Downscaling metawebs: propagation of uncertainties in species distribution and interaction probability

Gabriel Dansereau ^{1,2} Ceres Barros ³ Timothée Poisot ^{1,2}

Correspondance to:

Gabriel Dansereau — gabriel.dansereau@umontreal.ca

This work is released by its authors under a CC-BY 4.0 license

Last revision: September 12, 2023

¹ Université de Montréal ² Québec Centre for Biodiversity Sciences ³ University of British Columbia

Introduction

Sampling ecological networks in space and time is a challenging task as species interactions display high turnover and low encounter rates, which require large sampling efforts to properly document (Jordano 2016). Most studies on food webs have previously focused on local webs limited in size and extent, and are rarely replicated in space and time (Mestre et al. 2022). Interactions can show important variations in space (Poisot et al. 2015; **Zarnetske2017IntLan?**), yet available network data also show important geographical bias, limiting our ability to answer questions in many biomes and over broad spatial extents (Poisot et al. 2021). Moreover, global network monitoring is insufficient to properly describe and understand how ecosystems are reacting to global change (Windsor et al. 2023). As a result, there have been repeated calls for globally distributed interaction and network data and repeated sampling in time and space (Mestre et al. 2022; Windsor et al. 2023). 10 Approaches to predict species interactions (e.g., Morales-Castilla et al. 2015; Desjardins-Proulx et al. 2017) are 11 increasingly used as an alternative to determine potential interactions and can handle limited data to circumvent data scarcity (Strydom et al. 2021), but are rarely used to make explicitly spatial predictions. Given limited 13 resources, sampling can be optimized to assess targeted network properties (e.g., McLeod et al. 2021); yet, doing this across whole networks and various taxa over broad spatial scales remains a challenge. The metaweb is an increasingly used concept to address the issue of data scarcity, and it further holds potential 16 to analyse networks at large spatial extents. A metaweb contains all possible interactions between species found 17 in a given regional species pool (Dunne 2006). When assembled by integrating databases and computing tools, the metaweb allows to overcome sampling limitations to upscale network data to a global scale (Albouy2019MarFis?). Recent studies have focused on assembling metawebs for various taxa through 20 literature surveys and expert elicitation (European tetrapods, Maiorano et al. 2020) or using predictive tools (marine fish food web, Albouy2019MarFis?; Canadian mammals, Strydom et al. 2022a). However, the 22 metaweb holds more information than the possible interactions and is also key to analyse networks across space. 23 Empirical networks, which are local realizations of a regional metaweb (Poisot et al. 2012), inherit the metaweb structure with little influence from habitat and dynamical constraints (Saravia et al. 2022). Given this, Strydom 25 et al. (2022b) called the prediction of the metaweb structure the core goal of predictive network ecology and the 26 key to produce accurate downscaled and local predictions. Establishing or predicting the metaweb should 27 therefore be the first target for systems where we lack information about local realizations. This is not the same

as using interactions to improve predictions of species distributions as recent studies have done (for example,

- Moens et al. 2022; Poggiato et al. 2022; Lucas et al. 2023), although these are incredibly relevant and answer
- long-standing calls to include interactions within such models (Wisz et al. 2013). Instead, predicting networks
- 32 in space is a different task and it serves a different goal, focusing first on the distribution of networks and its
- drivers rather than on the distribution of species.
- Explicit spatial predictions such as downscaled metaweb predictions are essential as they will allow
- comparisons with extant work for species communities. Recent approaches to downscaling for European
- tetrapods combined the metaweb with species distribution maps to generate local assemblages (Braga et al.
- 2019; O'Connor et al. 2020; Galiana et al. 2021; Gaüzère et al. 2022). These downscaled assemblages allowed
- studying network structures in novel ways, for instance, assessing changes in food web structure across space
- ³⁹ (Braga et al. 2019) and the scaling of network area relationships (Galiana et al. 2021). Other examples have
- shown that the metaweb can be used to investigate large scale variation in food web structure, indicating high
- 41 geographical connections and heterogeneous robustness against species extinctions (marine fish food webs,
- 42 **Albouy2019MarFis?**). Further comparisons are relevant as they may go in unexpected directions and highlight
- new elements regarding network biogeography. For instance, Frelat et al. (2022) found a strong spatial coupling
- between community composition and food web structure but a temporal mismatch depending on the spatial
- scale. Poisot et al. (2017) found that interaction uniqueness captures more composition variability than
- 46 community uniqueness and that sites with exceptional compositions might not be the same for networks and
- 47 communities. Spatialized network data will allow these comparisons and allow identifying important
- 48 conservation targets for networks and whether they differ geographically from areas currently prioritized for
- ⁴⁹ biodiversity conservation.
- A key challenge remains in how to downscale a regional metaweb towards local network predictions reflecting
- the spatial variability of interactions. A potential limitation to previous downscaling approaches is that they
- assume interactions are constant across space, which ignores behaviour variability and does not consider the
- effect of environmental conditions on interaction realization (Braga et al. 2019). In contrast, recent studies
- argued that seeing interactions as probabilistic events (rather than binary ones) allows to account for their
- variability in space (Poisot et al. 2016) and that this should also be reflected in metawebs (Strydom et al.
- 56 2022b). Gravel et al. (2019) introduced a probabilistic framework describing how the metaweb can generate
- local realizations and showed how it could be used for interaction distribution modelling. This approach to
- downscaling is useful when combined with in situ observations of interactions and local networks to train
- interaction models (in this case with willow-galler-parasitoid networks). However, such data is rarely available

- across broad spatial extents (Hortal et al. 2015; Poisot et al. 2021; Windsor et al. 2023). Spatially replicated
- 61 interaction data required for such model is especially challenging to document with large food web systems such
- as European tetrapod and Canadian mammal metawebs (Maiorano et al. 2020; Strydom et al. 2022a). We
- 63 currently lack a downscaling framework that is both probabilistic and can be trained without replicated in situ
- 64 interaction data. Additionally, a probabilistic view can allow propagating uncertainty, which can play a key role
- in evaluating the quality of the predictions. Assessing model uncertainty would enable us to determine to which
- degree we should trust our predictions and to identify what to do to improve the current knowledge.
- 67 Here, we present a method to downscale a metaweb in space by spatially reconstructing local instances of a
- 68 probabilistic metaweb of Canadian mammals. We do so using a probabilistic approach to both species
- 69 distributions and interactions in a system without spatially replicated interaction data. We then explore how the
- ₇₀ spatial structure of the downscaled metaweb varies in space and how the uncertainty of interactions can be
- made spatially explicit. We further show that the downscaled metaweb can highlight important biodiversity
- areas and bring novel ecological insights compared to traditional community measures like species richness.

73 Methods

- Fig. 1 shows a conceptual overview of the methodological steps leading to the downscaled metaweb. The
- components were grouped as non-spatial and spatial inputs, localized site steps (divided into
- ₇₆ single-species-level, two-species-level, and network-level steps), and the final downscaled and spatialized
- metaweb. Throughout these steps, we highlight the importance of presenting the uncertainty of interactions and
- of their distribution in space. We argue that this requires adopting a probabilistic view and incorporating
- variation between scales.

[Figure 1 about here.]

81 Data

80

82 Metaweb

- The main source of interaction data was the metaweb for Canadian mammals from Strydom et al. (2022a),
- which is a-spatial, i.e., it represents interactions between mammals that can occur anywhere in Canada. The

- 85 species list for the Canadian metaweb was extracted from the International Union for the Conservation of
- Nature (IUCN) checklist (Strydom et al. 2022a). Briefly, the metaweb was developed using graph embedding
- and phylogenetic transfer learning based on the metaweb of European mammals, which is itself based on a
- comprehensive survey of interactions reported in the scientific literature (Maiorano et al. 2020). The Canadian
- metaweb is probabilistic, which has the advantage of reflecting the likelihood of an interaction taking place
- 90 given the phylogenetic and trait match between two species. This allows incorporating interaction variability
- between species (i.e., taking into account that two species may not always interact whenever or wherever they
- occur); however, we highlight that other factors beyond trait and phylogenetic matching (e.g., population
- densities) will also contribute to observed interaction frequencies.

94 Species occurrences

- The downscaling of the metaweb involved combining it with species occurrence and environmental data. First,
- we extracted species occurrences from the Global Biodiversity Information Facility (GBIF; www.gbif.org) for
- 97 the Canadian mammals after reconciling species names between the Canadian metaweb and GBIF using the
- 98 GBIF Backbone Taxonomy (GBIF Secretariat 2021). This step removed potential duplicates by combining
- 99 species listed in the Canadian metaweb which were considered as a single entity by GBIF. We collected
- occurrences for the updated species list (159 species) using the GBIF download API on October 21st 2022
- (GBIF.org 2022). We restricted our query to occurrences with coordinates between longitudes 175°W to 45°W
- and latitudes 10°N to 90°N. This was meant to collect training data covering a broader range than our prediction
- target (Canada only) and include observations in similar environments. Then, since GBIF observations
- represent presence-only data and most predictive models require absence data, we generated pseudo-absence
- data using the surface range envelope method, which selects random non-observed sites within the spatial range
- delimited by the presence data (Barbet-Massin *et al.* 2012).

107 Environmental data

- We used species distribution models (SDMs, Guisan & Thuiller 2005) to project Canadian mammal habitat
- suitability across the country, which we treated as information on potential distribution. For each species, we
- related occurrences and pseudo-absences with 19 bioclimatic variables from CHELSA (Karger et al. 2017) and
- 12 consensus land-cover variables from EarthEnv (Tuanmu & Jetz 2014). The CHELSA bioclimatic variables

(bio1-bio19) represent various measures of temperature and precipitation (e.g., annual averages, monthly 112 maximum or minimum, seasonality) and are available for land areas across the globe. We used the most recent 113 version, the CHELSA v2.1 dataset (Karger et al. 2021), and subsetted it to land surfaces only using the 114 CHELSA v1.2 (Karger et al. 2018), which does not cover open water. The EarthEnv land-cover variables represent classes such as Evergreen broadleaf trees, Cultivated and managed vegetation, Urban/Built-up, and 116 Open Water. Values range between 0 and 100 and represent the consensus prevalence of each class in 117 percentage within a pixel (hereafter called sites). We coarsened both the CHELSA and EarthEnv data from their original 30 arc-second resolution to a 2.5 arc-mininute one (around 4.5 km at the Equator) using GDAL 119 (GDAL/OGR contributors 2021). This resolution compromised capturing both local variations and broad scale 120 patterns, while limiting computation costs to a manageable level as memory requirements increase rapidly with 121 spatial resolution.

123 Analyses

Species distribution models

Our selection criteria for choosing an SDM algorithm was to have a method that generated probabilistic results (similar to Gravel et al. 2019), including both a probability of occurrence for a species in a specific site and the uncertainty associated with the prediction. These were crucial to obtaining a probabilistic version of the 127 metaweb as they were used to create spatial variations in the localized interaction probabilities (see next 128 section). One suitable method for this is Gradient Boosted Trees with a Gaussian maximum likelihood from the EvoTrees.jl Julia package (https://github.com/Evovest/EvoTrees.jl). This method returns a prediction for 130 every site with an average value and a standard deviation, which we used as a measure of uncertainty to build a 131 Normal distribution for the probability of occurrence of a given species at all sites (represented as probability distributions on Fig. 1). We trained models across the extent chosen for occurrences (longitudes 175°W to 133 45°W and latitudes 10°N to 90°N), then predicted species distributions only for Canada. We used the 2021 134 Census Boundary Files from Statistics Canada (Statistics Canada 2022) to set the boundaries for our 135 predictions, which gave us 970,698 sites in total.

Building site-level instances of the metaweb

The next part of the method was the localized steps which produce local metawebs for every site. This 138 component was divided into single-species, two-species, and network-level steps (Localized steps box on Fig. 1). 139 The single-species steps represented four possible ways to account for uncertainty in the species distributions 140 and bring variation to the spatial metaweb. We explored four different options to select a value (P(occurrence); 141 Fig. 1) from the occurrence distributions obtained in the previous steps: 1) taking the mean from the distribution as the probability of occurrence (option 1 on Fig. 1); 2) converting the mean value to a binary one 143 using a specific threshold per species (option 2); 3) sampling a random value within the Normal distribution 144 (option 3); or 4) converting a random value into a binary result (option 4, using a separate draw from option 3 and the same threshold as in option 2). The threshold (τ on Fig. 1) used was the value that maximized Youden's J informedness statistic (Youden 1950), the same metric used by Strydom et al. (2022a) at an intermediate step 147 while building the metaweb. The four sampling options were intended to explore how uncertainty and variation 148 in the species distributions can affect the metaweb result. We expected thresholding to have a more pronounced 149 effect on network structure as it should reduce the number of links by removing many of the rare interactions 150 (Poisot et al. 2016). Meanwhile, we expected random sampling to create spatial heterogeneity compared to the 151 mean probabilities, as including some extreme values should confound the potential effects of environmental gradients. We chose option 1 as the default to present results as it is intuitive and essentially represents the 153 result of a probabilistic SDM (as in Gravel et al. 2019). 154 Next, the two-species steps were aimed at assigning a probability of observing an interaction between two 155 species in a given site. For each species pair, we multiplied the product of the two species' occurrence 156 probabilities (P(co-occurrence); Fig. 1) (obtained using the one of the sampling options above) by their 157 interaction probability in the Canadian metaweb. For cases where species in the Canadian metaweb were 158 considered as the same species by the GBIF Backbone Taxonomy (the reconciliation step mentioned earlier), we 159 used the highest interaction probabilities involving the duplicated species. 160 The network-level steps then created the probabilistic metaweb for the site. We assembled all the local 161 interaction probabilities (from the two-species steps) into a probabilistic network (Poisot et al. 2016). We then 162 sampled several random network realizations to represent the potential local realization process (Poisot et al. 2015). This resulted in a distribution of localized networks, which we averaged over the number of simulations to obtain a single probabilistic network for the site.

166 Downscaled metaweb

The final output of our method was the downscaled metaweb, which contains a localized probabilistic metaweb 167 in every site across the study area (Outputs box on Fig. 1). A metaweb essentially serves to set an upper bound 168 on the potential interactions (Strydom et al. 2022b); therefore, the downscaled metaweb is a refined upper boundary at the local scale taking into account co-occurrences. It is still potential in nature and differs from a 170 local realization, from which it should have a different structure. Nonetheless, from the downscaled metaweb we 171 can create maps of network properties (e.g. number of links, connectance) measured on the local probabilities, display their spatial distribution, and compute some traditional community-level measures such as species 173 richness. We chose to compute and display the expected number of links (measured on probabilistic networks 174 following Poisot et al. 2016; also see Gravel et al. 2019 for a similar example) as its relationship with species richness has been highlighted in a spatial context in recent studies (Galiana et al. 2021; Galiana2022EcoNet?). 176 We also computed the uncertainty associated with the community and network measurements (richness 177 variance and link variance, respectively) and compared their spatial distribution (see Supplementary Material).

179 Analyses of results by ecoregions

Since both species composition and network summary values display a high spatial variation and complex patterns, we simplified the representation of their distribution by grouping sites by ecoregion, as species and interaction composition have been shown to differ between ecoregions across large spatial scales (Martins *et al.* 2022). To do so, we rasterized the Canadian subset of the global map of ecoregions from Dinerstein *et al.* (2017; also used by Martins *et al.* 2022), which resulted in 44 different ecoregions. For every measure we report (e.g. species richness, number of links), we calculated the median site value for each ecoregion. We also measured within-ecoregion variation as the 89% interquantile range of the site values in each ecoregion (threshold chosen to avoid confusion with conventional significance tests; McElreath 2020).

Analyses of ecological uniqueness

We compared the compositional uniqueness of the networks and the communities to assess whether they indicated areas of exceptional composition. We measured uniqueness using the local contributions to beta diversity (LCBD, Legendre & De Cáceres 2013), which identify sites with exceptional composition by quantifying how much one site contributes to the total variance in the community composition. While many

studies used LCBD values to evaluate uniqueness on local scales or few study sites (for example, da Silva & Hernández 2014; Heino & Grönroos 2017), recent studies used the measure on predicted species compositions 194 over broad spatial extents and a large number of sites (Vasconcelos et al. 2018; Dansereau et al. 2022). LCBD 195 values can also be used to measure uniqueness for networks by computing the values over the adjacency matrix, which has been shown to capture more unique sites and uniqueness variability than through species 197 composition (Poisot et al. 2017). Here, we measured and compared the uniqueness of our localized community 198 and network predictions. For species composition, we assembled a site-by-species community matrix with the 199 probability of occurrence at every site from the species distribution models. For network composition, we 200 assembled a site-by-interaction matrix with the localized interaction values from the spatial probabilistic 201 metaweb. We applied the Hellinger transformation on both matrices and computed the LCBD values from the 202 total variance in the matrices (Legendre & De Cáceres 2013). High LCBD values indicate a high contribution to the overall variance and a unique species or interaction composition compared to other sites. Since values 204 themselves are very low given our high number of sites (as in Dansereau et al. 2022), what matters primarily is 205 the magnitude of the difference between the sites. Given this, we divided values by the maximum value in each matrix (species or network) and suggest that these should be viewed as relative contributions compared to the 207 highest observed contribution. As with other measures, we then summarized the local uniqueness values by 208 ecoregion by taking the median LCBD value and measuring the 89% interquantile range within all ecoregions. We used Julia v1.9.0 (Bezanson et al. 2017) to implement all our analyses. We used packages GBIF.jl 210 (Dansereau & Poisot 2021) to reconcile species names using the GBIF Backbone Taxonomy, 211 SpeciesDistributionToolkit.jl (https://github.com/PoisotLab/SpeciesDistributionToolkit.jl) to handle raster layers, species occurrences and generate pseudoabsences, EvoTrees.jl 213 (https://github.com/Evovest/EvoTrees.jl) to perform the Gradient Boosted Trees, EcologicalNetworks.jl 214 (Poisot et al. 2019) to analyse network and metaweb structure, and Makie.jl (Danisch & Krumbiegel 2021) to produce figures. Our data sources (CHELSA, EarthEnv, Ecoregions) were all unprojected and we did not use a 216 projection in our analyses, but we displayed the results using a Lambert conformal conic projection more 217 appropriate for Canada using GeoMakie.jl (https://github.com/MakieOrg/GeoMakie.jl). All the code used to implement our analyses is available on GitHub (https://github.com/PoisotLab/SpatialProbabilisticMetaweb) and 219 includes instructions on how to run a smaller example at a coarser resolution. Note that running our analyses at 220 full scale is resource and memory intensive and required the use of compute clusters provided by Calcul Québec and the Digital Research Alliance of Canada. Final scripts ran for 0.0109 CPU core-years and peaked at 460 GB

24 Results

Our method allowed us to display the spatial distribution of ecoregion-level community measures (here expected species richness) and network measures (expected number of links; Fig. 2). We highlight that the community and network-level measures presented here are not actual predictions of the measure itself (e.g., we 227 do not present a prediction of actual species richness at each location). Instead, they are the reflection of these 228 metrics from the localized predictions of the communities and networks obtained from the downscaling of the metaweb, then summarized for the ecoregions (median value). Expected ecoregion richness (Fig. 2A) and 230 expected number of links (Fig. 2B) displayed similar distributions with a latitudinal gradient and higher values 231 in the south. However, within-ecoregion variability was distributed differently, as some ecoregions along the coasts displayed higher interquantile ranges while ecoregions around the southern border displayed narrower 233 ones (Fig. 2C-D). All results shown are based on the first sampling strategy (option 1) mentioned in the 234 Building site-level instances of the metaweb section, where species occurrence probabilities were taken as the 235 mean value of the distribution (results for other sampling strategies are discussed in Supplementary Material).

[Figure 2 about here.]

Direct comparison of the spatial distributions of species richness and expected number of links showed some areas with mismatches, both regarding the median estimates and regarding the within-ecoregion variability 239 (Fig. 3). Median values for the ecoregions showed a similar bivariate distribution with ecoregions in the south mostly displaying high species richness and a high number of links (Fig. 3A). The northernmost ecoregions 241 (Canadian High Artic Tundra and Davis Highlands Tundra) displayed higher richness (based on the quantile 242 rank) compared to the number or links. Inversely, ecoregions further south (Canadian Low Artic Tundra, 243 Northern Canadian Shield Taiga, Southern Hudson Bay Taiga) ranked higher for the number of links than for species richness. On the other hand, within-ecoregion variability showed different bivariate relationships and a 245 less constant latitudinal gradient (Fig. 3B). This indicates that richness and links do not co-vary completely 246 (i.e. their variability is not closely connected) although they may show similar distributions for median values.

237

Our results also indicate a mismatch between the uniqueness of communities and networks (Fig. 4). Uniqueness was higher mostly in the north and along the south border for communities, but only in the north for networks 250 (Fig. 4A-B). Consequently, ecoregions with both unique community composition and unique network 251 composition were mostly in the north (Fig. 4C). Meanwhile, some areas were unique for one element but not the other. For instance, the New England-Acadian forests ecoregion (south-east, near 70°W and 48°N) had a highly 253 unique species composition but a more common network composition (Fig. 4C). Opposite areas with unique 254 network compositions only were observed at higher between latitudes 52°N and 70°N (Eastern Canadian Shield 255 Taiga, Northern Canadian Shield Taiga, Canadian Low Artic Tundra). Also, network uniqueness values for 256 ecoregions spanned a narrower range between the 44 ecoregions than species LCBD values (Fig. 4D, left). 257 Within-ecoregion variation was also lower for network values with generally lower 89% interquantile ranges among the site-level LCBD values (Fig. 4D, right). Moreover, mismatched sites (unique for only one element) formed two distinct groups when evaluating the relationship between species richness and the number of links 260 (see Supplementary Material). The areas only unique for their species composition had both a high richness and 261 number of links. On the other hand, the sites only unique for their networks had both lower richness and a lower number of links, although they were not the sites with the lowest values for both. 263

[Figure 4 about here.]

5 Discussion

264

Our approach presents a way to downscale a metaweb, produce localized predictions using probabilistic networks as inputs and outputs, and incorporatie uncertainty, as called for by Strydom et al. (2022b). It gives us an idea of what local metawebs or networks could look like in space, given the species distributions and their variability, as well as the uncertainty around the interactions. We also provide the first spatial representation of 269 the metaweb of Canadian mammals (Strydom et al. 2022a) and a probabilistic equivalent to how the European tetrapod metaweb (Maiorano et al. 2020) was used to predict localized networks in Europe (Braga et al. 2019; 271 O'Connor et al. 2020; Galiana et al. 2021; Gaüzère et al. 2022; Botella et al. 2023). Therefore, our approach 272 could open similar possibilities of investigations in North America with food webs of Canadian mammals, for 273 instance on the structure of food webs over space (Braga et al. 2019) and on the effect of land-use intensification on food webs (Botella et al. 2023). Interesting research areas could include assessing climate 275 change impacts on network structure or investigating linkages between network structure and stability.

Moreover, since our approach is probabilistic, it does not assume species interact whenever they co-occur, and incorporates variability based on environmental conditions, which could lead to different results by introducing 278 a different association between species richness and network properties. Galiana et al. (2021) found that species 279 richness had a large explanatory power over network properties but mentioned it could potentially be due to interactions between species being fixed in space. Here, we found mismatches in the distribution of species 281 richness and interactions, and especially regarding their within-ecoregion variability (Fig. 3), highlighting that 282 interactions might vary differently than species distributions in space. Network measures (links on Fig. 3A) 283 were also lower in the north, contrarily to previous studies where connectance was higher in the north, although 284 those were in Europe for all tetrapods (Braga et al. 2019; Galiana et al. 2021) and willow-galler-parasitoid 285 networks (Gravel et al. 2019). Further research should investigate why these results might be different between the two continents and whether it is due to the methodology, data, or biogeographical processes. Our LCBD and uniqueness results highlighted that areas with unique network composition might differ from sites with unique species composition. In other words, the joint distribution of community and network uniqueness highlights different diversity hotspots. Poisot et al. (2017) showed a similar result with host-parasite 290 communities of rodents and ecto-fleas. Our results further show how these differences could be distributed 291 across ecoregions and a broad spatial extent. Areas unique for only one element (species or network composition) differed in their combination of species richness and number of links (supplementary material), 293 with species-unique sites displaying high values of both measures and network-unique sites displaying low 294 values. Moreover, LCBD scores essentially highlight variability hotspots and are a measure of the variance of community or network structure. Here they also serve as an inter-ecoregion variation measure which can be compared to the within-ecoregion variation highlighted by the interquantile ranges. The narrower range of 297 values for network LCBD values and the lower IQR values indicate that both the inter-ecoregion and within-ecoregion variation are lower for network than for species (Fig. 4). Additionally, higher values for network LCBD also indicate that most ecoregions can hold ecologically unique sites. 300 When to use the method we presented here will depend on the availability of interaction data or existing metawebs and on the intent to incorporate interaction variability, as well as ecoregion-level variability. In 302 systems where in situ interaction and network data are available, the approach put forward by Gravel et al. 303 (2019) achieves a similar purpose as we attempted here, but is more rigourous and allows modelling the effect of the environment on the interactions. Without such data, establishing or predicting the metaweb should be the first step towards producing localized predictions (Strydom et al. 2022b). Well-documented binary metawebs

such as the European tetrapod metaweb could be partly be combined with our approach if used with
probabilistic SDMs and summarized by ecoregions (as they would only lack an initial probabilistic metaweb,
but would still obtain a more probabilistic output). Our approach will essentially differ from previous attempts
in how it perceives uncertainty and variability. For instance, rare interactions should not be over-represented
(Poisot *et al.* 2016) and should have lesser effects over computed network measures. Summarizing results by
ecoregion allows showing variation within and between ecologically-meaningful biogeographic boundaries
(Martins *et al.* 2022), which as our results showed is not constant across space and can help identify contrasting
diversity hotspots.

5 References

- Barbet-Massin, M., Jiguet, F., Albert, C.H. & Thuiller, W. (2012). Selecting pseudo-absences for species distribution models: How, where and how many? *Methods in Ecology and Evolution*, 3, 327–338.
- Bezanson, J., Edelman, A., Karpinski, S. & Shah, V.B. (2017). Julia: A fresh approach to numerical computing.

 SIAM Review, 59, 65–98.
- Botella, C., Gaüzère, P., O'Connor, L., Ohlmann, M., Renaud, J., Dou, Y., et al. (2023). Land-use intensity influences European tetrapod food-webs (Preprint). Authorea.
- Braga, J., Pollock, L.J., Barros, C., Galiana, N., Montoya, J.M., Gravel, D., *et al.* (2019). Spatial analyses of multi-trophic terrestrial vertebrate assemblages in Europe. *Global Ecology and Biogeography*, 28, 1636–1648.
- da Silva, P.G. & Hernández, M.I.M. (2014). Local and regional effects on community structure of dung beetles in a mainland-island scenario. *PLOS ONE*, 9, e111883.
- Danisch, S. & Krumbiegel, J. (2021). Makie.jl: Flexible high-performance data visualization for Julia. *Journal*of Open Source Software, 6, 3349.
- Dansereau, G., Legendre, P. & Poisot, T. (2022). Evaluating ecological uniqueness over broad spatial extents using species distribution modelling. *Oikos*, 2022, e09063.
- Dansereau, G. & Poisot, T. (2021). SimpleSDMLayers.jl and GBIF.jl: A framework for species distribution modeling in Julia. *Journal of Open Source Software*, 6, 2872.
- Desjardins-Proulx, P., Laigle, I., Poisot, T. & Gravel, D. (2017). Ecological interactions and the Netflix problem. *PeerJ*, 5, e3644.
- Dinerstein, E., Olson, D., Joshi, A., Vynne, C., Burgess, N.D., Wikramanayake, E., *et al.* (2017). An Ecoregion-Based Approach to Protecting Half the Terrestrial Realm. *BioScience*, 67, 534–545.
- Dunne, J. (2006). The network structure of food webs. In: *Ecological Networks: Linking Structure to Dynamics*in Food Webs. pp. 27–86.
- Frelat, R., Kortsch, S., Kröncke, I., Neumann, H., Nordström, M.C., Olivier, P.E.N., *et al.* (2022). Food web structure and community composition: A comparison across space and time in the North Sea. *Ecography*, 2022.

- Galiana, N., Barros, C., Braga, J., Ficetola, G.F., Maiorano, L., Thuiller, W., *et al.* (2021). The spatial scaling of food web structure across European biogeographical regions. *Ecography*, 44, 653–664.
- Gaüzère, P., O'Connor, L., Botella, C., Poggiato, G., Münkemüller, T., Pollock, L.J., *et al.* (2022). The diversity of biotic interactions complements functional and phylogenetic facets of biodiversity. *Current Biology*.
- 346 GBIF Secretariat. (2021). GBIF Backbone Taxonomy.
- 347 GBIF.org. (2022). GBIF occurrence download.
- GDAL/OGR contributors. (2021). *GDAL/OGR geospatial data abstraction software library*. Manual. Open
 Source Geospatial Foundation.
- Gravel, D., Baiser, B., Dunne, J.A., Kopelke, J.-P., Martinez, N.D., Nyman, T., *et al.* (2019). Bringing Elton and Grinnell together: A quantitative framework to represent the biogeography of ecological interaction networks. *Ecography*, 42, 401–415.
- Guisan, A. & Thuiller, W. (2005). Predicting species distribution: Offering more than simple habitat models. *Ecology Letters*, 8, 993–1009.
- Heino, J. & Grönroos, M. (2017). Exploring species and site contributions to beta diversity in stream insect assemblages. *Oecologia*, 183, 151–160.
- 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, 523–549.
- Jordano, P. (2016). Sampling networks of ecological interactions. Functional Ecology, 30, 1883–1893.
- Karger, D.N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R.W., *et al.* (2017). Climatologies at high resolution for the earth's land surface areas. *Scientific Data*, 4, 170122.
- Karger, D.N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R.W., *et al.* (2018). Data from:

 Climatologies at high resolution for the earth's land surface areas.
- Karger, D.N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R.W., *et al.* (2021). Climatologies at high resolution for the earth's land surface areas.
- Legendre, P. & De Cáceres, M. (2013). Beta diversity as the variance of community data: Dissimilarity coefficients and partitioning. *Ecology Letters*, 16, 951–963.

- Lucas, P., Thuiller, W., Talluto, M., Polaina, E., Albrecht, J., Selva, N., et al. (2023). Including biotic
- interactions in species distribution models improves the understanding of species niche: A case of study
- with the brown bear in Europe.
- Maiorano, L., Montemaggiori, A., Ficetola, G.F., O'Connor, L. & Thuiller, W. (2020). TETRA-EU 1.0: A
- species-level trophic metaweb of European tetrapods. Global Ecology and Biogeography, 29, 1452–1457.
- Martins, L.P., Stouffer, D.B., Blendinger, P.G., Böhning-Gaese, K., Buitrón-Jurado, G., Correia, M., et al.
- (2022). Global and regional ecological boundaries explain abrupt spatial discontinuities in avian frugivory
- interactions. *Nature Communications*, 13, 6943.
- McElreath, R. (2020). Statistical rethinking: A bayesian course with examples in R and Stan. Second.
- Chapman and Hall/CRC, New York.
- McLeod, A., Leroux, S.J., Gravel, D., Chu, C., Cirtwill, A.R., Fortin, M.-J., et al. (2021). Sampling and
- asymptotic network properties of spatial multi-trophic networks. *Oikos*, 130, 2250–2259.
- Mestre, F., Gravel, D., García-Callejas, D., Pinto-Cruz, C., Matias, M.G. & Araújo, M.B. (2022). Disentangling
- food-web environment relationships: A review with guidelines. *Basic and Applied Ecology*, 61, 102–115.
- Moens, M., Biesmeijer, J., Huang, E., Vereecken, N. & Marshall, L. (2022). The importance of biotic
- interactions in distribution models depends on the type of ecological relations, spatial scale and range.
- Morales-Castilla, I., Matias, M.G., Gravel, D. & Araújo, M.B. (2015). Inferring biotic interactions from
- proxies. Trends in Ecology & Evolution, 30, 347–356.
- O'Connor, L.M.J., Pollock, L.J., Braga, J., Ficetola, G.F., Maiorano, L., Martinez-Almoyna, C., et al. (2020).
- Unveiling the food webs of tetrapods across Europe through the prism of the Eltonian niche. *Journal of*
- 389 Biogeography, 47, 181–192.
- Poggiato, G., Andréoletti, J., Shirley, L. & Thuiller, W. (2022). Integrating food webs in species distribution
- models improves ecological niche estimation and predictions (Preprint). Authorea.
- Poisot, T., Bélisle, Z., Hoebeke, L., Stock, M. & Szefer, P. (2019). EcologicalNetworks.jl: Analysing ecological
- networks of species interactions. *Ecography*, 42, 1850–1861.
- Poisot, T., Bergeron, G., Cazelles, K., Dallas, T., Gravel, D., MacDonald, A., et al. (2021). Global knowledge
- gaps in species interaction networks data. Journal of Biogeography, 48, 1552–1563.

- Poisot, T., Canard, E., Mouillot, D., Mouquet, N. & Gravel, D. (2012). The dissimilarity of species interaction networks. *Ecology Letters*, 15, 1353–1361.
- 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, 303–312.
- Poisot, T., Guéveneux-Julien, C., Fortin, M.-J., Gravel, D. & Legendre, P. (2017). Hosts, parasites and their interactions respond to different climatic variables. *Global Ecology and Biogeography*, 26, 942–951.
- Poisot, T., Stouffer, D.B. & Gravel, D. (2015). Beyond species: Why ecological interaction networks vary through space and time. *Oikos*, 124, 243–251.
- Saravia, L.A., Marina, T.I., Kristensen, N.P., De Troch, M. & Momo, F.R. (2022). Ecological network

 assembly: How the regional metaweb influences local food webs. *Journal of Animal Ecology*, 91, 630–642.
- Statistics Canada. (2022). *Boundary files, reference guide second edition, Census year 2021*. Second edition.

 Statistics Canada = Statistique Canada, Ottawa.
- Strydom, T., Bouskila, S., Banville, F., Barros, C., Caron, D., Farrell, M.J., *et al.* (2022a). Food web reconstruction through phylogenetic transfer of low-rank network representation. *Methods in Ecology and Evolution*, 13, 2838–2849.
- Strydom, T., Bouskila, S., Banville, F., Barros, C., Caron, D., Farrell, M.J., *et al.* (2022b). Predicting metawebs:

 Transfer of graph embeddings can help alleviate spatial data deficiencies.
- Strydom, T., Catchen, M.D., Banville, F., Caron, D., Dansereau, G., Desjardins-Proulx, P., et al. (2021). A
 roadmap towards predicting species interaction networks (across space and time). Philosophical
 Transactions of the Royal Society B: Biological Sciences, 376, 20210063.
- Tuanmu, M.-N. & Jetz, W. (2014). A global 1-km consensus land-cover product for biodiversity and ecosystem modelling. *Global Ecology and Biogeography*, 23, 1031–1045.
- Vasconcelos, T.S., Nascimento, B.T.M. do & Prado, V.H.M. (2018). Expected impacts of climate change threaten the anuran diversity in the Brazilian hotspots. *Ecology and Evolution*, 8, 7894–7906.
- Windsor, F.M., van den Hoogen, J., Crowther, T.W. & Evans, D.M. (2023). Using ecological networks to answer questions in global biogeography and ecology. *Journal of Biogeography*, 50, 57–69.
- Wisz, M.S., Pottier, J., Kissling, W.D., Pellissier, L., Lenoir, J., Damgaard, C.F., *et al.* (2013). The role of biotic interactions in shaping distributions and realised assemblages of species: Implications for species

- distribution modelling. *Biological Reviews*, 88, 15–30.
- Youden, W.J. (1950). Index for rating diagnostic tests. *Cancer*, 3, 32–35.

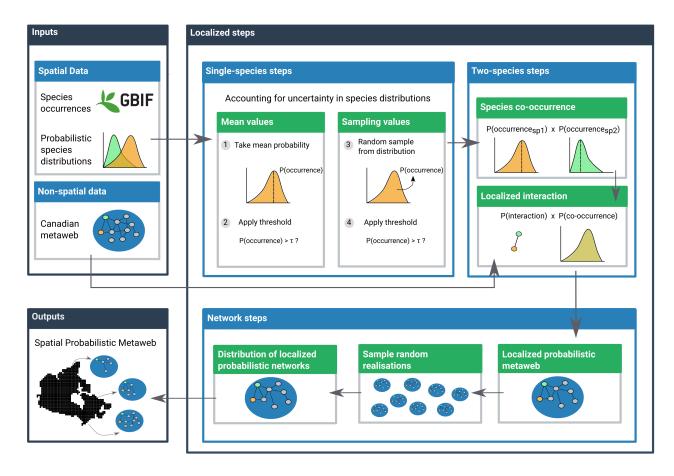


Figure 1: Conceptual figure of the workflow to obtain the spatial probabilistic metaweb (Chapter 1). The workflow has three components: the inputs, the localized steps, and the final spatial output. The inputs are composed of the spatial data (data with information in every cell) and the non-spatial data (constant for all of Canada). The localized steps use these data and are performed separately in every cell, first at a single-species level (using distribution data), then for every species pair (adding interaction data from the metaweb), and finally at the network level by combining the results of all species pairs. The final output coming out of the network-level steps contains a spatialized probabilistic metaweb for every cell across the study extent.

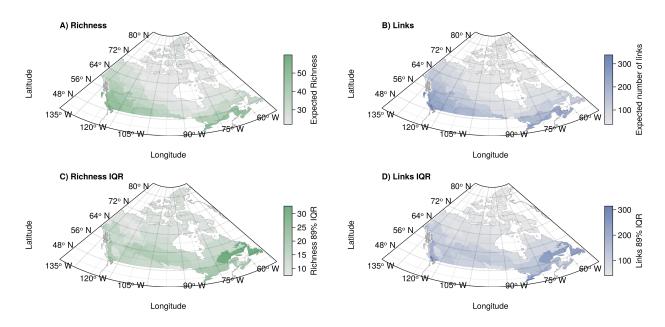


Figure 2: (A-B) Example of a community measure (A, expected species richness) and a network one (B, expected number of links). Both measures are assembled from the predicted probabilistic communities and networks, respectively. Values are first measured separately for all sites, then the median value is taken to represent the ecoregion-level value. (C-B) Representation of the 89% interquantile range of values within the ecoregion for expected richness (C) and expected number of links (D).

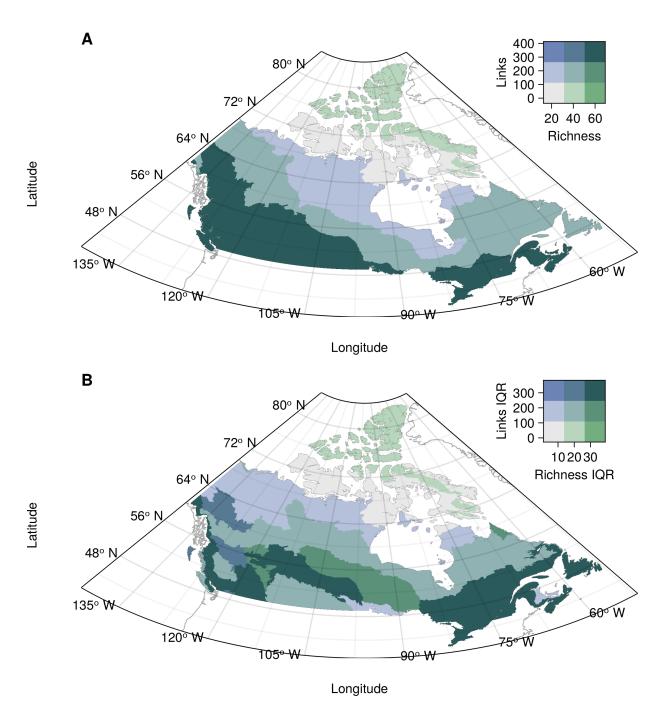


Figure 3: Bivariate relationship between community and network measures for the median ecoregion value (A) and the within-ecoregion 89% interquantile range (B). Values are grouped into three quantiles separately for each variable. The colour combinations represent the nine possible combinations of quantiles. Species richness (horizontal axis) goes left to right from low (light grey, bottom left) to high (green, bottom right). The number of links goes bottom-up from low (light grey, bottom left) to high (blue, top left).

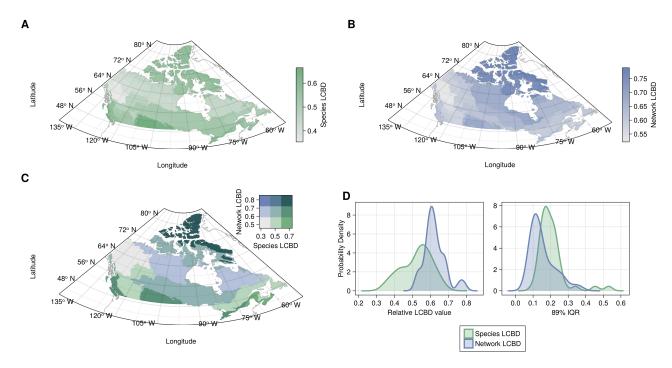


Figure 4: (A-B) Representation of the ecoregion uniqueness values based on species composition (a) and network composition (b). LCBD values were first computed across all sites and scaled relative to the maximum value observed. The ecoregion LCBD value is the median value for the sites in the ecoregion. (C) Bivariate representation of species and network composition LCBD. Values are grouped into three quantiles separately for each variable. The colour combinations represent the nine possible combinations of quantiles. The species uniqueness (horizontal axis) goes left to right from low uniqueness (light grey, bottom left) to high uniqueness (green, bottom right). The network composition uniqueness goes bottom-up from low uniqueness (light grey, bottom left) to high uniqueness (blue, top left). (D) Probability densities for the ecoregion LCBD values for species and network LCBD (left), highlighting the variability of the LCBD between ecoregions, and the 89% interquartile range of the values within each ecoregion (right), highlighting the variability within the ecoregions.