

METHOD

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

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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 emphasise the importance of analysing 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 analysing their variation across environmental gradients and time.

Keywords

Hill numbers, interaction network diversity, Metanetwork, species aggregation level.

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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 analysing 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 analyse 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 generalises 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 conceptualised as subsets of a regional species pool, local ecological networks are realisations 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 organisation of life on Earth (Pellissier *et al.* 2017) and its effects on ecosystem functioning and associated services (Brose & Hillebrand 2016). The realisation, 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 behavioural 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.

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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 four mathematical properties (see Jost 2010): (1) α and β should be mathematically unrelated; (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) γ should be completely determined by α and β ; (4) α cannot be larger than γ . A fifth 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 four properties, and the fifth 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 generalisation 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 summarise the structure of a network through a single quantity (Poisot *et al.* 2012, 2016; Pellissier *et al.* 2017) – but none of them satisfy the five 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 formalise 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 characterising 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 data set 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 in the R package *econetwork* available on CRAN (<https://cran.r-project.org>), 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 generalise 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 realisation of an interaction event at the individual level (Albert *et al.* 2010; Gonzalez-Varo & Traveset 2016). 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:

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

$$L_{ql} = \pi_{ql} p_q p_l \tag{2}$$

where

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

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 .

$$\tilde{p}_q = \sum_{k \in C_q} p_k \tag{4}$$

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 .

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

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

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

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

$$s = \frac{Q}{n} \tag{7}$$

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

Table 1 Notations, name of the different indices and ranges of values

Object	Name	Total margin
\mathbf{p}	Vector of relative group abundances	$\sum_{1 \leq q \leq Q} p_q = 1$
\mathbf{L}	Matrix of link abundances	$\sum_{1 \leq q, l \leq Q} L_{ql} = C$
$\mathbf{\Pi}$	Matrix of link probabilities (adjacency matrix of the weighted network)	$\sum_{1 \leq q, l \leq Q} \pi_{ql}$
\mathbf{P}	Matrix of group abundances of groups (metanetwork case)	$\sum_{q=1}^Q \sum_{k=1}^K P_{qk} = K$
\mathbf{L}	Tensor of links abundances (metanetwork case)	$\sum_{q,l=1}^Q \sum_{k=1}^K L_{qlk} = \sum_{k=1}^K C_k$
$\mathbf{\Pi}$	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^n	Overall α -diversity in group abundances	
		Average diversity in group abundances across local networks	$1 \leq A_p^n \leq Q$
	A_L^n	Overall α -diversity in link abundances	
		Average diversity in link abundances across local networks	$1 \leq A_L^n \leq N_L$
	A_{Π}^n	Overall α -diversity in link probabilities	
		Average diversity in link probabilities across local network	$1 \leq A_{\Pi}^n \leq N_L$
γ -diversity	G_p^n	γ -diversity in group abundances	
		Diversity in group abundances of the metanetwork	$1 \leq G_p^n \leq Q$
	G_L^n	γ -diversity in link abundances	
		Diversity in link abundances of the metanetwork	$1 \leq G_L^n \leq N_L$
	G_{Π}^n	γ -diversity in link probabilities	
		Diversity in link probabilities of the metanetwork	$1 \leq G_{\Pi}^n \leq N_L$
β -diversity	B_p^n	β -diversity of group abundances	
		Effective numbers of distinct communities of groups	$1 \leq B_p^n \leq K$
	B_L^n	β -diversity of link abundances	
		Effective numbers of distinct networks	$1 \leq B_L^n \leq K$
	B_{Π}^n	β -diversity of link probabilities	
		Effective numbers of distinct networks (with abundances rescaled at evenly distributed values)	$1 \leq B_{\Pi}^n \leq K$
dissimilarity	δ_p^n	Dissimilarity of group abundances	
		Effective average proportion of shared groups	$0 \leq \delta_p^n \leq 1$
	δ_L^n	Dissimilarity of link abundances	
		Effective average proportion of shared links	$0 \leq \delta_L^n \leq 1$
	δ_{Π}^n	Dissimilarity of link probabilities	
		Effective average proportion of shared links (with abundances rescaled at evenly distributed values)	$0 \leq \delta_{\Pi}^n \leq 1$

Notes. 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 .

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.

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

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:

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

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 $\eta = 1$, eqn 8 is not defined but it converges towards the exponential of the Shannon entropy :

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

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:

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

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:

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

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

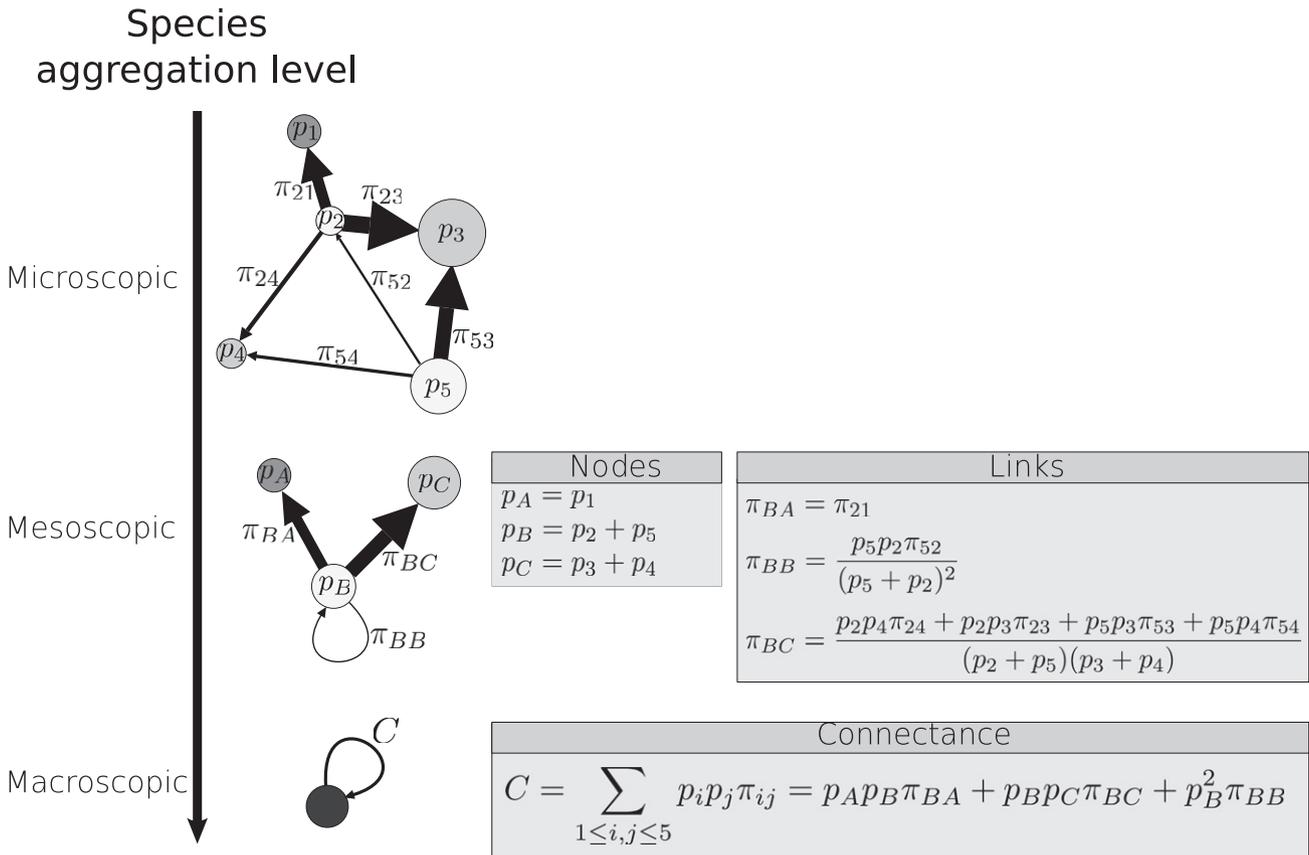


Figure 1 Navigating through species aggregation levels. From the original weighted network to image networks at mesoscopic and macroscopic scales, with the formulas giving the group abundances and link probabilities of the image networks.

$D^n(\Pi)$ is unrelated to $D^n(\mathbf{p})$ (*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 $D^n(\mathbf{L})$ which are therefore related. These last two indices translate into an effective numbers of links, either weighted ($D^n(\mathbf{L})$) or not ($D^n(\Pi)$) by the group abundances. Note that ($D^n(\Pi)$) 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 realisations 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 four 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:

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

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:

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

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

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

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:

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

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:

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

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

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

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

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

$$B_P = \frac{G_P}{A_P} \tag{19}$$

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:

$$B_L = \frac{G_L}{A_L} \tag{20}$$

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:

$$B_{\Pi} = \frac{G_{\Pi}}{A_{\Pi}} \tag{21}$$

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

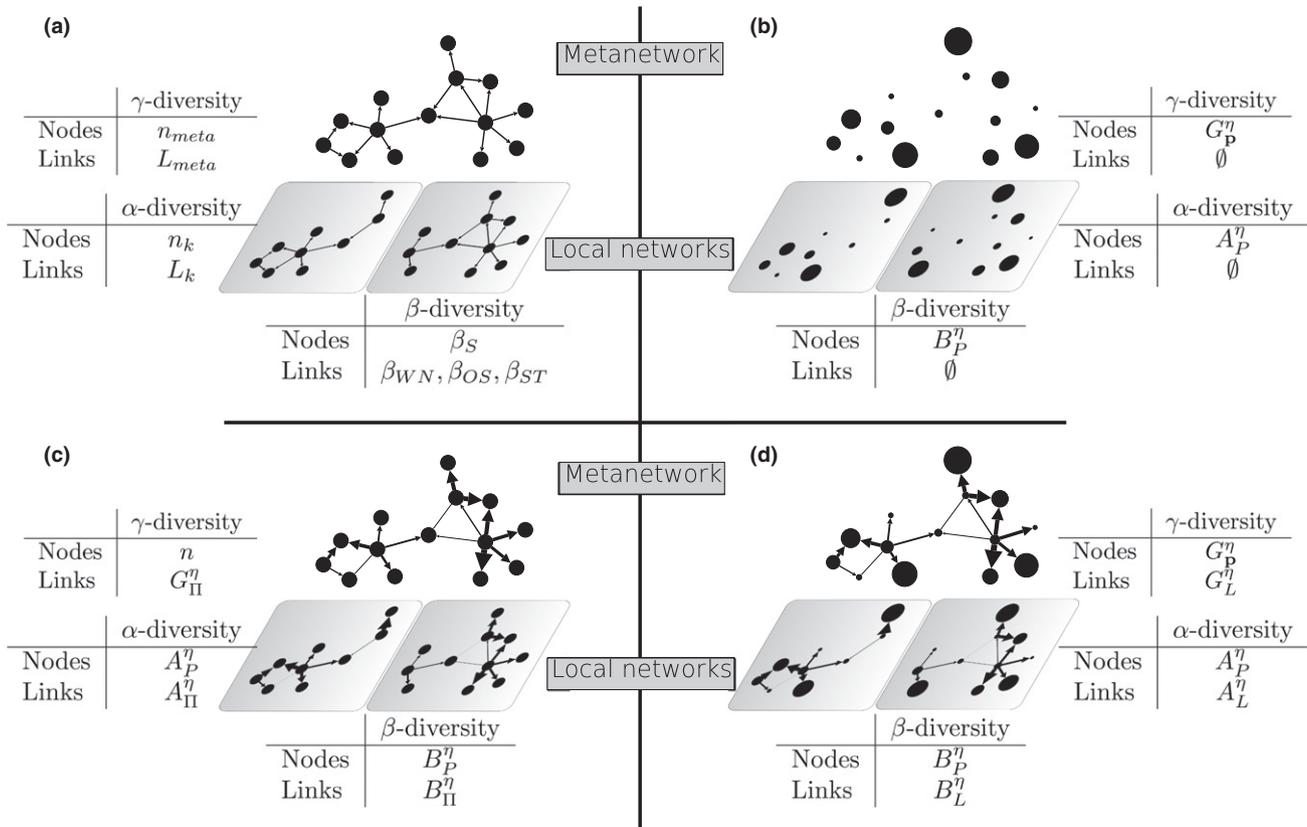


Figure 2 The metanetwork and the local realised networks in different cases: (a) binary network, unweighted links and without node abundances, (b) node abundances but absence of links, (c) weights on links but no node abundances and (d) weights and links and node abundances. The different indices to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

Overlap measures can be built from β -diversity to obtain dissimilarity measures (Jost 2007, 2010; Chao & Chiu 2016). A class of parameterised 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 the R package *econetwork* available on CRAN (<https://www.cran.r-project.org>).

APPLICATION TO A CASE STUDY: WHEN THE AGGREGATION LEVEL REVERSES THE ASSESSMENT OF THE DRIVERS OF NETWORK DISSIMILARITY

Here, we re-analysed a data set used in Thompson & Townsend (2003). Using groups built *a priori* with 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 novel framework together with trophic groups built using the topology of the metanetwork (Allesina & Pascual 2009; Gauzens *et al.* 2015). We hypothesised 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 data set 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

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)	Herzlzer	<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

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 analyse the mesoscopic network dissimilarity is 14/532. We thereafter computed the dissimilarity matrices of link and group abundances at the microscopic and mesoscopic scales (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 was 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

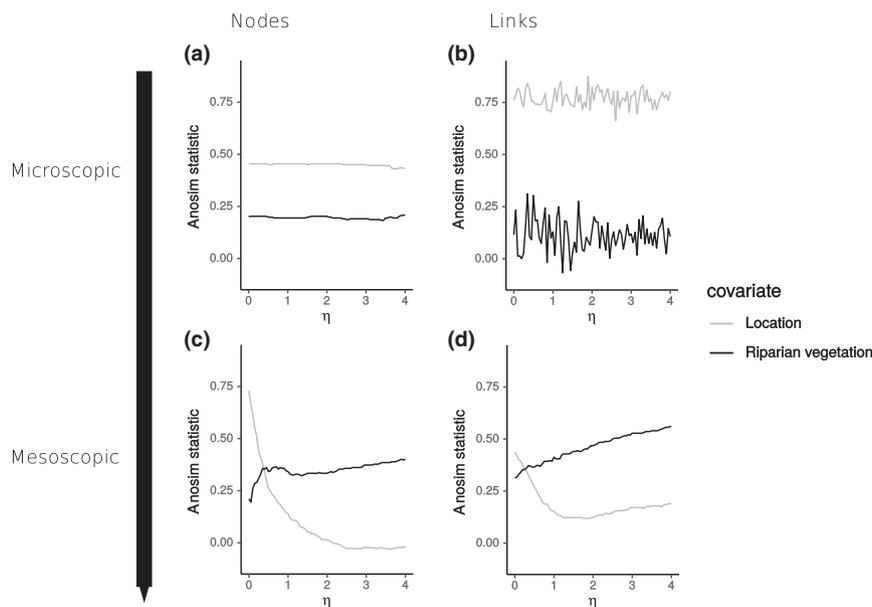


Figure 3 Assessing the drivers of dissimilarity in group abundances and link abundances at different species aggregation levels. Relative importance (ANOSIM statistic) of the location vs. the riparian vegetation regarding the (a) microscopic pairwise dissimilarity in groups abundances (δ_P^η at a microscopic scale) (b) microscopic pairwise β -diversity in link abundances (δ_L^η at a microscopic scale) (c) mesoscopic pairwise dissimilarity in group abundances (δ_P^η at a mesoscopic scale) (d) mesoscopic pairwise dissimilarity in link abundances (δ_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 dissimilarity).

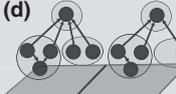
Local network		Networks in space and time														
Network aggregation	(a)  To what extent do ecological processes shape network structure?	(c)  To what extent do ecological processes shape networks across space and time at a species level?														
	<i>Studies:</i> Cohen et al. 2003 Dormann et al. 2017 (review)	<i>Studies:</i> Caradonna et al. 2017 Tylianakis & Morris 2017 (review)														
	<i>Hypothesis:</i> Traits and eco-evolutionary processes shape network structure	<i>Hypothesis:</i> Species composition and interactions change across space and time														
	<i>Diversity index</i> $C, D^n(\mathbf{p}), D^n(\mathbf{L}), D^n(\mathbf{\Pi})$	<table border="1" style="width: 100%; text-align: center;"> <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>A_P^n, G_P^n</td> <td>A_{Π}^n, G_{Π}^n</td> <td>A_L^n, G_L^n</td> </tr> <tr> <td>B_P^n, δ_P^n</td> <td>$B_{\Pi}^n, \delta_{\Pi}^n$</td> <td>$B_L^n, \delta_L^n$</td> </tr> </tbody> </table>				<i>Mechanisms</i>			Change in species composition	Change that alters probability of interactions	Change in energy fluxes	A_P^n, G_P^n	A_{Π}^n, G_{Π}^n	A_L^n, G_L^n	B_P^n, δ_P^n	$B_{\Pi}^n, \delta_{\Pi}^n$
<i>Mechanisms</i>																
Change in species composition	Change that alters probability of interactions	Change in energy fluxes														
A_P^n, G_P^n	A_{Π}^n, G_{Π}^n	A_L^n, G_L^n														
B_P^n, δ_P^n	$B_{\Pi}^n, \delta_{\Pi}^n$	B_L^n, δ_L^n														
(b)  To what extent can species in a network be aggregated into groups while preserving the overall structure?	(d)  To what extent do ecological processes shape networks across space and time at a (trophic) group level?															
<i>Studies:</i> Allesina & Pascual 2009 Gauzens et al. 2015 Cirtwill et al. 2018 (review)	<i>Studies:</i> Thompson & Townsend 2003 (groups formed a priori) This study															
<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	<i>Hypothesis:</i> (Trophic) groups composition and interactions change across space and time															
<i>Diversity index</i> $D^n(\mathbf{p}), D^n(\mathbf{L}), D^n(\mathbf{\Pi})$ (meso)	<table border="1" style="width: 100%; text-align: center;"> <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>A_P^n, G_P^n (meso)</td> <td>A_{Π}^n, G_{Π}^n (meso)</td> <td>A_L^n, G_L^n (meso)</td> </tr> <tr> <td>B_P^n, δ_P^n</td> <td>$B_{\Pi}^n, \delta_{\Pi}^n$</td> <td>$B_L^n, \delta_L^n$</td> </tr> </tbody> </table>				<i>Mechanisms</i>			Change in (trophic) groups composition	Change that alters probability of interactions between groups	Change in energy fluxes	A_P^n, G_P^n (meso)	A_{Π}^n, G_{Π}^n (meso)	A_L^n, G_L^n (meso)	B_P^n, δ_P^n	$B_{\Pi}^n, \delta_{\Pi}^n$	B_L^n, δ_L^n
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B_P^n, δ_P^n	$B_{\Pi}^n, \delta_{\Pi}^n$	B_L^n, δ_L^n														

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.

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 (Thompson *et al.* 2012; Pellissier *et al.* 2017; 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 (Poisot *et al.* 2016; Pellissier *et al.* 2017). 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 a set of diversity indices that address each of these

requirements. The proposed framework is a generalisation of the Hill numbers 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 data set 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 and expert 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 (Alessina & 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, summarises 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 (Supporting Information) 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 hypothesise 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 (Héroult 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.

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AUTHORSHIP

MO developed a draft version of the framework that was further elaborated with WT. VM, SD, WT and MO conceptualised the final version of the framework. LO and LC gave additional perspectives to the paper. MO and WT wrote the first version of the paper and all authors contributed substantially to the revisions.

DATA ACCESSIBILITY STATEMENT

We used an open data set : https://www.nceas.ucsb.edu/interactionweb/resources.html#predator_prey. The code used to generate the simulated data is provided in section 5 of the Supporting Information. We implemented the method in the

R package *econetwork* available on CRAN (<https://cran.r-project.org>).

REFERENCES

- Albert, C.H., Thuiller, W., Yoccoz, N.G., Douzet, R., Aubert, S. & Lavorel, S. (2010). A multi-trait approach reveals the structure and the relative importance of intra- vs. interspecific variability in plant traits. *Funct. Ecol.*, *24*, 1192–1201.
- Allesina, S. & Pascual, M. (2009). Food web models: a plea for groups. *Ecol. Lett.*, *12*, 652–662.
- Barnes, A.D., Jochum, M., Mumme, S., Haneda, N.F., Farajallah, A., Widarto, T.H. & Brose, U. (2014). Consequences of tropical land use for multitrophic biodiversity and ecosystem functioning. *Nat. Commun.*, *5*, 5351.
- Belmaker, J., Sekercioglu, C.H. & Jetz, W. (2012). Global patterns of specialization and coexistence in bird assemblages. *J. Biogeogr.*, *39*, 193–203.
- Bersier, L.F., Banasek-Richter, C. & Cattin, M.F. (2002). Quantitative descriptors of food-web matrices. *Ecology*, *83*, 2394–2407.
- Bohan, D.A., Vacher, C., Tamaddoni-Nezhad, A., Raybould, A., Dumbrell, A.J. & Woodward, G. (2017). Next-generation global biomonitoring: large-scale, automated reconstruction of ecological networks. *Trends Ecol. Evol.*, *32*, 477–487.
- Brose, U. & Hillebrand, H. (2016). Biodiversity and ecosystem functioning in dynamic landscapes. *Philos. Trans. R. Soc. Lond. B, Biol. Sci.*, *371*.
- CaraDonna, P.J., Petry, W.K., Ross, M.B., Cunningham, J.L., Bronstein, J.L., Waser, N.M. *et al.* (2017). Interaction rewiring and the rapid turnover of plant–pollinator networks. *Ecol. Lett.*, *20*, 385–394.
- Carstensen, D.W., Sabatino, M., Trøjsgaard, K. & Morellato, L.P.C. (2014). Beta diversity of plant–pollinator networks and the spatial turnover of pairwise interactions. *PLoS ONE*, *9*, 1–7.
- Chalmandrier, L., Münkemüller, T., Lavergne, S. & Thuiller, W. (2015). Effects of species' similarity and dominance on the functional and phylogenetic structure of a plant meta-community. *Ecology*, *96*, 143–153.
- Chao, A. & Chiu, C.H. (2016). Bridging the variance and diversity decomposition approaches to beta diversity via similarity and differentiation measures. *Methods Ecol. Evol.*, *7*, 919–928.
- Chao, A., Chiu, C.H. & Jost, L. (2014a). Unifying species diversity, phylogenetic diversity, functional diversity, and related similarity and differentiation measures through hill numbers. *Annu. Rev. Ecol. Evol. Syst.*, *45*, 297–324.
- Chao, A., Gotelli, N.J., Hsieh, T.C., Sander, E.L., Ma, K.H., Colwell, R.K. *et al.* (2014b). Rarefaction and extrapolation with hill numbers: a framework for sampling and estimation in species diversity studies. *Ecol. Monogr.*, *84*, 45–67.
- Clarke, K.R. (1993). Non-parametric multivariate analyses of changes in community structure. *Aust. J. Ecol.*, *18*, 117–143.
- Daudin, J.J., Picard, F. & Robin, S. (2008). A mixture model for random graphs. *Stat. Comput.*, *18*, 173–183.
- Dunne, J. (2006). The network structure of food webs. In: *Ecological Networks: Linking Structure to Dynamics in Food Webs* (eds Pascual, M. & Dunne, J.A.). Oxford University Press, Oxford, pp. 27–86.
- Ellison, A.M. (2010). Partitioning diversity. *Ecology*, *91*, 1962–1963.
- Elton, C.S. (1927). *Animal Ecology*. Macmillan Co., New York. <https://www.biodiversitylibrary.org/bibliography/7435>
- Gaston, K.J. (2003). *The Structure and Dynamics of Geographic Ranges*. Oxford University Press on Demand, Oxford.
- Gauzens, B., Thébault, E., Lacroix, G. & Legendre, S. (2015). Trophic groups and modules: two levels of group detection in food webs. *J. R. Soc. Interface*, *12*, 20141176.
- Gonzalez-Varo, J.P. & Traveset, A. (2016). The labile limits of forbidden interactions. *Trends Ecol. Evol.*, *31*, 700–710.
- Graham, C.H., Storch, D. & Machac, A. (2018). Phylogenetic scale in ecology and evolution. *Glob. Ecol. Biogeogr.*, *27*, 175–187.
- Gravel, D., Massol, F., Canard, E., Mouillot, D. & Mouquet, N. (2011). Trophic theory of island biogeography. *Ecol. Lett.*, *14*, 1010–1016.
- Hawkins, B.A., Field, R., Cornell, H.V., Currie, D.J., Guégan, J.F., Kaufman, D.M. *et al.* (2003). Energy, water, and broad-scale geographic patterns of species richness. *Ecology*, *84*, 3105–3117.
- Héroult, B. (2007). Reconciling niche and neutrality through emergent group approach. *Perspect. Plant. Ecol.*, *9*, 71–78.
- Hill, M.O. (1973). Diversity and evenness: a unifying notation and its consequences. *Ecology*, *54*, 427–432.
- von Humboldt, A. (1805). *Essai sur la géographie des plantes; accompagné d'un tableau physique des régions équinoxiales*. Levrault, Paris.
- Jost, L. (2006). Entropy and diversity. *Oikos*, *113*, 363–375.
- Jost, L. (2007). Partitioning diversity into independent alpha and beta components. *Ecology*, *88*, 2427–2439.
- Jost, L. (2010). Independence of alpha and beta diversities. *Ecology*, *91*, 1969–1974.
- Kéfi, S., Miele, V., Wieters, E.A., Navarrete, S.A. & Berlow, E.L. (2016). How structured is the entangled bank? The surprisingly simple organization of multiplex ecological networks leads to increased persistence and resilience. *PLoS Biol.*, *14*, 1–21.
- Lavorel, S. & Garnier, E. (2002). Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the holy grail. *Funct. Ecol.*, *16*, 545–556.
- Leger, J.B., Daudin, J.J. & Vacher, C. (2015). Clustering methods differ in their ability to detect patterns in ecological networks. *Methods Ecol. Evol.*, *6*, 474–481.
- Lindeman, R.L. (1942). The trophic-dynamic aspect of ecology. *Ecology*, *23*, 399–417.
- Luck, G.W., Lavorel, S., McIntyre, S. & Lumb, K. (2012). Improving the application of vertebrate trait-based frameworks to the study of ecosystem services. *J. Anim. Ecol.*, *81*, 1065–1076.
- Luczkovich, J.J., Borgatti, S.P., Johnson, J.C. & Everett, M.G. (2003). Defining and measuring trophic role similarity in food webs using regular equivalence. *J. Theor. Biol.*, *220*, 303–321.
- Massol, F., Dubart, M., Calcagno, V., Cazelles, K., Jacquet, C., Kéfi, S. & Gravel, D. (2017). Island biogeography of food webs. *Adv. Ecol. Res.*, *56*, 183–262.
- Mazel, F., Wüest, R.O., Lessard, J.P., Renaud, J., Ficetola, F.G., Lavergne, S. *et al.* (2017). Global patterns of beta-diversity along the phylogenetic time-scale: the role of climate and plate tectonics. *Glob. Ecol. Biogeogr.*, *26*, 1211–1221.
- Münkemüller, T., Gallien, L., Lavergne, S., Renaud, J., Roquet, C., Abdulhak, S. *et al.* (2014). Scale decisions can reverse conclusions on community assembly processes. *Glob. Ecol. Biogeogr.*, *23*, 620–632.
- Newman, M. & Leicht, E. (2007). Mixture models and exploratory analysis in networks. *Proc. Natl Acad. Sci.*, *104*, 9564–9569.
- Pellissier, L., Albouy, C., Bascompte, J., Farwig, N., Graham, C., Loreau, M. *et al.* (2017). Comparing species interaction networks along environmental gradients. *Biol. Rev.*, *93*, 785–800.
- Poisot, T., Canard, E., Mouillot, D., Mouquet, N. & Gravel, D. (2012). The dissimilarity of species interaction networks. *Ecol. Lett.*, *15*, 1353–1361.
- Poisot, T., Cirtwill, A.R., Cazelles, K., Gravel, D., Fortin, M.J. & Stouffer, D.B. (2016). The structure of probabilistic networks. *Methods Ecol. Evol.*, *7*, 303–312.
- Reeve, R., Leinster, T., Cobbold, C., Thompson, J.N., Brummitt, M. & Matthews, L. (2014). How to partition diversity. *arXiv:1404.6520*.
- Rényi, A. (1961). On measures of entropy and information. In: *Proceedings of the Fourth Berkeley Symposium on Mathematical Statistics and Probability, Volume 1: Contributions to the Theory of Statistics* (ed Neyman, J.). University of California Press, Berkeley, CA, pp. 547–561.

- Routledge, R. (1979). Diversity indices: which ones are admissible? *J. Theor. Biol.*, 76, 503–515.
- Thompson, R.M. & Townsend, C.R. (2003). Impacts on stream food webs of native and exotic forest: an intercontinental comparison. *Ecology*, 84, 145–161.
- Thompson, R.M., Brose, U., Dunne, J.A., Hall, R.O., Hladyz, S., Kitching, R.L. *et al.* (2012). Food webs: reconciling the structure and function of biodiversity. *Trends Ecol. Evol.*, 27, 689–697.
- Tucker, C.M., Cadotte, M.W., Carvalho, S.B., Davies, T.J., Ferrier, S., Fritz, S.A. *et al.* (2016). A guide to phylogenetic metrics for conservation, community ecology and macroecology. *Biol. Rev.*, 92, 698–715.
- Tylianakis, J.M. & Morris, R.J. (2017). Ecological networks across environmental gradients. *Annu. Rev. Ecol. Syst.*, 48, 25–48.
- Whittaker, R.H. (1960). Vegetation of the siskiyou mountains, oregon and california. *Ecol. Monogr.*, 30, 279–338.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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