

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

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

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