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Diversity indices for ecological networks: a unifying framework using Hill numbers

Marc Ohlmann¹, Vincent Miele², Stéphane Dray², Loïc Chalmandrier^{3,4,5}, Louise O'Connor⁶ and Wilfried Thuiller¹

¹ Univ. Grenoble Alpes, CNRS, Univ. Savoie Mont Blanc; CNRS, LECA, Laboratoire d'Écologie Alpine, F-38000 Grenoble, France

² Université de Lyon, F-69000 Lyon; Université Lyon 1; CNRS, UMR5558, Laboratoire de Biométrie et Biologie Evolutive, F-69622 Villeurbanne, France.

³Landscape Ecology, Institute of Terrestrial Ecosystems, ETH Zürich, CH- 8092 Zürich, Switzerland

⁴ Swiss Federal Research Institute WSL, CH-8903 Birmensdorf, Switzerland

⁵ Department of Botany, University of Wyoming, Laramie, WY 82071, USA;

⁶ Ecole Normale Supérieure, F-75005 Paris, France;

Email addresses: Marc Ohlmann (marc.ohlmann@univ-grenoble-alpes.fr), Vincent Miele (vincent.miele@univ-lyon1.fr), Stéphane Dray (stephane.dray@univ-lyon1.fr), Loïc Chalmandrier (chalman@uwyo.edu), Louise O'Connor (louise.o.connor@ens.fr), Wilfried Thuiller (wilfried.thuiller@univ-grenoble-alpes.fr)

Corresponding author: Marc Ohlmann, LECA, UMR UGA-USMB-CNRS 5553, Université 27 Grenoble Alpes, CS 40700 38058 Grenoble cedex 9, France, tel : +33 4 76 51 42 78, fax :+33 4 76 28 51 42 79

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https://www.nceas.ucsb.edu/interactionweb/resources.html#predator_prey.

Simulated data are available upon request. We implemented the method in a R package *NetDiv* available at <https://gricad-gitlab.univ-grenoble-alpes.fr/ohlmannm/NetDiv>.

Abstract

Describing how ecological interactions change over space and time and how they are shaped by environmental conditions is crucial to understand and predict ecosystem trajectories. However, it requires having an appropriate framework to measure network diversity locally, regionally and between samples (α -, γ - and β - diversity). Here, we propose a unifying framework that builds on Hill numbers and accounts both for the probabilistic nature of biotic interactions and the abundances of species or groups. We emphasize the importance of analyzing network diversity across different species aggregation levels (e.g., from species to trophic groups) to get a better understanding of network structure. We illustrate our framework with a simulation experiment and an empirical analysis using a global food-web database. We discuss further usages of the framework and show how it responds to recent calls on comparing ecological networks and analyzing their variation across environmental gradients and time.

Introduction

Since the pioneering work of Humboldt (von Humboldt 1805), understanding the patterns of biodiversity across space and time has been a question central to both biogeography and community ecology (Gaston 2003). The recent upsurge of large-scale databases has made possible to produce comprehensive syntheses of biodiversity patterns (Belmaker *et al.* 2012; Mazel *et al.* 2017) by analyzing local assemblages on the one hand (α -diversity, Hawkins *et al.* 2003) and composition turnover between such assemblages on the other (β -diversity, Mazel *et al.* 2017). A plethora of diversity indices and unifying frameworks have thus been proposed to partition biodiversity into α - and β -diversity components (Whittaker 1960; Routledge 1979; Ellison 2010; Chao *et al.* 2014b; Chao & Chiu 2016). However, not only does biodiversity reflect species coexistence but also the trophic and non-trophic interactions that link them to one another (Kéfi *et al.* 2016). The development of the trophic theory of island biogeography (Gravel *et al.* 2011; Massol *et al.* 2017) has recently paved the way for a new biogeography synthesis by accounting for trophic interactions in theoretical predictions of biodiversity patterns. Similarly, empiricists do not only investigate species distribution patterns but also analyze how ecological interactions (i.e. ecological networks) vary over space and time (Pellissier *et al.* 2017; Tylianakis & Morris 2017). To this aim, the *metanetwork* concept generalizes the regional species-pool of classic community ecology by adding to this representation of biodiversity the potential trophic and non-trophic interactions between species (Dunne 2006; Kéfi *et al.* 2016) at a regional scale. Thus, in the same way local assemblages are conceptualized as subsets of a regional species pool, local ecological networks are realizations of a subset of the regional metanetwork. This opens new perspectives in understanding the processes that shape the distribution of biodiversity in space and time. For instance, mapping, describing and comparing ecological networks along environmental or disturbance gradients are the first steps of a fascinating era to understand the organization of life on Earth (Pellissier *et al.* 2017) and its effects on ecosystem functioning and associated services (Brose & Hillebrand 2016). The realization, the frequency and the intensity of interactions within networks across space and time are driven by the compositional turnover of species or groups of species, changes in their abundances, their plasticity or behavioral variations, and finally by the environmental constraints on biotic interactions. Any of these variations may have direct or indirect consequences on ecosystem functioning (Barnes *et al.* 2014). Such knowledge would thus help not only to improve our understanding of multi-trophic assemblages and their influence on ecosystem functioning but also to help build a more robust predictive ecology at the interface between trophic ecology, community ecology and ecosystem ecology (Thompson *et al.* 2012).

There is thus a strong need to develop a framework to understand the structure and composition of ecological networks across spatial and temporal scales and along environmental gradients (Pellissier *et al.* 2017). To date, such a framework remains hampered by several issues.

First, no appropriate diversity measure is available to describe the diversity of ecological networks, and partition it into α , β and γ components, that would account for both species abundances and the probabilistic nature of interactions, and that would relate to existing frameworks in biogeography or community ecology (Pellissier *et al.* 2017). Recent years have seen a prolific development of frameworks to measure diversity at both the taxonomic (Jost 2007; Ellison 2010; Chao & Chiu 2016) and phylogenetic or trait levels (Chao *et al.* 2014a; Tucker *et al.* 2016). These indices need to satisfy five mathematical properties (see Jost 2010): (1) α and β should be mathematically independent; (2) α , β and γ should be effective numbers (this enables to interpret a given measure of diversity in terms of the diversity of an evenly distributed community and therefore guarantees the comparability of diversity measures); (3) overall α should represent an average of local diversity measures; (4) γ should be completely determined by α and β ; (5) α cannot be larger than γ . A sixth additional practical property of β -diversity, *invariance under shattering* (Reeve *et al.* 2014) assumes that each community represents a portion of the geographical space. This assumption implies that if a community is split into two and the abundances of the two resulting communities are equal, then the β -diversity of the overall metacommunity should not change. The framework recently proposed by Reeve *et al.* (2014) satisfies each of these fundamental properties (only when similarities between species are not considered) while Jost's framework satisfies the first five properties, and the sixth only for some particular cases. These indices are based on Hill numbers (Hill 1973), which are derived from Rényi's entropy (Rényi 1961) and have enabled a generalization of the well-established diversity measures such as the Shannon entropy or the Simpson diversity index. An additional and interesting feature of Hill numbers is the introduction of a *viewpoint*

parameter linked to the weight given to dominant vs. rare species onto assembly rules (Chalmandrier *et al.* 2015). While this framework could potentially be very useful for ecological networks, it is not yet applicable. So far, the few network-specific metrics are built on graph theory, with the aim to summarize the structure of a network through a single quantity (Poisot *et al.* 2012, 2016; Pellissier *et al.* 2017) – but none of them satisfy the six requirements listed above, nor are they able to manipulate species abundances or the probability of a given interaction occurring. Second, diversity metrics depend on the way individuals are aggregated into larger groups (e.g., species, guilds, functional groups). In trophic networks, species can be aggregated based on their equivalent roles. Indeed, species richness or taxonomic turnover do not reveal much on how assemblages are truly structured in terms of resource exploitation, niche partitioning and co-existence mechanisms (Thompson *et al.* 2012), whereas functional or trophic groups enable to encapsulate more of the underlying ecological processes. In this respect, insights from graph theory (Luczkovich *et al.* 2003) and random models of networks (Group model, Allesina & Pascual 2009 or stochastic block model, Newman & Leicht 2007) have helped to mathematically formalize equivalence relationships between species using the topology of the ecological network alone. However, aggregating species in trophic or functional groups is often challenging (e.g., choosing an optimal number of groups) and there is no way of knowing whether a given grouping will provide a better understanding of the diversity pattern than others. To address this issue, we believe it is necessary to describe and analyze patterns at different levels of species aggregation, as is now done in community phylogenetic analyses (Chalmandrier *et al.* 2015; Graham *et al.* 2018). In fact, analyses of ecological networks diversity (α , β , γ) should be carried out along a profile of species aggregation levels, ranging from characterizing all species (their abundances, the abundance of their links and their probability of interactions, hereafter named the *microscopic scale*), to various species aggregation levels (hereafter coined the *mesoscopic scale*) until the *macroscopic scale*, represented by the single value of connectance (the probability of interaction between any two species). This multi-scale approach should provide novel insights to understand the processes that shape ecological networks. To overcome these limitations, we introduce a novel framework that allows measuring α , β , and γ diversities of ecological networks and combines Hill numbers (Hill 1973, Jost 2006, Chao & Chiu 2016) with different species aggregation levels. First, we build on the existing mathematical frameworks to derive new indices for ecological network diversity, which we partition into α , β , and γ components. We then demonstrate that existing network diversity indices (Bersier *et al.* 2002; Poisot *et al.* 2012, 2016) are particular cases of the proposed unified framework. We further extend our framework so it can be used across multiple levels of species aggregation. We then apply this framework to an intercontinental dataset of stream water trophic networks (Thompson & Townsend 2003) and show that the drivers of the dissimilarity of ecological networks vary with the level of species aggregation. We finally provide an implementation of the framework with our R package *NetDiv*, guidelines for the interpretation of the results, and recommendations for the analyses of networks across space and time.

Diversity for a single network

For the sake of simplicity, we first introduce the formalism behind our new indices with a single trophic network. We then generalize the framework to the case of a metanetwork, and provide the details and mathematical proofs in the Supporting Information.

A probabilistic model of interaction networks

We propose a generic model of ecological networks that considers both species abundances and the probabilities of interaction between species. It is an extension of the probabilistic network model (Poisot *et al.* 2016) with the additional property that it accounts for species abundances.

We consider a given region that contains individuals belonging to n different species with relative abundances $p = (p_1, \dots, p_n)$. p_q represents the probability of picking an individual of species q . We also assume that the probability of interaction between two individuals of species q and l follows a Bernoulli law of parameter π_{ql} . This allows to account for the potential variability on the realization of an interaction event at the individual level (Gonzalez-Varo & Traveset 2016; Albert *et al.* 2010). We also assume that all interactions occur independently. We represent this regional model using a weighted network G , with p_q the relative abundance of the node V_q , and π_{ql} the weight of the link (V_q, V_l) ($\mathbf{\Pi}$ is the adjacency matrix of G , see Table 1). The probability of picking

a link that connects two individuals of species q and l is thus:

$$L_{ql} = Pr(i \rightarrow j, i \in q, j \in l) \quad (1)$$

$$L_{ql} = \pi_{ql} p_q p_l \quad (2)$$

where

$$\pi_{ql} = Pr(i \rightarrow j \mid i \in q, j \in l) \quad (3)$$

If this model represents the most complete case of a single network (abundances on nodes and weights on links), simpler cases can easily be derived by omitting the weights on links (i.e. for binary networks, π_{ql} is either 0 or 1) or the abundances of nodes (i.e. assuming evenly distributed species abundances).

Navigating across species aggregation levels

We initially described the probabilistic network model at a species level. However, species can have similar positions, roles (e.g., Eltonian niche, [Elton 1927](#)) or functions ([Lindeman 1942](#); [Lavorel & Garnier 2002](#); [Luck et al. 2012](#)), leading to inflated or deflated estimates with respect to functional diversity. It is thus crucial to represent and analyze the diversity of ecological networks at different aggregation levels, by grouping species into larger and more relevant entities. Here we propose to use mathematical methods that group nodes using the topology of the ecological network without any prior knowledge (see Supporting Information for a brief review of these methods).

Assuming that we have established Q groups (C_1, \dots, C_Q) from the previous network ($Q \leq n$), we can represent the network at a coarser resolution (Fig. 1, mesoscopic scale), called the image network ([Luczkovich et al. 2003](#); [Allesina & Pascual 2009](#)). The new set of nodes is $\tilde{V} = (\tilde{V}_1, \dots, \tilde{V}_Q)$ and each node is assigned a weight \tilde{p}_q that corresponds to the abundance of the group q .

$$\tilde{p}_q = \sum_{k \in C_q} p_k \quad (4)$$

Similarly, each link of the image network is assigned a weight $\tilde{\pi}_{ql}$ that corresponds to the probability of interaction between individuals from classes C_q and C_l .

$$\tilde{\pi}_{ql} = \frac{\sum_{k \in C_q, k' \in C_l} \pi_{kk'} p_k p_{k'}}{\sum_{k \in C_q} p_k \sum_{k' \in C_l} p_{k'}} \quad (5)$$

The link abundances between individuals of classes q and l , \tilde{L}_{ql} thus equates to:

$$\tilde{L}_{ql} = \sum_{k \in C_q, k' \in C_l} \pi_{kk'} p_k p_{k'} \quad (6)$$

We thus define the scale of the image network considered as:

$$s = \frac{Q}{n} \quad (7)$$

If $s = 1$, the network is considered at a microscopic scale (the image network corresponds to the original one). If $s = \frac{1}{n}$, the network is considered at a macroscopic scale. In this case, the image network is then made of a single node (with abundance 1, the sum of species relative abundances) and a single link. The weight of this link represents the probability that any two nodes of the original networks are connected and is, consequently, the connectance of the original network.

$$C = \sum_{1 \leq q, l \leq n} \pi_{ql} p_q p_l \quad (8)$$

If $\frac{1}{n} < s < 1$, the network is considered at a mesoscopic scale.

Measuring diversity at different species aggregation levels

For a community vector $\mathbf{p} = (p_1, \dots, p_Q)$, the Hill number of order η is defined as:

$$D^\eta(\mathbf{p}) = \left(\sum_{i=1}^Q p_i^\eta \right)^{\frac{1}{1-\eta}}, \eta \geq 0, \eta \neq 1 \quad (9)$$

This number ranges between 1 and Q (Table 1), and translates into an effective number of groups (which can be species or group of species i.e., we define diversity indices on the image network while keeping the notations of the original one for the sake of simplicity). A Hill measure of Δ hence means that the system holds a diversity equivalent to a system made of Δ equally distributed groups. η is considered as a viewpoint parameter that modulates the weight given to group abundances. When $\eta = 0$, all groups equally contribute to the index and D^0 is the richness of groups. For $\eta = 1$, Eq. 8 is not defined but it converges towards the exponential of the Shannon entropy :

$$D^1(\mathbf{p}) = \lim_{\eta \rightarrow 1} D^\eta(\mathbf{p}) = \exp \left(\sum_{i=1}^Q -p_i \log p_i \right) \quad (10)$$

We propose to extend the use of Hill numbers to compute the diversity in link abundances and the diversity in link probabilities between groups. More precisely, we measure the entropy of the random variable associated to the experience: "A link is drawn uniformly in the network, what is the label of this link (the label is defined by the identity of the two groups that are connected by the link)". Assuming that \mathbf{L} is the matrix of link abundances, the diversity in link abundances is:

$$D^\eta(\mathbf{L}) = \left(\sum_{1 \leq q, l \leq Q} \left(\frac{L_{ql}}{C} \right)^\eta \right)^{\frac{1}{1-\eta}} \quad (11)$$

where $C = \sum_{1 \leq q, l \leq Q} L_{ql}$.

Similarly, assuming that $\mathbf{\Pi}$ is the adjacency matrix of the image graph, the diversity in link probabilities is defined as:

$$D^\eta(\mathbf{\Pi}) = \left(\sum_{1 \leq q, l \leq Q} \left(\frac{\pi_{ql}}{\pi_{++}} \right)^\eta \right)^{\frac{1}{1-\eta}} \quad (12)$$

where $\pi_{++} = \sum_{1 \leq q, l \leq Q} \pi_{ql}$.

$D^\eta(\mathbf{\Pi})$ is unrelated to $D^\eta(\mathbf{p})$ (*sensu* Chao & Chiu 2016), since the value of one of this measure does not constrain the value of the other. When $\eta = 0$, it measures the number of links of the image network. When $\eta \rightarrow 1$, it converges towards the exponential of the Shannon entropy of the probability of links (Bersier *et al.* 2002)

Both group abundances and the interaction probabilities determine the range of values of $D^\eta(\mathbf{L})$ which are therefore related. These last two indices translate into an effective numbers of links, either weighted ($D^\eta(\mathbf{L})$) or not ($D^\eta(\mathbf{\Pi})$) by the group abundances. Note that ($D^\eta(\mathbf{\Pi})$) could be used in studies where groups have different relative abundances, but these are not important in the analysis.

Diversity for a metanetwork

Measuring α -, β - and γ -diversity at different species aggregation levels

Mirroring the single network case, we propose to analyze the diversity of the metanetwork and its local realizations through different species aggregation levels. Importantly, we assume that any grouping is defined on the metanetwork. We thus define α -, β - and γ -diversity measures on the set of local networks and on the metanetwork at different species aggregation levels. We measure the diversity of group abundances, link abundances and link probabilities using Hill numbers. We extend the framework presented in Chao & Chiu 2016 since it satisfies the first five properties listed in the introduction and elegantly link the variance and decomposition perspective on β -diversity (see Chao & Chiu 2016 for details). For the sake of simplicity, we present the case $\eta \rightarrow 1$ (and therefore omit the exponent in the indices). The general case is presented in Supporting

Information, together with our framework as an extension of Jost's and Reeve's framework and the mathematical links between the existing network diversity indices and the proposed unified framework. The proposed indices can be applied in several subcases (Fig. 2).

We use the same probabilistic network model as presented before. The metanetwork is thus a weighted network, divided in K local networks (see Table 1 for notations and total margins).

α -diversity

For each local network, the α diversity is computed using Hill numbers (for $\eta \rightarrow 1$, it converges towards Shannon entropy). The overall α -diversity of groups across local networks is:

$$A_P = \exp \left(\sum_{q=1}^Q \sum_{k=1}^K -\frac{P_{qk}}{P_{++}} \log \left(\frac{P_{qk}}{P_{++}} \right) - \log(K) \right) \quad (13)$$

where $P_{++} = \sum_{1 \leq k \leq K} \sum_{1 \leq q \leq Q} P_{qk}$.

This is the mean equivalent number of groups across local networks. Similarly, the overall α -diversities in link abundances and link probabilities are equal to:

$$A_L = \exp \left(\sum_{q,l=1}^Q \sum_{k=1}^K -\frac{L_{qlk}}{L_{+++}} \log \left(\frac{L_{qlk}}{L_{+++}} \right) - \log(K) \right) \quad (14)$$

where $L_{+++} = \sum_{1 \leq k \leq K} \sum_{1 \leq q,l \leq Q} L_{qlk}$.

$$A_{\Pi} = \exp \left(\sum_{q,l=1}^Q \sum_{k=1}^K -\frac{\pi_{qlk}}{\pi_{+++}} \log \left(\frac{\pi_{qlk}}{\pi_{+++}} \right) - \log(K) \right) \quad (15)$$

where $\Pi_{+++} = \sum_{1 \leq k \leq K} \sum_{1 \leq q,l \leq Q} \pi_{qlk}$.

γ -diversity

The γ -diversity of group abundances is defined as:

$$G_P = \exp \left(\sum_{q=1}^Q -\frac{P_{q+}}{P_{++}} \log \left(\frac{P_{q+}}{P_{++}} \right) \right) \quad (16)$$

where $P_{q+} = \sum_{1 \leq k \leq K} P_{qk}$.

This corresponds to the equivalent number of groups in the metanetwork. The γ -diversity of the link abundances is defined as:

$$G_L = \exp \left(\sum_{q,l=1}^Q -\frac{L_{ql+}}{L_{+++}} \log \left(\frac{L_{ql+}}{L_{+++}} \right) \right) \quad (17)$$

where $L_{ql+} = \sum_{1 \leq k \leq K} L_{qlk}$.

This corresponds to the equivalent number of links in the metanetwork. The γ -diversity in link probabilities is defined as:

$$G_{\Pi} = \exp \left(\sum_{q,l=1}^Q -\frac{\pi_{ql+}}{\pi_{+++}} \log \left(\frac{\pi_{ql+}}{\pi_{+++}} \right) \right) \quad (18)$$

where $\Pi_{ql+} = \sum_{1 \leq k \leq K} \pi_{qlk}$.

This corresponds to the equivalent number of links in a network that contains the same probabilities of links as in the metanetwork but where the relative abundances of groups are arbitrarily considered evenly distributed.

β -diversity and dissimilarity measures

The overall β -diversity can be calculated in group abundances, link abundances and link probabilities. The β -diversity in groups abundance is equal to:

$$B_P = \frac{G_P}{A_P} \quad (19)$$

This is the effective number of equally large and completely distinct communities of groups. It represents how many completely distinct communities of groups are present in the set of networks. The β -diversity in link abundances is equal to:

$$B_L = \frac{G_L}{A_L} \quad (20)$$

This is the effective number of equally large and completely distinct networks i.e., the number of networks made of distinct links across the considered region. The β -diversity in link probabilities is equal to:

$$B_{\Pi} = \frac{G_{\Pi}}{A_{\Pi}} \quad (21)$$

This translates to an effective number of equally large and completely distinct networks where group abundances would have arbitrarily been considered equal.

Overlap measures can be built from β -diversity to obtain dissimilarity measures (Jost 2007; Jost 2010; Chao & Chiu 2016). A class of parameterized Sorensen's based dissimilarity measures can be defined as non-linear transformation of β -diversity. When $\eta=1$, it equals to the Horn dissimilarity index (the general case is presented in Supporting Information).

$$\delta_P = \frac{\log(G_P) - \log(A_P)}{\log K} \quad (22)$$

$$\delta_L = \frac{\log(G_L) - \log(A_L)}{\log K} \quad (23)$$

$$\delta_{\Pi} = \frac{\log(G_{\Pi}) - \log(A_{\Pi})}{\log K} \quad (24)$$

These measures quantify the effective average proportion of shared groups/links/probability of links across networks and range between 0 and 1.

The framework is implemented in a R package *NetDiv*, available at <https://gricad-gitlab.univ-grenoble-alpes.fr/ohlmannm/NetDiv>.

Application to a case study: when the aggregation level reverses the assessment of the drivers of network dissimilarity

Here, we re-analysed a dataset used in Thompson & Townsend 2003. Using groups built *a priori* using three trophic levels, the authors concluded that stream water networks surrounded by pine or tussock grassland in New Zealand differ in their structure at a mesoscopic level. They attributed this change of structure to differences of energy supply in the two systems. We proposed to extend this analysis to the entire dataset (ten stream water trophic networks sampled in the United States of America (USA hereafter) and New Zealand surrounded either by pines or not (Table 1)) using our quantitative dissimilarity framework together with trophic groups built using the topology of the metanetwork (Allesina & Pascual 2009; Gauzens *et al.* 2015). We hypothesized that at a species level, geographic location should have a major impact on network dissimilarity due to the different biogeographical histories of the two continents (e.g., dispersal limitation that leads to small species overlap, different life history traits due to different environmental constraints), whereas at a trophic group level, vegetation should have much more impact due to energy supply provided by the riparian vegetation (e.g., vegetation types select for certain groups of species and network structure, which is not discernible at a species level).

The dataset consists of ten stream water trophic networks sampled in the USA and New Zealand (Thompson & Townsend 2003, https://www.nceas.ucsb.edu/interactionweb/resources.html#predator_prey, Fig. S1). The riparian vegetation of the American networks is a native species of pine, *Pinus Strobus*. Two of the New Zealand networks are surrounded by planted pines, *Pinus radiata* (Table 2). All other networks in New Zealand are surrounded by bush and tussock. The networks contain species of algae, invertebrates and fishes. We kept only the largest connected component of the metanetwork (Fig. S2). It contains 532 species and has a connectance value of 0.01.

To work at the mesoscale, we first determined the most relevant trophic groups using the stochastic block model implemented in the R package 'mixer' (Daudin *et al.* 2008). The optimal number of groups, 14, was identified using an information criterion (for simplicity we only used the optimal number of groups, but could have navigated through a wider range of aggregation levels). Therefore, the scale used to analyze the mesoscopic network dissimilarity is 14/532. We thereafter computed the dissimilarity matrices of link and group abundances at the microscopic and mesoscopic scale (using pairwise δ_L^η at two different aggregation levels) and the dissimilarity matrix of groups (using pairwise δ_P^η at two different aggregation levels) along a profile of weights attributed to abundant groups or links by varying the values of η . We then assessed the influence of the riparian vegetation (presence/absence of pine trees) and the location (USA or New Zealand) on the four dissimilarity matrices per value of η using ANOSIM (Clarke 1993) for both covariates (location and riparian vegetation) along the range of η values. (Fig. 3).

These analyses revealed that at a microscopic scale, the pairwise dissimilarities of both group and link abundances (δ_P^η and δ_L^η) are best explained by the geographic location. At the mesoscopic scale however the riparian vegetation is the variable that best explains both the dissimilarity of group and link abundances for medium to high values of η ($\eta > 0.35$ for the groups dissimilarity and $\eta > 0.15$ for the links dissimilarity).

Since New Zealand and the USA have drastically different biogeographical histories, they have very few species in common (New Zealand and USA streams share, for example, almost no invertebrate species, Thompson & Townsend 2003). Consequently, the location is indeed expected to be a more powerful explanatory variable of the species dissimilarity (i.e., δ_P^η at a microscopic scale). Moreover, given that species turnover is partially responsible for the links turnover (i.e. δ_L^η at a microscopic scale), the latter is also expected to be predominantly explained by the location. Studying δ_P^η and δ_L^η at a mesoscopic scale allows to look beyond species turnover, and accounts for the role of the riparian vegetation in diversity, both for the group abundances and the link abundances. Importantly, riparian vegetation best explains group and link dissimilarities for medium to high values of η . So, the abundances of the largest trophic groups and the links between these groups are shaped by the riparian vegetation whereas their presence (i.e., while omitting their abundances) is explained by the location.

Discussion

Diversity indices aim to describe and quantify the structure of ecological communities across space and time. There is currently a paradigm shift in the representation of a community, from a species assemblage to an interaction network (Pellissier *et al.* 2017, Thompson *et al.* 2012, Tylianakis & Morris 2017). While deciding which species belong to a community is made easier using a network representation of biodiversity (since a community is no more than a connected network), measuring and partitioning the diversity of these interaction networks is much more complex (Pellissier *et al.* 2017, Poisot *et al.* 2016). Diversity indices using Hill numbers provide a robust framework when ignoring interactions, as it gradually takes into account species abundances and satisfies theoretical properties. To be generic enough and to embrace the complexity of natural systems, these indices should take into account species abundances and the probabilistic nature of biotic interactions, while unifying the existing diversity frameworks. Moreover, they should be able to measure diversity at different species aggregation levels, so as to not inflate diversity indices or overestimate link turnover. In this paper, we defined diversity indices that address each of these requirements. The proposed framework is a generalization of the Hill numbers framework to measure α -, β - and γ -diversity in link abundances and link probabilities. By doing so, we have extended the existing indices of network diversity (e.g., Poisot *et al.* 2012), while benefiting from key properties of Hill numbers. In other words, using this single framework on a single dataset would enable one to not only investigate traditional relationships between species richness and energy as well as understand the compositional turnover across space, but also explore further by deciphering how variations in species abundance, probability of interactions and environmental gradients influence ecological networks.

The proposed framework is based on a probabilistic model of networks where parameters are species abundances and probabilities of interaction between species or groups of species. Consequently, it represents interactions as a random event rather than a deterministic event, thus assuming a plasticity of interactions at an individual level. While this constitutes an appealing representation from a theoretical standpoint, empirical datasets of interaction networks are often binary and lack

abundance estimates. Binary networks constitute particular cases of our framework, that then connect with existing frameworks (Poisot *et al.* 2012). Our framework can also be applied to any weighted network (i.e., network containing interaction strength) even if the weights do not strictly represent a probability of interaction. The viewpoint parameter η can then be used to modulate the weight given to interaction strength when assessing network diversity. The proposed diversity indices are based on Hill numbers that satisfy properties regarding group abundances but also link abundances. This is a fundamental condition to describe adequately network diversity over space and time and to build a robust spatial network ecology.

Additionally, our framework allows to compute diversity indices at different species aggregation levels (Fig. 4). In this paper, we have focused on methods that aggregate species based on the topology of the metanetwork (regular equivalence and stochastic block modelling). These methods aim to form trophic groups (Gauzens *et al.* 2015) and, in the general case, reduce the complexity of the network (i.e., the number of nodes) while preserving the overall structure. Grouping species using ecological knowledge and computing diversity indices is possible using the developed framework. In this latter case, however, there is no guarantee that the structure of the image network will reflect the structure of the original network (Allesina & Pascual 2009; Gauzens *et al.* 2015; Leger *et al.* 2015).

Whatever the clustering method used, the image network can be viewed as a map at a coarser resolution than the original species network. A map which, depending on the method used, summarizes more or less faithfully the structure of the original network. Importantly, it changes the assessment of link turnover. Indeed, what appears as link turnover at a species level could disappear at a group level, provided that the species considered belong to the same group. In other words, network diversity patterns depend on the aggregation level we choose to study the network. This introduces a new notion of scale in the analysis of ecological networks and adds to the spatial and temporal scale used to describe network biogeographic patterns (Fig. 4). Studies aiming to describe network biogeography have so far mostly described macroscopic (i.e., connectance, Thompson & Townsend 2003) or microscopic (link turnover at a species level, Poisot *et al.* 2012, 2016; Carstensen *et al.* 2014; CaraDonna *et al.* 2017) scale patterns and occasionally mesoscopic scale using a priori groups based on the trophic level concept (Thompson & Townsend 2003). Statistical methods, such as the stochastic block model and regular equivalence, allow to select an optimal number of groups to cluster the nodes of a network, thus defining an appropriate scale to study network diversity when no ecological knowledge is available for the species described in the network. As shown by the case study, network diversity can be shaped by different ecological processes depending on the aggregation level considered, in the same way that species diversity is shaped by different processes depending on the spatial and aggregation level considered (Münkemüller *et al.* 2014). This encourages to study network diversity at micro-, macroscopic scale and along a profile of mesoscopic scales (i.e., by changing gradually the number of groups of the image network) to study the processes that govern network structure across space. Indeed, given that some empirical evidence suggests that network structure might be random at a species level (CaraDonna *et al.* 2017), one purpose of aggregating species into equivalent groups is to investigate beyond the stochastic plasticity of biotic interactions. For example, the simulation (Supp. Info) suggests a stochastic plasticity at a species level but not at a group level since the image network is fixed at a given point of the ecological gradient. We hypothesize that, in the real world, there is an aggregation level below which stochastic processes drive the patterns of network diversity, and above which deterministic processes (i.e., ecological processes) are the main drivers. This hypothesis mirrors the use of the concept of emergent groups of organisms to assess the contribution of niche and neutral theory to community assembly (Hérault 2007).

Moreover, since ecological networks are now built using a wide spectrum of organisms, especially microorganisms with the advent of Next Generation Sequencing (Bohan *et al.* 2017) where the notion of species is hard to handle, using indices that allow to understand network diversity through different species aggregation levels will allow overcoming issues in the definition of the biological entity.

We thus believe that this unified framework should now pave the way for a better understanding of the spatial and temporal structure of biodiversity while considering biotic interactions. Indeed, it reconciles two perspectives on ecological networks analysis while building the associated indices. On the one hand, the study of how ecological processes shape an isolated network (Fig. 4a) and how meaningful groups can be derived from the topology of an ecological network (Fig. 4b), and on the other hand how networks vary across space and time (Fig. 4c). Importantly, it allows

testing key ecological hypotheses on the processes shaping the spatial and temporal variation of ecological networks (case study, Fig. 3), by varying different aspects of the networks (Fig. 4d). Consequently, it should foster the emergence of spatial network ecology and allow the comparison, analysis and partitioning of multiple ecological networks, from the local community to the global metacommunity they are a part of, while considering various definitions of the organisms involved.

Acknowledgements

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Tables and boxes

Table 1: Notations, name of the different indices and ranges of values. C is the connectance of the considered network, Q is the number of groups of the considered metanetwork and N_L its number of different links and C_k is the connectance of the local network k .

Object	Name	Total margin
p	Vector of relative group abundances	$\sum_{1 \leq q \leq Q} p_q = 1$
L	Matrix of link abundances	$\sum_{1 \leq q, l \leq Q} L_{ql} = C$
II	Matrix of link probabilities (adjacency matrix of the weighted network)	$\sum_{1 \leq q, l \leq Q} \pi_{ql}$
P	Matrix of group abundances of groups (metanetwork case)	$\sum_{q=1}^Q \sum_{k=1}^K P_{qk} = K$
L	Tensor of links abundances (metanetwork case)	$\sum_{q,l=1}^Q \sum_{k=1}^K L_{qlk} = \sum_{k=1}^K C_k$
II	Tensor of link probabilities (metanetwork case)	$\sum_{q,l=1}^Q \sum_{k=1}^K \pi_{qlk}$

	Diversity index	Name & interpretation	Range
α -diversity	A_P^η	<i>Overall α-diversity in group abundances</i> Average diversity in group abundances across local networks	$1 \leq A_P^\eta \leq Q$
	A_L^η	<i>Overall α-diversity in link abundances</i> Average diversity in link abundances across local networks	$1 \leq A_L^\eta \leq N_L$
	A_{II}^η	<i>Overall α-diversity in link probabilities</i> Average diversity in link probabilities across local network	$1 \leq A_{II}^\eta \leq N_L$
γ -diversity	G_P^η	<i>γ-diversity in group abundances</i> Diversity in group abundances of the metanetwork	$1 \leq G_P^\eta \leq Q$
	G_L^η	<i>γ-diversity in link abundances</i> Diversity in link abundances of the metanetwork	$1 \leq G_L^\eta \leq N_L$
	G_{II}^η	<i>γ-diversity in link probabilities</i> Diversity in link probabilities of the metanetwork	$1 \leq G_{II}^\eta \leq N_L$
β -diversity	B_P^η	<i>β-diversity of group abundances</i> Effective numbers of distinct communities of groups	$1 \leq B_P^\eta \leq K$
	B_L^η	<i>β-diversity of link abundances</i> Effective numbers of distinct networks	$1 \leq B_L^\eta \leq K$
	B_{II}^η	<i>β-diversity of link probabilities</i> Effective numbers of distinct networks (with abundances rescaled at evenly distributed values)	$1 \leq B_{II}^\eta \leq K$
dissimilarity	δ_P^η	<i>Dissimilarity of group abundances</i> Effective average proportion of shared groups	$0 \leq \delta_P^\eta \leq 1$
	δ_L^η	<i>Dissimilarity of link abundances</i> Effective average proportion of shared links	$0 \leq \delta_L^\eta \leq 1$
	δ_{II}^η	<i>Dissimilarity of link probabilities</i> Effective average proportion of shared links (with abundances rescaled at evenly distributed values)	$0 \leq \delta_{II}^\eta \leq 1$

Table 2: The set of trophic networks and the covariates (adapted from [Thompson & Townsend 2003](#))

Location	Site	Vegetation
Maine (USA)	Troy	<i>Pinus strobus</i>
Maine (USA)	Martins	<i>Pinus strobus</i>
North Carolina (USA)	Herlzler	<i>Pinus strobus</i>
North Carolina (USA)	Cooper	<i>Pinus strobus</i>
New Zealand	Venlaw	<i>Pinus radiata</i>
New Zealand	Berwick	<i>Pinus radiata</i>
New Zealand	North col	native bush
New Zealand	Powder	native bush
New Zealand	Trib C	tussock
New Zealand	Sutton	tussock

Figures caption

Figure 1 Navigating through species aggregation levels. From the original weighted network to image networks at mesoscopic and macroscopic scales, with the formulas giving the group abundances and link probabilities of the image networks.

Figure 2 The metanetwork and the local realized networks in different cases: a. binary network, unweighted links and without node abundances, b. node abundances but absence of links, c. weights on links but no node abundances and d. weights and links and node abundances. The different indices to measure α -, β - and γ -diversity are associated to each particular case and presented more generally in Table 1.

Figure 3 Assessing the drivers of β -diversity in group abundances and link abundances at different species aggregation levels. Relative importance (ANOSIM statistic) of the location vs. the riparian vegetation regarding the a. microscopic pairwise β -diversity in groups abundances (B_P^η at a microscopic scale) b. microscopic pairwise β -diversity in link abundances (B_L^η at a microscopic scale) c. mesoscopic pairwise β -diversity in group abundances (B_P^η at a mesoscopic scale) d. mesoscopic pairwise β -diversity in link abundances (B_L^η at a mesoscopic scale) across a range of η values (i.e the viewpoint parameter controlling the weight given to entities (group abundances or link abundances) in the measure of the β -diversity). n_k is the number of nodes of the network k and L_k its number of links.

Figure 4 Reconciling two perspectives in ecological network analyses. Here, we represent the key questions, seminal studies and underlying hypotheses usually considered in studies of ecological networks, and our specific indices for investigating them. (a) Studying the structure of a local network. (b) Studying the structure of a network where species have been aggregated in meaningful groups (trophic groups in the case of trophic networks). (c) Studying how networks vary in space and time. (d) Studying how networks change in space and time at various aggregation levels (trophic groups in the case of trophic networks). (meso) means the diversity indices are computed at a mesoscopic scale.

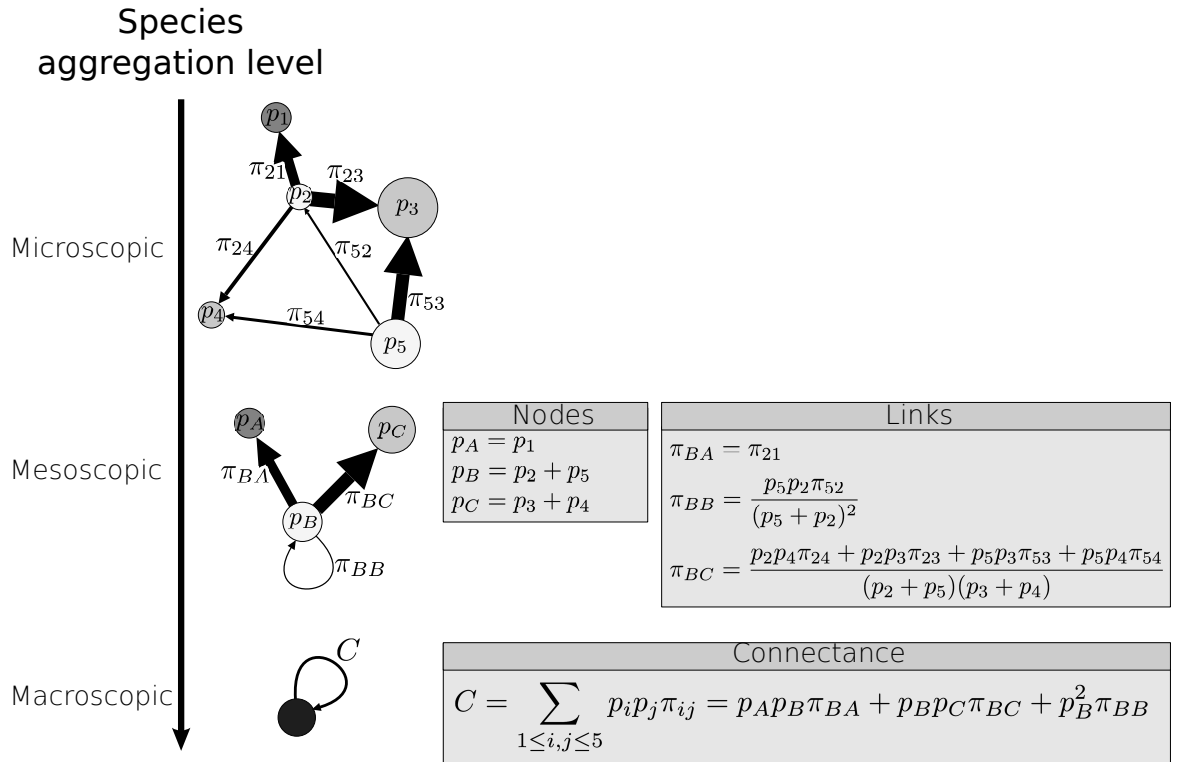


Figure 1

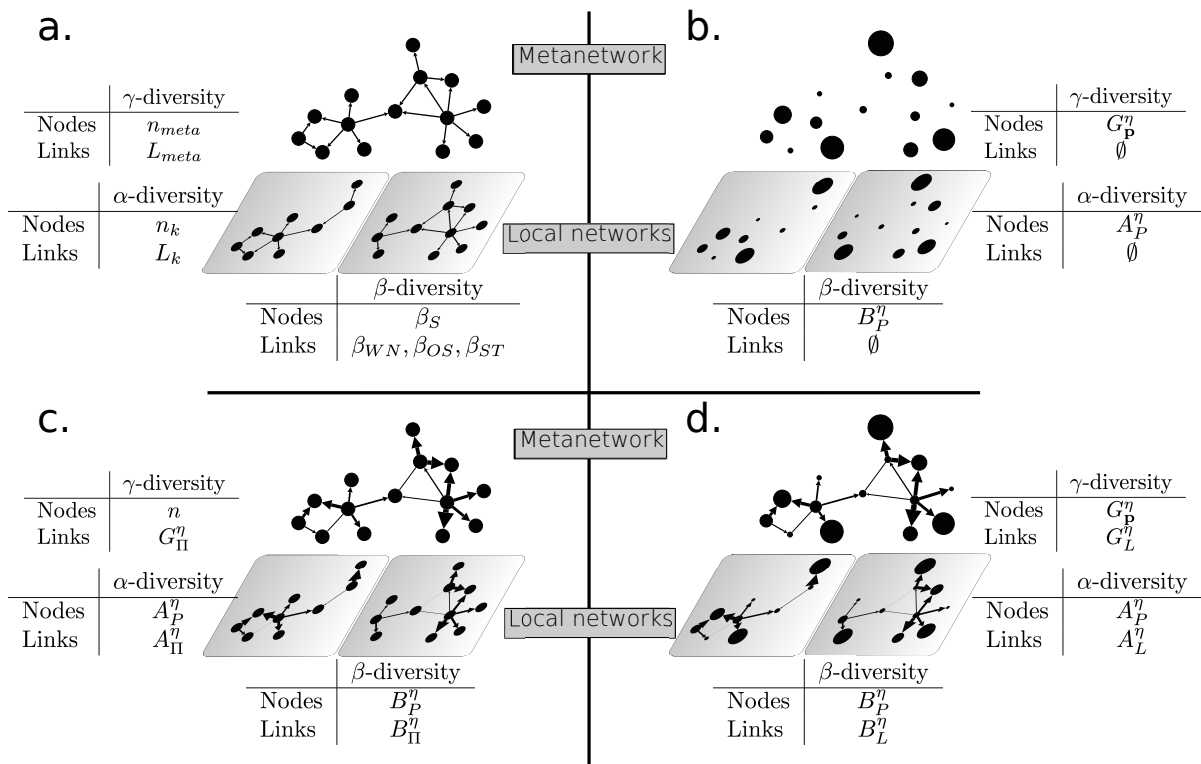


Figure 2

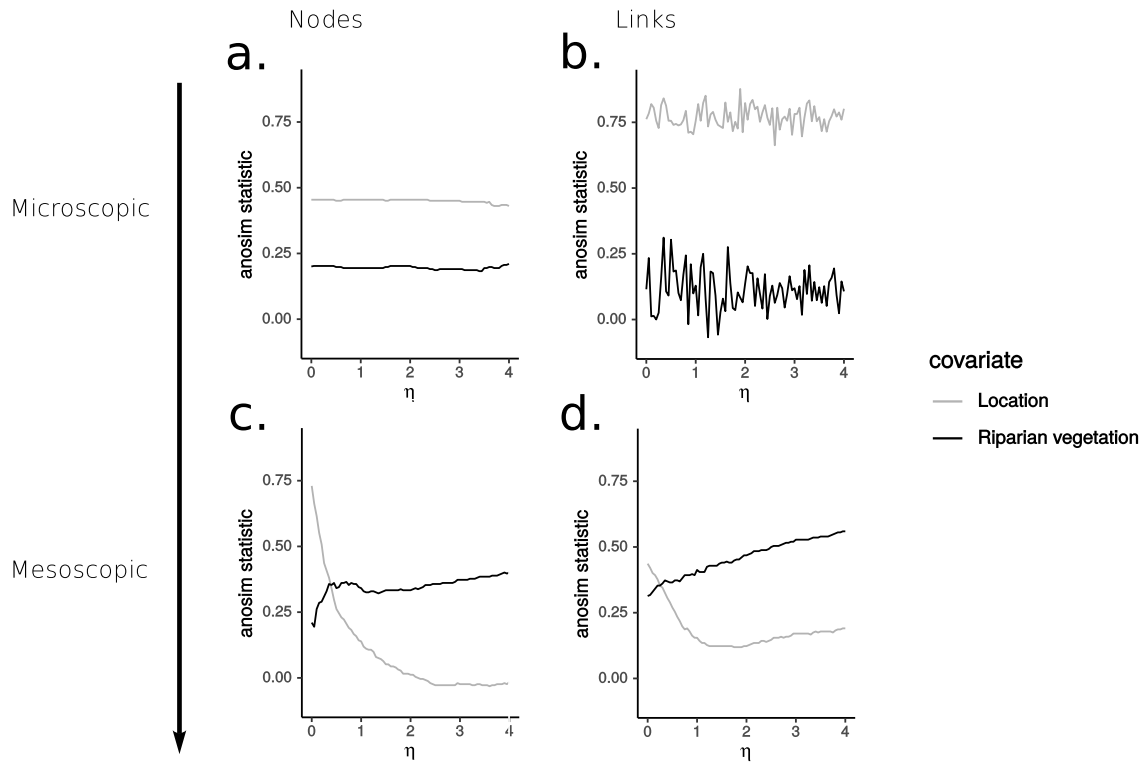


Figure 3





Local network		Networks in space and time								
Network aggregation	<p>a.  To what extent do ecological processes shape network structure?</p>	<p>c.  To what extent do ecological processes shape networks across space and time at a species level?</p>								
	<p><i>Studies:</i> Cohen et al. 2003 Dormann et al. 2017 (review)</p>	<p><i>Studies:</i> Caradonna et al. 2017 Tylianakis & Morris 2017 (review)</p>								
	<p><i>Hypothesis:</i> Traits and eco-evolutionary processes shape network structure</p>	<p><i>Hypothesis:</i> Species composition and interactions change across space and time</p>								
	<p><i>Diversity index</i> $C, D^n(\mathbf{p}), D^n(\mathbf{L}), D^n(\mathbf{II})$</p>	<table border="1"> <thead> <tr> <th colspan="3"><i>Mechanisms</i></th> </tr> <tr> <th>Change in species composition</th> <th>Change that alters probability of interactions</th> <th>Change in energy fluxes</th> </tr> </thead> <tbody> <tr> <td><i>Diversity index</i> A_P^n, G_P^n B_P^n, δ_P^n</td> <td>A_{II}^n, G_{II}^n B_{II}^n, δ_{II}^n</td> <td>A_L^n, G_L^n B_L^n, δ_L^n</td> </tr> </tbody> </table>	<i>Mechanisms</i>			Change in species composition	Change that alters probability of interactions	Change in energy fluxes	<i>Diversity index</i> A_P^n, G_P^n B_P^n, δ_P^n	A_{II}^n, G_{II}^n B_{II}^n, δ_{II}^n
<i>Mechanisms</i>										
Change in species composition	Change that alters probability of interactions	Change in energy fluxes								
<i>Diversity index</i> A_P^n, G_P^n B_P^n, δ_P^n	A_{II}^n, G_{II}^n B_{II}^n, δ_{II}^n	A_L^n, G_L^n B_L^n, δ_L^n								
<p>b.  To what extent can species in a network be aggregated into groups while preserving the overall structure?</p>	<p>d.  To what extent do ecological processes shape networks across space and time at a (trophic) group level?</p>									
<p><i>Studies:</i> Allesina & Pascual 2009 Gauzens et al. 2015 Cirtwill et al. 2018 (review)</p>	<p><i>Studies:</i> Thompson & Townsend 2003 (groups formed a priori) This study</p>									
<p><i>Hypothesis:</i> Species that have similar traits are equivalent in terms of position in the network. Interpretation as trophic group (or trophospecies) in the case of trophic networks</p>	<p><i>Hypothesis:</i> (Trophic) groups composition and interactions change across space and time</p>									
<p><i>Diversity index</i> $D^n(\mathbf{p}), D^n(\mathbf{L}), D^n(\mathbf{II})$ (meso)</p>	<table border="1"> <thead> <tr> <th colspan="3"><i>Mechanisms</i></th> </tr> <tr> <th>Change in (trophic) groups composition</th> <th>Change that alters probability of interactions between groups</th> <th>Change in energy fluxes</th> </tr> </thead> <tbody> <tr> <td><i>Diversity index</i> A_P^n, G_P^n (meso) B_P^n, δ_P^n (meso)</td> <td>A_{II}^n, G_{II}^n (meso) B_{II}^n, δ_{II}^n (meso)</td> <td>A_L^n, G_L^n (meso) B_L^n, δ_L^n (meso)</td> </tr> </tbody> </table>	<i>Mechanisms</i>			Change in (trophic) groups composition	Change that alters probability of interactions between groups	Change in energy fluxes	<i>Diversity index</i> A_P^n, G_P^n (meso) B_P^n, δ_P^n (meso)	A_{II}^n, G_{II}^n (meso) B_{II}^n, δ_{II}^n (meso)	A_L^n, G_L^n (meso) B_L^n, δ_L^n (meso)
<i>Mechanisms</i>										
Change in (trophic) groups composition	Change that alters probability of interactions between groups	Change in energy fluxes								
<i>Diversity index</i> A_P^n, G_P^n (meso) B_P^n, δ_P^n (meso)	A_{II}^n, G_{II}^n (meso) B_{II}^n, δ_{II}^n (meso)	A_L^n, G_L^n (meso) B_L^n, δ_L^n (meso)								

Figure 4

Supporting Information

1 Proofs

1.1 Proof of Eq. 2

The abundance of the group q is:

$$p_q = Pr(i \in q)$$

The abundance of the link between group q and l is :

$$L_{ql} = Pr(i \rightarrow j, i \in q, j \in l)$$

Using Bayes formula, we have :

$$L_{ql} = Pr(i \rightarrow j | i \in q, j \in l) Pr(i \in q) Pr(j \in l)$$

$$L_{ql} = \pi_{ql} p_q p_l$$

1.2 Proof of Eq. 3

By definition

$$\tilde{p}_q = Pr(i \in C_q)$$

Moreover :

$$C_q = \dot{\bigcup}_{k \in C_q} V_k$$

where $\dot{\bigcup}$ denotes the disjoint union. So :

$$\tilde{p}_q = \sum_{k \in C_q} p_k$$

1.3 Proof of Eq. 4 and 5

By definition :

$$\tilde{\pi}_{ql} = Pr(i \rightarrow j | i \in C_q, j \in C_l)$$

Using Bayes' formula :

$$\tilde{\pi}_{ql} = \frac{Pr(i \rightarrow j, i \in C_q, j \in C_l)}{Pr(i \in C_q) Pr(j \in C_l)}$$

By definition :

$$\tilde{L}_{ql} = Pr(i \rightarrow j, i \in C_q, j \in C_l)$$

Using the law of total probabilities :

$$\tilde{L}_{ql} = \sum_{k \in C_q, k' \in C_l} Pr(i \rightarrow j | i \in V_k, j \in V_{k'}) Pr(i \in V_k) Pr(j \in V_{k'})$$

$$\tilde{L}_{ql} = \sum_{k \in C_q, k' \in C_l} \pi_{kk'} p_k p'_{k'}$$

Since :

$$Pr(i \in C_q, j \in C_l) = \left(\sum_{k \in C_q} p_k \right) \left(\sum_{k' \in C'_l} p'_{k'} \right)$$

It follows:

$$\tilde{\pi}_{ql} = \frac{\sum_{k \in C_q, k' \in C'_l} \pi_{kk'} p_k p'_{k'}}{\left(\sum_{k \in C_q} p_k \right) \left(\sum_{k' \in C'_l} p'_{k'} \right)}$$

1.4 Proof of Eq. 7

By definition, :

$$C = Pr(i \rightarrow j)$$

Moreover :

$$L_{ql} = Pr(i \rightarrow j | i \in q, j \in l)$$

By summing over q and l , it follows that

$$C = \sum_{q,l} L_{ql}$$

$$C = \sum_{q,l} \pi_{ql} p_q p_l$$

This last result is a generalization of the weighted connectance presented in [Poisot *et al.* \(2016\)](#).

2 Clustering methods

We focus here on two network clustering methods that are particularly appropriate to aggregate nodes without any *a priori*: regular equivalence ([Luczkovich *et al.* 2003](#)) and the stochastic block model ([Daudin *et al.* 2008](#); [Allesina & Pascual 2009](#); [Newman & Leicht 2007](#)). These methods have already been used to study interaction networks (regular equivalence [Gauzens *et al.* 2015](#); the stochastic block model [Kéfi *et al.* 2016](#)). Importantly, in the case of trophic networks, the groups formed are interpreted in terms of trophic groups ([Allesina & Pascual 2009](#); [Gauzens *et al.* 2015](#)). We acknowledge that other methods exist (see e.g., [Henderson *et al.* 2012](#)) and could be applied to trophic networks. In regular equivalence, two nodes belong to the same equivalence class (i.e, same groups) if they have the same links (with the same weight in the case of weighted networks) to all other equivalence classes. Regular equivalence can thus be applied to binary or weighted networks. In contrast, the stochastic block model is a probabilistic perspective. Two nodes belong to the same group if they share the same probability of being linked to all the other groups. Similar to regular equivalence, the method is applicable to both binary networks ([Daudin *et al.* 2008](#)) and weighted networks ([Mariadassou *et al.* 2010](#)). A broader review of the links between clustering methods based on the topology of a network and the concepts of species' role in trophic networks can be found in [Cirtwill *et al.* \(2018\)](#).

3 General framework

In this section, we present the general way to partition network diversity using the framework presented in [Chao & Chiu \(2016\)](#) as the frameworks presented in [Jost \(2007\)](#) and [Reeve *et al.* \(2014\)](#).

3.1 Chao's framework

The main text present the diversity indices for $\eta = 1$. Here are presented the indices for any *eta* value. The interpretations of the indices are the same than these presented in the main document as the ranges presented in table 1.

For $\eta \neq 1$, the α -diversities are :

$$A_P^\eta = \frac{1}{K} \left(\sum_{q=1}^Q \sum_{k=1}^K \left(\frac{P_{qk}}{P_{+++}} \right)^\eta \right)^{\frac{1}{1-\eta}}$$

$$A_L^\eta = \frac{1}{K} \left(\sum_{q,l=1}^Q \sum_{k=1}^K \left(\frac{L_{qlk}}{L_{++++}} \right)^\eta \right)^{\frac{1}{1-\eta}}$$

$$A_\Pi^\eta = \frac{1}{K} \left(\sum_{q,l=1}^Q \sum_{k=1}^K \left(\frac{\pi_{qlk}}{\pi_{++++}} \right)^\eta \right)^{\frac{1}{1-\eta}}$$

For $\eta \neq 1$, the γ -diversities are :

$$G_P^\eta = \frac{1}{K} \left(\sum_{q=1}^Q \sum_{k=1}^K \left(\frac{P_{q+}}{P_{+++}} \right)^\eta \right)^{\frac{1}{1-\eta}}$$

$$G_L^\eta = \frac{1}{K} \left(\sum_{q,l=1}^Q \sum_{k=1}^K \left(\frac{L_{ql+}}{L_{++++}} \right)^\eta \right)^{\frac{1}{1-\eta}}$$

$$G_\Pi^\eta = \frac{1}{K} \left(\sum_{q,l=1}^Q \sum_{k=1}^K \left(\frac{\pi_{ql+}}{\pi_{++++}} \right)^\eta \right)^{\frac{1}{1-\eta}}$$

And the β -diversities are defined as :

$$B_P^\eta = \frac{G_P^\eta}{A_P^\eta}$$

$$B_L^\eta = \frac{G_L^\eta}{A_L^\eta}$$

$$B_\Pi^\eta = \frac{G_\Pi^\eta}{A_\Pi^\eta}$$

Overlap measures between the K local networks can be built using β -diversities giving the following dissimilarity measures (for $\eta \neq 1$) :

$$\delta_P^\eta = \frac{1 - (1/B_P^\eta)^{\eta-1}}{1 - (1/K)^{\eta-1}}$$

$$\delta_L^\eta = \frac{1 - (1/B_L^\eta)^{\eta-1}}{1 - (1/K)^{\eta-1}}$$

$$\delta_\Pi^\eta = \frac{1 - (1/B_\Pi^\eta)^{\eta-1}}{1 - (1/K)^{\eta-1}}$$

3.2 Jost's and Reeve's frameworks

In this section, we present network diversity indices using the frameworks presented in [Jost \(2007\)](#) and in [Reeve et al. \(2014\)](#). These two frameworks allow to measure diversity while weights (that are not necessarily evenly distributed) on local networks. Jost's framework satisfies the invariance under shattering property for $\eta \in 0, 1$ (and to all order for equal weights) while Reeve's framework satisfies this property whatever η . However, this last framework is not correct for similarity sensitive case i.e., when phylogenetic or functional information is incorporated to the indices (see Appendix 1 of [Chao et al. \(2014\)](#) for a counter example). However, the framework is correct when no phylogenetic or functional information is used (as in the presented diversity indices) as shown in S2.1.2 of [Reeve et al. \(2014\)](#). We encourage the reader to use Reeve's framework with special care.

3.2.1 Notations

The relative abundance of the group q in the local network k is p_{qk} , giving the matrix \mathbf{P} of group abundances (so that $\sum_{1 \leq q \leq Q, 1 \leq k \leq K} P_{qk} = 1$). The relative group abundances in the local network k is $\mathbf{P}_{\cdot \mathbf{k}}$ and it constitutes a fraction $\omega_k^p = \sum_{1 \leq q \leq Q} P_{qk}$ of total group abundances. The normalized relative group abundances in the local network k is $\overline{\mathbf{P}}_{\cdot \mathbf{k}} = \frac{\mathbf{P}_{\cdot \mathbf{k}}}{\omega_k^p}$ (so that $\sum_{1 \leq q \leq Q} \overline{P}_{qk} = 1$). It follows that $p^{meta} = \sum_{1 \leq k \leq K} \omega_k^p \overline{\mathbf{P}}_{\cdot \mathbf{k}}$

Similarly, the relative link abundance between groups q and l in the local network k is L_{qlk}^* , giving the matrix of link abundances in the local network k , $\mathbf{L}_{\cdot \cdot \mathbf{k}}^*$ and the tensor of order three $\mathbf{L}^* = (L_{qlk}^*)$ of link abundances (so that $\sum_{1 \leq q, l \leq Q, 1 \leq k \leq K} L_{qlk}^* = 1$). If we note C_k the connectance of the local network k and $\overline{\mathbf{L}}_{\cdot \cdot \mathbf{k}}$ the normalized link abundances of the network k (so that $\sum_{1 \leq q, l \leq n} \overline{L}_{qlk} = 1$), we have $\overline{\mathbf{L}}_{\cdot \cdot \mathbf{k}} = \frac{\mathbf{L}_{\cdot \cdot \mathbf{k}}^*}{\omega_k^L}$, with $\omega_k^L = \frac{C_k}{\sum C_p}$ (see next subsection for proof). We have then $\mathbf{L}_{meta}^* = \sum_{1 \leq k \leq K} \omega_k^L \overline{\mathbf{L}}_{\cdot \cdot \mathbf{k}}$ (see next subsection for a proof).

Moreover, the relative link probability between groups q and l in the local network k is π_{qlk}^* , giving the matrix of link probabilities in the local network k , $\mathbf{\Pi}_{\cdot, \mathbf{k}}^*$, and the tensor of order three $\mathbf{\Pi}^* = (\pi_{qlk}^*)$ of link probabilities (so that $\sum_{1 \leq q, l \leq Q, 1 \leq k \leq K} \pi_{qlk}^* = 1$). The matrix of link probabilities in the local network k , $\mathbf{\Pi}_{\cdot, \mathbf{k}}^*$, constitutes a fraction $\omega_k^\pi = \sum_{1 \leq q, l \leq Q} \pi_{qlk}^*$ of total link probabilities. The normalized matrix of link probabilities in the local network k is $\overline{\mathbf{\Pi}}_{\cdot, \mathbf{k}} = \frac{\mathbf{\Pi}_{\cdot, \mathbf{k}}^*}{\omega_k^\pi}$ (so that $\sum_{1 \leq q, l \leq Q} \overline{\mathbf{\Pi}}_{\cdot, \mathbf{k}} = 1$). We have then $\mathbf{\Pi}_{\text{meta}}^* = \sum_{1 \leq k \leq K} \omega^\pi \overline{\mathbf{\Pi}}_{\cdot, \mathbf{k}}$

3.2.2 Weights on the networks when assessing link diversity

By definition :

$$\omega_k^L = \sum_{1 \leq q, l \leq Q} L_{qlk}^*$$

where L_{qlk}^* is an element of the tensor of relative link abundances L . This tensor is normalized so that $\sum_{1 \leq q, l \leq Q, 1 \leq k \leq K} L_{qlk}^* = 1$. By denoting L_{qlk} the absolute link abundance between group q and l in the network k and C_k the connectance of the network k , we have (from Eq. 7) :

$$C_k = \sum_{q, l} L_{qlk}$$

and

$$\sum_k C_k = \sum_{q, l, k} L_{qlk}$$

Since $\frac{\sum_{q, l} L_{qlk}^*}{\sum_{q, l, k} L_{qlk}^*} = \frac{\sum_{q, l} L_{qlk}}{\sum_{q, l, k} L_{qlk}}$, it follows :

$$\omega_k^L = \frac{C_k}{\sum_k C_k}$$

3.3 Reeve's framework

We first define the power mean function of order η of \mathbf{X} weighted by \mathbf{u} , where \mathbf{X} and \mathbf{u} are either a vectors or matrices.

If \mathbf{X} and \mathbf{u} are vectors and μ a positive real number:

$$M_\mu(\mathbf{u}, \mathbf{X}) = \begin{cases} \left(\sum_q u_q X_q^\mu \right)^{\frac{1}{\mu}} & \text{if } \mu \neq 0 \\ \exp \left(\sum_q u_q \log(X_q) \right) & \text{if } \mu = 0 \end{cases}$$

If \mathbf{X} and \mathbf{u} are matrices and μ a positive real number:

$$M_\mu(\mathbf{u}, \mathbf{X}) = \begin{cases} \left(\sum_{q, l} u_{ql} X_{ql}^\mu \right)^{\frac{1}{\mu}} & \text{if } \mu \neq 0 \\ \exp \left(\sum_{q, l} u_{ql} \log(X_{ql}) \right) & \text{if } \mu = 0 \end{cases}$$

The local α -diversities (groups, link abundances and link probabilities) of the network k are defined as :

$$\alpha_{P, k}^\eta = M_{1-\eta} \left(\overline{\mathbf{P}}_{\cdot, \mathbf{k}}, \frac{1}{\overline{\mathbf{P}}_{\cdot, \mathbf{k}}} \right)$$

$$\alpha_{L, k}^\eta = M_{1-\eta} \left(\overline{\mathbf{L}}_{\cdot, \mathbf{k}}, \frac{1}{\overline{\mathbf{L}}_{\cdot, \mathbf{k}}} \right)$$

$$\alpha_{\Pi, k}^\eta = M_{1-\eta} \left(\overline{\mathbf{\Pi}}_{\cdot, \mathbf{k}}, \frac{1}{\overline{\mathbf{\Pi}}_{\cdot, \mathbf{k}}} \right)$$

The overall α -diversities are :

$$A_P^\eta = M_{1-\eta}(\omega^P, \alpha_P^\eta)$$

$$A_L^\eta = M_{1-\eta}(\omega^L, \alpha_L^\eta)$$

$$A_\Pi^\eta = M_{1-\eta}(\omega^\pi, \alpha_\Pi^\eta)$$

The local β -diversities of the network k are defined as :

$$\beta_{P,k}^\eta = \frac{1}{M_{1-\eta}(\overline{\mathbf{P}\cdot k}, \overline{\mathbf{p}^{\text{meta}}/\mathbf{P}\cdot k})}$$

$$\beta_{L,k}^\eta = \frac{1}{M_{1-\eta}(\overline{\mathbf{L}\cdot k}, \overline{\mathbf{L}^{\text{meta}}/\mathbf{L}\cdot k})}$$

$$\beta_{\Pi,k}^\eta = \frac{1}{M_{1-\eta}(\overline{\mathbf{\Pi}\cdot k}, \overline{\mathbf{\Pi}^{\text{meta}}/\mathbf{\Pi}\cdot k})}$$

The overall β -diversities are defined as :

$$B_P^\eta = M_{1-\eta}(\omega^{\mathbf{P}}, \beta_P^\eta)$$

$$B_L^\eta = M_{1-\eta}(\omega^{\mathbf{L}}, \beta_L^\eta)$$

$$B_\Pi^\eta = M_{1-\eta}(\omega^\pi, \beta_\Pi^\eta)$$

The local γ -diversities of the network k are defined as :

$$\gamma_{P,k}^\eta = M_{1-\eta}(\overline{\mathbf{P}\cdot k}, 1/\mathbf{p}^{\text{meta}})$$

$$\gamma_{L,k}^\eta = M_{1-\eta}(\overline{\mathbf{L}\cdot k}, 1/\mathbf{L}^{\text{meta}})$$

$$\gamma_{\Pi,k}^\eta = M_{1-\eta}(\overline{\mathbf{\Pi}\cdot k}, 1/\mathbf{\Pi}^{\text{meta}})$$

The overall γ -diversities are defined as :

$$G_P^\eta = M_{1-\eta}(\omega^{\mathbf{P}}, \gamma_P)$$

$$G_L^\eta = M_{1-\eta}(\omega^{\mathbf{L}}, \gamma_L)$$

$$G_\Pi^\eta = M_{1-\eta}(\omega^\pi, \gamma_\Pi)$$

The range of variation of the overall diversity indices are the same as these presented in table 1 for $\eta = 1$ using the Chao's framework.

3.3.1 Jost's Framework

The α -diversities for $\eta \neq 1$ are defined as :

$$A_P^\eta = \frac{\left(\sum_k (\omega_k^P)^\eta \left(\sum_q \overline{P_{qk}^\eta} \right) \right)^{\frac{1}{1-\eta}}}{\left(\sum_k (\omega_k^P)^\eta \right)}$$

For $\eta = 1$, it converges towards the same index than the one presented in the previous section (i.e. A_P^1). It ranges between 1 and the number of groups in the metanetwork.

$$A_L^\eta = \frac{\left(\sum_k (\omega_k^L)^\eta \left(\sum_{q,l} \overline{L_{qlk}^\eta} \right) \right)^{\frac{1}{1-\eta}}}{\left(\sum_k (\omega_k^L)^\eta \right)}$$

For $\eta = 1$, it converges towards the same index than the one presented in the previous section (i.e. A_L^1). It ranges between 1 and the number of links in the metanetwork.

$$A_\Pi^\eta = \frac{\left(\sum_k (\omega_k^\Pi)^\eta \left(\sum_{q,t} \overline{\Pi_{qtk}^\eta} \right) \right)^{\frac{1}{1-\eta}}}{\left(\sum_k (\omega_k^\Pi)^\eta \right)}$$

For $\eta = 1$, it converges towards the same index than the one presented in the previous section (i.e. A_Π^1). It ranges between 1 and the number of links in the metanetwork.

The γ -diversities are defined as :

$$G_P^\eta = M_{1-\eta}(\mathbf{p}^{\text{meta}}, 1/\mathbf{p}^{\text{meta}})$$

It ranges between 1 and the number of groups in the metanetwork.

$$G_L^\eta = M_{1-\eta}(\mathbf{L}^{\text{meta}}, 1/\mathbf{L}^{\text{meta}})$$

$$G_{\Pi}^\eta = M_{1-\eta}(\mathbf{\Pi}^{\text{meta}}, 1/\mathbf{\Pi}^{\text{meta}})$$

It ranges between 1 and the number of links in the metanetwork. The β -diversities are defined as

$$B_P^\eta = \frac{G_P^\eta}{A_P^\eta}$$

$$B_L^\eta = \frac{G_L^\eta}{A_L^\eta}$$

$$B_{\Pi}^\eta = \frac{G_{\Pi}^\eta}{A_{\Pi}^\eta}$$

However, for $\eta \neq 1$, α -diversity can exceed γ -diversity (Jost 2007). So, these indices must be used for $\eta = 1$ (or with equal weights for any η value). In this case ($\eta = 1$), the β diversities have the following ranges (Jost 2007) :

$$1 \leq B_P^1 \leq M_1(\omega^{\mathbf{P}}, \frac{1}{\omega^{\mathbf{P}}})$$

$$1 \leq B_L^1 \leq M_1(\omega^{\mathbf{L}}, \frac{1}{\omega^{\mathbf{L}}})$$

$$1 \leq B_{\Pi}^1 \leq M_1(\omega^{\mathbf{\Pi}}, \frac{1}{\omega^{\mathbf{\Pi}}})$$

Dissimilarity measures can be built from β -diversity as presented in section 2.1 (using only $\eta = 1$ for the case of unequal weights).

3.4 Link with existing frameworks

While we originally defined our framework and associated indices for the general case of weighted networks (weights on links and abundances of nodes), they are obviously applicable to unweighted networks. In this particular instance, our framework generalizes the metrics developed by Poisot *et al.* (2012) to assess the diversity of unweighted networks. In addition to species turnover (β_S , Sorensen index on species composition), the authors proposed to measure the dissimilarity of links (β_{WN} , Sorensen index on links) and to partition it in an additive way between a component that measures the plasticity of interactions (β_{OS}) and a component that measures the links turnover due to species turnover (β_{ST}). We propose to show that, at a microscopic scale for a binary network, $\delta_P^0 = \beta_S$, $\delta_L^0 = \beta_{WN}$ and $\delta_{\Pi}^0 = \beta_{OS}$ (using Chao's framework).

Let consider two networks G_1 and G_2 , we note V_1, V_2 the corresponding sets of nodes and E_1, E_2 the corresponding set of edges. Let G_{meta} be the metanetwork, defined (in the case of binary networks) as the union of G_1 and G_2 (i.e. $V_{meta} = V_1 \cup V_2$ and $E_{meta} = E_1 \cup E_2$).

Poisot's diversity indices (β_S and β_{WN}) consist in Sorensen dissimilarity index on sets of nodes and links of the two networks. We have :

$$\beta_S = \frac{|V_1| + |V_2| - 2|V_1 \cap V_2|}{|V_1| + |V_2|}$$

where $|\cdot|$ denotes the cardinal function. Moreover :

$$\beta_{WN} = \frac{|E_1| + |E_2| - 2|E_1 \cap E_2|}{|E_1| + |E_2|}$$

δ_P^0 consists in Sorensen dissimilarity index on nodes of G_1 and G_2 (i.e. species composition, Chao & Chiu 2016), so $\delta_P^0 = \beta_S$. Similarly, δ_L^0 consists in Sorensen dissimilarity index on edges of G_1 and G_2 , so $\delta_L^0 = \beta_{WN}$.

We now show that $\delta_{\Pi}^0 = \beta_{OS}$. To do so, we introduce the induced subgraph function *ind.sub*. Let G be a network and V a subset of $V(G)$. *ind.sub*(G, V) is the network whose nodes are V and edges are $E = E(G) \setminus (q, l) / (q \notin V \vee l \notin V)$. We note $V^\cap = V_1 \cap V_2$, $G_1^\cap = \text{ind.sub}(G_1, V^\cap)$ and $G_2^\cap = \text{ind.sub}(G_2, V^\cap)$. The set of nodes of these graphs are V^\cap and we note E_1^\cap and E_2^\cap their

sets of edges.. In order to estimate the probability of interaction between species q and l in the network k , π_{qlk}^* , we need to observe at least one individual of species q and l in the network k . Consequently, in order to compute probabilities of interaction, we only consider species that belong to V^\cap . In the case of the two considered networks, the dimension of Π is then $|V^\cap| * |V^\cap| * 2$. Poiset's measure of plasticity of interactions is :

$$\beta_{OS} = \frac{|E_1^\cap| + |E_2^\cap| - 2|E_1^\cap \cap E_2^\cap|}{|E_1^\cap| + |E_2^\cap|}$$

At a microscopic level, δ_Π^0 consists in the Sorensen dissimilarity index on the edges of G_1^\cap and G_2^\cap . Consequently, $\delta_\Pi^0 = \beta_{OS}$.

4 Simulation study

Here, we simulate the change in the structure of an ecological network along a gradient (Fig. S3a) and show that the observed network diversity strongly depends on the aggregation level at which the network is considered. For simplicity, we hypothesized that we have a prior knowledge of the groups.

We assume that we observe three groups (C_1, C_2, C_3), each containing 100 species, along an environmental gradient. We assume no species turnover along the gradient. In other words, at each location of the gradient, the local species pool is the regional species pool. At a given location t within the gradient, the matrix of link probabilities Π_t^* between the groups is thus given by:

$$\begin{pmatrix} C_1 & C_2 & C_3 \\ 0 & 0 & 0 \\ c-t & 0 & 0 \\ c+t & 0 & 0 \end{pmatrix} \begin{matrix} C_1 \\ C_2 \\ C_3 \end{matrix} \quad (1)$$

At a species level, the network is binary and its edges are drawn in independent Bernoulli laws of parameters depending on the group of species (the interaction between two species from group q and l is a random event that occurs with a probability of π_{qlt}^*). Two species belonging to the same group are equivalent in the sense that they have the same link probabilities with all the other species. However, globally, the species are not equivalent since they do not all have the same probability of interacting. Moreover, the link probabilities between groups change along the gradient. This simulation setting may reflect the interactions between a group of rodents (C1) and two groups of parasites (C2, C3), where we observed a variation in parasitic interactions following a shift in the rodents' phenology induced by climate (see [Poisot et al. 2017](#)).

We now propose to analyze network diversity at micro-, meso-, and macroscopic scales along the gradient. The groups are evenly distributed along the gradient since they contain 100 species each (i.e. $p_{C_1} = p_{C_2} = p_{C_3} = \frac{1}{3}$). The expected value of the connectance (i.e. macroscopic diversity) at a location t in the gradient, $E(C_t)$, is then (Eq. 8):

$$E(C_t) = \frac{c-t}{3} + \frac{c+t}{3} = \frac{2c}{3} \quad (2)$$

Therefore, the expected value of connectance is constant along the gradient and consequently, no pattern can appear at a macroscopic scale along the gradient.

We now propose to evaluate the dissimilarity of probabilities of interactions between each pair of networks along the gradient at both the microscopic (species-level) and mesoscopic (group level) scales using δ_Π^1 .

We used 21 values of t , regularly spaced across a range of -0.05 and 0.05 to represent the environmental gradient and set $c = 0.1$. At each point t of the gradient, we randomly sampled 200 networks. We then computed, on any two locations t_1 and t_2 in the gradient, the value of δ_Π^1 at a microscopic and mesoscopic scales. We then visualize δ_Π^1 at both aggregation level for each pair of values of t , revealing two different patterns (Fig. S3b and S3c). The simulation highlights that patterns of network diversity strongly depend on the aggregation level at which the network is considered. At the macroscopic scale, no spatial structure emerges, since the connectance is constant along the gradient. At the microscopic scale, the interaction rewiring is too high to distinguish

any structure. The dissimilarity values shifted from 0 along the diagonal to high values on the off-diagonal terms. However, at the mesoscopic scale, we can observe the dissimilarity pattern since the dissimilarity values slowly increase around the diagonal. As a result, this encourages one to look beyond species to investigate the spatial and temporal diversity of networks.

Points locations
Berghaus star projection

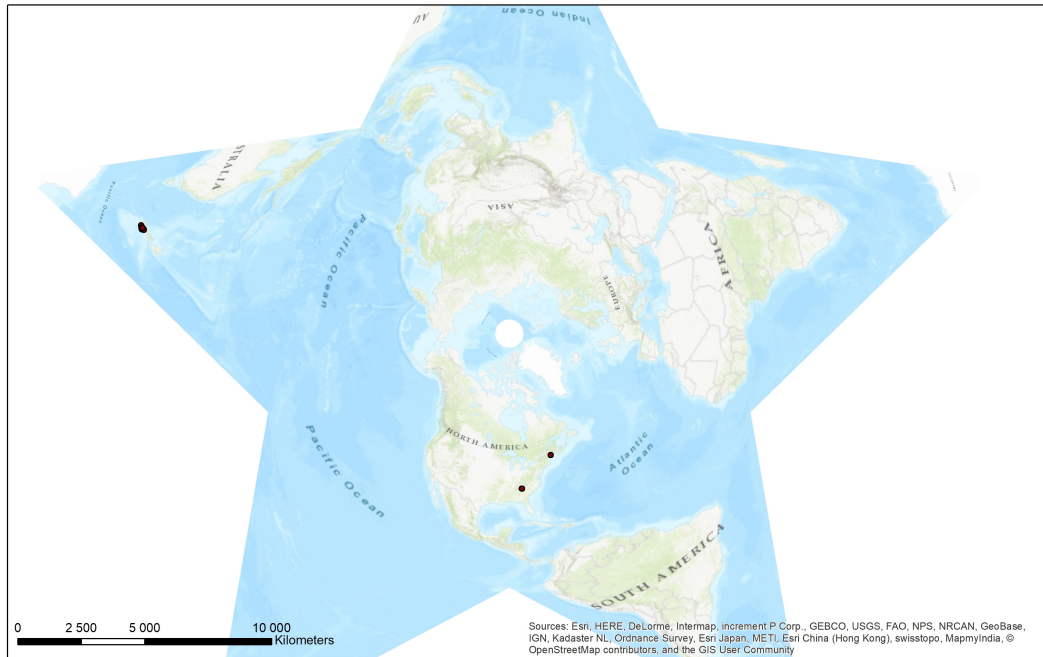


Figure S1: Locations of the ten trophic networks described in [Thompson & Townsend \(2003\)](#). Six networks were sampled in the USA and four networks in New Zealand



Figure S2: The metanetwork built from the 10 stream trophic networks. We only kept the largest connected component that contains 532 species and has a connectance value of 0.01. The network was visualized using the Gephi software (force Atlas 2 algorithm).

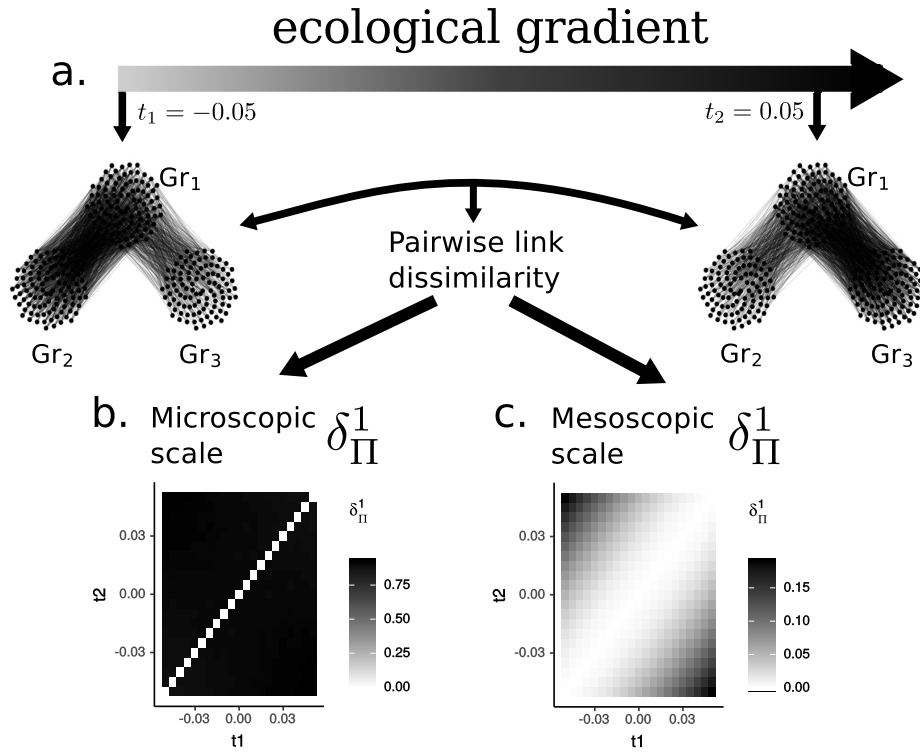


Figure S3: Change of network structure along an ecological gradient (a.) in function of two species aggregation levels (species and three equivalent groups of species in terms of probability of interactions with the others groups). We assess and represent the pairwise dissimilarity in link probabilities (δ_{Π}^1) at both a microscopic (b.) and mesoscopic scales (c.).

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