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

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Introduction

Sampling species interactions and ecological networks in repeated locations in space and time is a challenging task (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), 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 undestand how ecosystems are reacting to global change (Windsor et al. 2023). Predictive approaches are increasingly used to predict species interactions (Morales-Castilla et al. 2015; e.g. Desjardins-Proulx et al. 2017) and can handle limited data to circumvent data scarcity (Strydom et al. 2021), but they are rarely used to make explicitly spatial predictions. 10 As a result, there have been repeated calls for globally distributed interaction and network data and repeated 11 samplings in time and space (Poisot et al. 2021; Mestre et al. 2022; Windsor et al. 2023). The metaweb is an increasingly used concept to address the issue of data scarcity, and it further holds potential 13 to analyse networks at large spatial extents. A metaweb contains all the possible interactions between the species found in a given regional species pool (Dunne 2006). Recent studies have focused on assembling metawebs for 15 various taxa through extensive literature surveys (European tetrapods, Maiorano et al. 2020) or using predictive 16 tools (Canadian mammals, Strydom et al. 2022a). In comparison, empirical networks are local realizations of a 17 regional metaweb (Poisot et al. 2012, 2015) and inherit the metaweb structure with little influence from habitat and dynamical constraints (Saravia et al. 2022). Given this, Strydom et al. (2022b) called the prediction of the metaweb structure the core goal of predictive network ecology and the key to produce accurate downscaled and 20 local predictions. Establishing or predicting the metaweb should 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 22 species distributions as recent studies have done (Moens et al. 2022; for example, 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 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. A key challenge remains in how to downscale a regional metaweb towards local network predictions. Gravel et al. (2019) introduced a mathematical 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 (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 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). In contrast, 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). A potential limitation to this
- approach is that is assumes that 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). This is
- an advantage of the probabilistic framwork put forward by Gravel et al. (2019) and absent from the European
- 40 metaweb studies, as treating interactions as probabilistic events allows to account for their variability in space
- Strydom et al. (2022b). We currently lack a downscaling framework that is both probabilistic and does not
- require in situ data. Additionally, a probabilistic view can allow propagating uncertainty, which can play a key
- role in evaluating the quality of the predictions. Moreover, assessing model uncertainty would enable us to
- assess to which degree we should trust our predictions and to identify what to do to improve the current
- 45 knowledge. For instance, we could locate where our knowledge and models are the most uncertain and
- determine new sampling sites or areas where repeated sampling is necessary.
- 47 Explicit spatial predictions such as downscaled metaweb predictions are essential as they will allow
- 48 comparisons with extant work for species communities. Previous downscaling attempts allowed studying
- 49 network structures in novel ways, for instance, assessing changes in food web structure across space (Braga et
- ₅₀ al. 2019), the scaling of network area relationships (Galiana et al. 2021), or how sampling effort affects
- measured network structure (McLeod et al. 2021). Further comparisons are relevant as they may go in
- ⁵² unexpected directions and highlight new elements regarding network biogeography. For instance, Frelat *et al.*
- 53 (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 community uniqueness and that sites with exceptional compositions might not be
- the same for networks and communities. Spatialized network data will allow these comparisons and allow
- 57 identifying important conservation targets for networks and whether they differ geographically from areas
- 58 currently prioritized for biodiversity conservation.
- Here, we present a method to downscale a metaweb in space by spatially reconstructing local instances of a

- ₆₀ probabilistic metaweb of Canadian mammals. We do so using a probabilistic approach to both species
- 61 distributions and interactions in a system without spatially replicated interaction data. We then explore how the
- 52 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.

Methods

- ⁶⁶ 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 steps (divided into 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.]

Non-spatial inputs

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- The main source of interaction data was the metaweb for Canadian mammals from Strydom et al. (2022a),
- vhich is a-spatial, i.e., it represents interactions between mammals that can occur anywhere in Canada. The
- 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
- 78 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
- 80 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
- ₈₂ occur); however, we highlight that other factors beyond trait and phylogenetic matching (e.g., population
- densities) will also contribute to observed interaction probabilities.

84 Spatial inputs

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 the Canadian mammals after reconciling species names between the Canadian metaweb and GBIF using the GBIF Backbone Taxonomy (GBIF Secretariat 2021). Doing so, we removed potential duplicates where species listed in the Canadian metaweb are considered as a single entity by GBIF. We collected occurrences for our 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 94 method available in SimpleSDMLayers. jl (Dansereau & Poisot 2021). This method generates pseudo-absences by selecting random non-observed sites within the spatial range delimited by the presence data (Barbet-Massin et al. 2012). 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 100 12 consensus land-cover variables from EarthEnv (Tuanmu & Jetz 2014). The CHELSA bioclimatic variables 101 (bio1-bio19) represent various measures of temperature and precipitation (e.g., annual averages, monthly 102 maximum or minimum, seasonality) and are available for land areas across the globe. We used the most recent 103 version, the CHELSA v2.1 dataset (Karger et al. 2021), and subsetted it to land surfaces only using the 104 CHELSA v1.2 (Karger et al. 2018), which does not cover open water. The EarthEnv land-cover variables 105 represent classes such as Evergreen broadleaf trees, Cultivated and managed vegetation, Urban/Built-up, and 106 Open Water. Values range between 0 and 100 and represent the consensus prevalence of each class in 107 percentage within a pixel (hereafter considered as sites). We coarsened both the CHELSA and EarthEnv data 108 from their original 30 arc-second resolution to a 2.5 arc-mininute one (around 4.5 km at the Equator) using GDAL (GDAL/OGR contributors 2021). This resolution compromised capturing both local variations and 110 broad scale patterns, while limiting computation costs to a manageable level as memory requirements increase 111 rapidly with spatial resolution.

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 114 uncertainty associated with the prediction. These were crucial to obtaining a probabilistic version of the 115 metaweb as they were used to create spatial variations in the localized interaction probabilities (see next section). One suitable method for this is Gradient Boosted Trees with a Gaussian maximum likelihood from the 117 EvoTrees.jl Julia package (https://github.com/Evovest/EvoTrees.jl). This method returns a prediction for 118 every site with an average value and a standard deviation, which we used as a measure of uncertainty to build a Normal distribution for the probability of occurrence of a given species at all sites (represented as probability 120 distributions on Fig. 1). We trained models across the extent chosen for occurrences (longitudes 175°W to 121 45°W and latitudes 10°N to 90°N), then predicted species distributions only for Canada. We used the 2021 Census Boundary Files from Statistics Canada (Statistics Canada 2022) to set the boundaries for our predictions, which gave us 970,698 sites in total. 124

Localized steps: 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 126 component was divided into single-species, two-species, and network-level steps (Localized steps box on Fig. 1). The single-species steps represented four possible ways to account for uncertainty in the species distributions 128 and bring variation to the spatial metaweb. We explored four different options to select a value (P(occurrence); Fig. 1) from the occurrence distributions obtained in the previous steps (Inputs section): 1) taking the mean 130 from the distribution as the probability of occurrence (option 1 on Fig. 1); 2) converting the mean value to a 131 binary one using a specific threshold per species (option 2); 3) sampling a random value within the Normal 132 distribution (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 134 maximized Youden's J informedness statistic (Youden 1950), the same metric used by Strydom et al. (2022a) at 135 an intermediate step while building the metaweb. The four sampling options were intended to explore how uncertainty and variation in the species distributions can affect the metaweb result. We expected thresholding to 137 have a more pronounced effect on network structure as it should reduce the number of links by removing many of the rare interactions (Poisot et al. 2016). Meanwhile, we expected random sampling to create spatial heterogeneity compared to the 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 result of a probabilistic SDM (as in Gravel *et al.* 2019).
- Next, the two-species steps were aimed at assigning a probability of observing an interaction between two
- species in a given site. For each species pair, we multiplied the product of the two species' occurrence
- probabilities (P(co-occurrence); Fig. 1) (obtained using the one of the sampling options above) by their
- interaction probability in the Canadian metaweb. For cases where species in the Canadian metaweb were
- considered as the same species by the GBIF Backbone Taxonomy (the reconciliation step mentioned earlier), we
- used the highest interaction probabilities involving the duplicated species.
- The network-level steps then created the probabilistic metaweb for the site. We assembled all the local
- interaction probabilities (from the two-species steps) into a probabilistic network (Poisot et al. 2016). We then
- sampled several random network realizations to represent the potential local realization process (Poisot et al.
- 152 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.

Outputs: The downscaled metaweb

- The final output of our method was the downscaled metaweb, which contains a localized probabilistic metaweb
- in every site across the study area (Outputs box on Fig. 1). A metaweb essentially serves to set an upper bound
- 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
- local realization, from which it should have a different structure. Nonetheless, from the downscaled metaweb
- we 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 richness. We can also calculate the uncertainty associated with the network and community
- measurements and compare their spatial distribution (see Supplementary Material). We computed expected
- metrics on probabilistic networks following Poisot et al. (2016; see Gravel et al. 2019 for a similar example).

165 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 175 indicated areas of exceptional composition. We measured uniqueness using the local contributions to beta 176 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 178 studies used LCBD values to evaluate uniqueness on local scales or few study sites (for example, da Silva & 179 Hernández 2014; Heino & Grönroos 2017), recent studies used the measure on predicted species compositions over broad spatial extents and a large number of sites (Vasconcelos et al. 2018; Dansereau et al. 2022). LCBD 181 values can also be used to measure uniqueness for networks by computing the values over the adjacency matrix, 182 which has been shown to capture more unique sites and uniqueness variability than through species 183 composition (Poisot et al. 2017). Here, we measured and compared the uniqueness of our localized community and network predictions. For species composition, we assembled a site-by-species community matrix with the 185 probability of occurrence at every site from the species distribution models. For network composition, we 186 assembled a site-by-interaction matrix with the localized interaction values from the spatial probabilistic metaweb. We applied the Hellinger transformation on both matrices and computed the LCBD values from the 188 total variance in the matrices (Legendre & De Cáceres 2013). High LCBD values indicate a high contribution 189 to the overall variance and a unique species or interaction composition compared to other sites. Since values themselves are very low given our high number of sites (as in Dansereau et al. 2022), what matters primarily is 191 the magnitude of the difference between the sites. Given this, we divided values by the maximum value in each 192 matrix (species or network) and suggest that these should be viewed as relative contributions compared to the highest observed contribution. As with other measures, we then summarized the local uniqueness values by 194 ecoregion by taking the median LCBD value and measuring the 89% interquantile range within all ecoregions. 195 We used Julia v1.9.0 (Bezanson et al. 2017) to implement all our analyses. We used packages GBIF.jl (Dansereau & Poisot 2021) to reconcile species names using the GBIF Backbone Taxonomy,

SpeciesDistributionToolkit.jl to handle raster layers and species occurrences, EcologicalNetworks.jl
(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
projection in our analyses, but we displayed the results using a Lambert conformal conic projection more
appropriate for Canada using GeoMakie.jl. All the code used to implement our analyses is available on GitHub
(https://github.com/PoisotLab/SpatialProbabilisticMetaweb) and includes instructions on how to run a smaller
example at a coarser resolution. Note that running our analyses at 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.

207 **Results**

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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 209 community and network-level measures presented here are not actual predictions of the measure itself (e.g., we 210 do not present a prediction of actual species richness at each location). Instead, they are the reflection of these metrics from the localized predictions of the communities and networks obtained from the downscaling of the 212 metaweb, then summarized for the ecoregions (median value). Expected ecoregion richness (Fig. 2A) and 213 expected number of links (Fig. 2B) displayed similar distributions with a latitudinal gradient and higher values in the south. However, within-ecoregion variability was distributed differently, as some ecoregions along the 215 coasts displayed higher interquantile ranges while ecoregions around the southern border displayed narrower 216 ones (Fig. 2C-D). All results shown are based on the first sampling strategy (option 1) mentioned in the Localized steps section, where species occurrence probabilities were taken as the mean value of the distribution (results for other sampling strategies are discussed in Supplementary Material). 219

[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 (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

(Canadian High Artic Tundra and Davis Highlands Tundra) displayed higher richness (based on the quantile rank) compared to the number or links. Inversely, ecoregions further south (Canadian Low Artic Tundra, 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 less constant latitudinal gradient (Fig. 3B). This indicates that richness and links do not co-vary completely (i.e. their variability is not closely connected) although they may show similar distributions for median values.

[Figure 3 about here.]

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 (Fig. 4A-B). Consequently, ecoregions with both unique community composition and unique network 234 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 unique species composition but a more common network composition (Fig. 4C). Opposite areas with unique 237 network compositions only were observed at higher between latitudes 52°N and 70°N (Eastern Canadian Shield 238 Taiga, Northern Canadian Shield Taiga, Canadian Low Artic Tundra). Also, network uniqueness values for ecoregions spanned a narrower range between the 44 ecoregions than species LCBD values (Fig. 4D, left). 240 Within-ecoregion variation was also lower for network values with generally lower 89% interquantile ranges 241 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 (see Supplementary Material). The areas only unique for their species composition had both a high richness and 244 number of links. On the other hand, the sites only unique for their networks had both lower richness and a lower 245 number of links, although they were not the sites with the lowest values for both.

[Figure 4 about here.]

Discussion

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Our approach presents a way to downscale a metaweb and produce localized predicitions using probabilistic networks as inputs and outputs and incorporating 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 252 the metaweb of Canadian mammals (Strydom et al. 2022a) and a probabilistic equivalent to how the European 253 tetrapod metaweb (Maiorano et al. 2020) was used to predict localized networks in Europe (Braga et al. 2019; O'Connor et al. 2020; Galiana et al. 2021; Gaüzère et al. 2022; Botella et al. 2023). Therefore, our approach 255 could open similar possibilities of investigations in North America with food webs of Canadian mammals, for 256 instance on the structure of food webs over space (Braga et al. 2019) and on the effect of land-use 257 intensification on food webs (Botella et al. 2023). Interesting research areas could include assessing climate 258 change impacts on network structure or investigating linkages between network structure and stability. 259 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 a different association between species richness and network properties. Galiana et al. (2021) found that species 262 richness had a large explanatory power over network properties but mentioned it could potentially be due to 263 interactions between species being fixed in space. Here, we found mismatches in the distribution of species richness and interactions, and especially regarding their within-ecoregion variability (Fig. 3), highlighting that interactions might vary differently than species distributions in space. Network measures (links on Fig. 3A) were also lower in the north, contrarily to previous studies (e.g. connectance higher in the north, Braga et al. 2019; Galiana et al. 2021). 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 271 communities of rodents and ecto-fleas. Our results further show how these differences could be distributed 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), 274 with species-unique sites displaying high values of both measures and network-unique sites displaying low 275 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 278 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.

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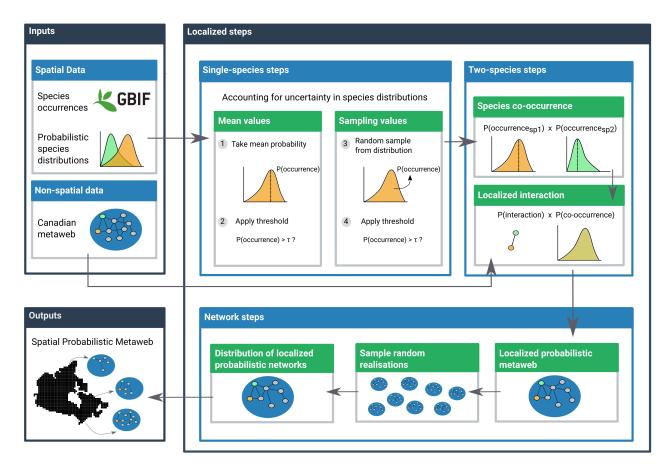


Figure 1: Conceptual figure of the workflow to obtain the spatial probabilistic metaweb (Chapter 1). The workflow has three components: the inputs, the localized steps, and the final spatial output. The inputs are composed of the spatial data (data with information in every cell) and the non-spatial 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.

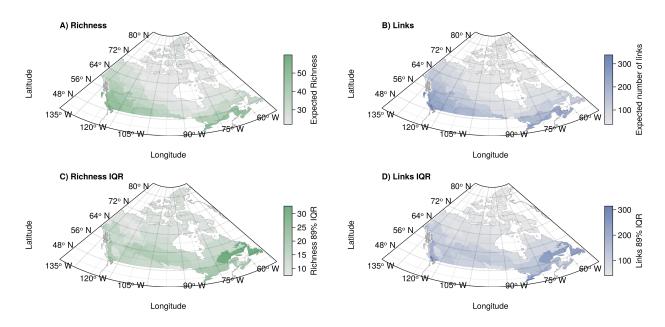


Figure 2: (A-B) Example of a community measure (A, expected species richness) and a network one (B, expected number of links). Both measures are assembled from the predicted probabilistic communities and networks, respectively. Values are first measured separately for all sites, then the median value 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).

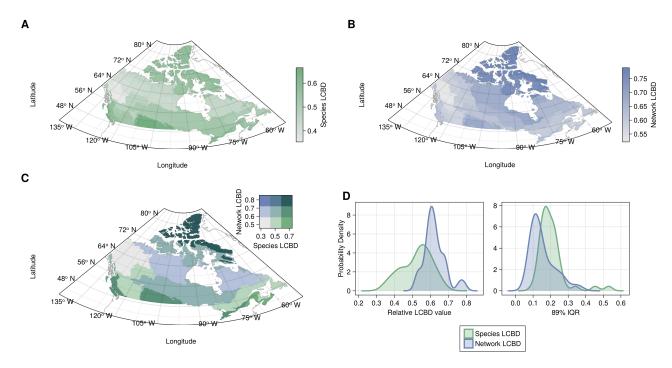


Figure 4: (A-B) Representation of the ecoregion uniqueness values based on species composition (a) and network composition (b). LCBD values were first computed across all sites and scaled relative to the maximum value observed. The ecoregion LCBD value is the median value for the sites in the ecoregion. (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.