LETTER

The dissimilarity of species interaction networks

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Abstract

In a context of global changes, and amidst the perpetual modification of community structure undergone by most natural ecosystems, it is more important than ever to understand how species interactions vary through space and time. The integration of biogeography and network theory will yield important results and further our understanding of species interactions. It has, however, been hampered so far by the difficulty to quantify variation among interaction networks. Here, we propose a general framework to study the dissimilarity of species interaction networks over time, space or environments, allowing both the use of quantitative and qualitative data. We decompose network dissimilarity into interactions and species turnover components, so that it is immediately comparable to common measures of β-diversity. We emphasise that scaling up β-diversity of community composition to the β-diversity of interactions requires only a small methodological step, which we foresee will help empiricists adopt this method. We illustrate the framework with a large dataset of hosts and parasites interactions and highlight other possible usages. We discuss a research agenda towards a biogeographical theory of species interactions.

Keywords

β-diversity, food web, metaweb, species interaction networks.

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INTRODUCTION

Integrating network theory to biogeography is among the most important and exciting challenges that macroecologists are currently facing (Cumming *et al.* 2010), yet the idea that species interactions have a biogeographical structure of their own is often overlooked (Beck *et al.* 2012). Achieving this integration is necessary to progress towards understanding species interactions through time and space (Kissling *et al.* 2011), and doing so to predict species geographical distributions and their variations in an ever-changing world. While the theoretical literature is progressing rapidly with this regard (e.g. Leibold *et al.* 2004; Gravel *et al.* 2011a,b; Massol *et al.* 2011; Pillai *et al.* 2011; Winegardner *et al.* 2012), the development of toolboxes and methodological frameworks to describe the variation of species interactions is in its infancy (Baselga 2010; Krasnov *et al.* 2011; Poulin *et al.* 2011). We suggest that such methods can be developed from the simple observation that local ecological networks are strongly contingent on local species composition, the realisation of their potential interactions and are drawn from a common regional pool of both species and interactions (Holt 1996, Holt 2002).

Dunne (2006) coined this regional pool of species and their potential interactions a metaweb. Understanding how local realisations relate to it paves the way to the development of a biogeography of species interactions. Given the multiple drivers of local community composition (species filtering, historical contingencies and stochasticity), only a subset of species will be present at each locality, thus potentially realising only a subsample (the α diversity)

of all the possible interactions found in the metaweb (the γ diversity; Fig. 1). For this reason, we call a local network drawn from a regional metaweb a *realisation*. The metaweb can be reconstructed by aggregating these local networks sampled at different times, in different localities or under different environmental conditions. Quantifying to which extent realisation varies, both between themselves and when compared to the metaweb, can bear important informations towards a better understanding of, at least, environmental (Woodward *et al.* 2010) and human impacts (O'Gorman *et al.* 2012) on network structure, especially as recent research highlighted how knowing the food-web structure is key in predicting both the functioning (Thébault & Loreau 2003) and the consequences of warming on functioning (Sarmento *et al.* 2010) in complex ecosystems. It will also help address the relative influence of neutral (Krishna *et al.* 2008; Canard *et al.* 2012) vs. niche processes on species interactions and the scaling of specialisation (Poulin *et al.* 2011). In addition, because local communities are non-random samples from the regional species pool (Ricklefs 1987), the properties of local networks will differ from the metaweb. Laying out this work is an important task, as it will allow characterizing the diversity of interactions in space, which is the first step in developing a predictive theory of spatial food-web ecology (Gravel *et al.* 2011a,b).

Networks are made of nodes (species) linked by edges (ecological interactions): both these objects can experience turnover over time and space, and contribute to the dissimilarity between local networks. Complexity arises from the fact that the occurrence of interactions is not independent from species composition, as both

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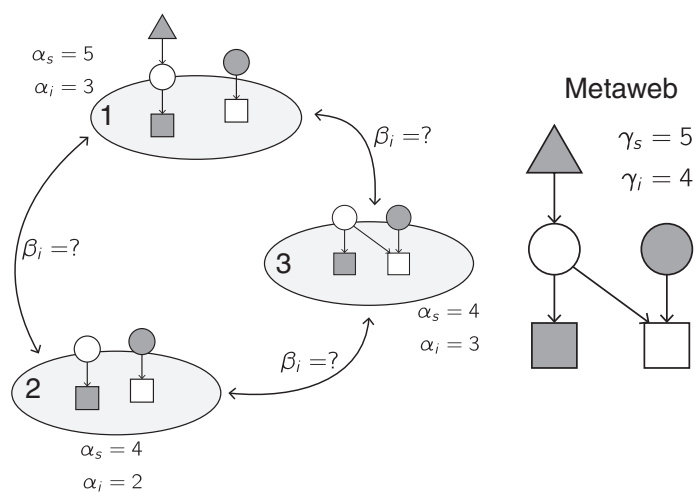
Figure 1 Five species regional network (metaweb – on the right-hand side), with two primary producers (squares), two consumers (circles) and one top predator (triangle). Three local realisations (in the grey patches) are shown. The metaweb can be built by integrating all the interactions at the largest possible scale. Complexity stems from the fact that some interactions found in the metaweb (i.e. between the white round and the white square species) may not occur at all locations. Although it is easy to measure α and γ diversities for the species (s subscript) or interactions (i subscript), there is no available method to measure the β-diversity of the later. We propose such an approach in this article.

of these objects can experience correlated or uncorrelated turnover over time and space, and contribute to the dissimilarity between local networks. Previous authors like Havens (1992) assumed that species co-occurence was a sufficient condition for a potential interaction to realise itself. Although it makes sense to view co-occurence as a necessary condition for the occurrence of an interaction, it is by no means a sufficient one (Allesina *et al.* 2008; Olesen *et al.* 2011). Typically, even when they co-occur, species of plants and pollinators may not interact because of phenological differences (Vázquez 2005) or because one of them is rare (Canard *et al.* 2012). Some other interactions may only be possible if a third species, or interaction between other species, is present (see examples in Golubski & Abrams 2011; Poisot *et al.* 2011a), or when the environment is favourable enough (Poisot *et al.* 2011b). This explains why even simple experimental designs resulted in complex patterns of network structure with major changes over an environmental gradient (Poisot *et al.* 2011b). All of these mechanisms may promote variation in network structure, even though there is little to no variation in species composition. Quantifying the dissimilarity of species interactions thus appears to be a more complex task than it is for dissimilarity of community composition.

The challenge lies in finding a meaningful way to measure the dissimilarity between interaction networks (Dale & Fortin 2010), which will account for the turnover of both species and their interactions. There were previous attempts at developing a methodology for network comparison in ecology. Some methods allow the algorithmic comparison of multiple networks in which no species are found in common (Faust & Skvoretz 2002; Dale & Fortin 2010), and are primarily concerned about the overall statistical properties of networks. Similarly, some authors used multivariate analyses of network metrics to estimate their level of similarity (e.g. Vermaat *et al.* 2009; Baiser *et al.* 2011, , 2012), or statistically compared a subset of metrics of interest (e.g. nestedness or modularity Flores *et al.* 2011; Poisot *et al.* 2011b). These methods are primarily concerned about the similarity of networks as mathematical objects (in that they focus on network-wide, emergent properties, such as nestedness, connectance and so forth), and less about the similarity of their ecology. Poisot *et al.* (2011b) proposed a method to evaluate the amount to which interactions are gained or lost along environmental gradients through pairwise network comparison, but this method neglects possible changes in species loss or gain. However, as local community composition is subjected to important variations (see e.g. Koleff *et al.* 2003; Anderson *et al.* 2011), dissimilarity of interaction networks needs to be partitioned between its compositional and purely 'interactive' components (Canard 2011).

We set a framework for the measurement of pairwise network dissimilarity, accounting both for species and interaction turnover through space, time or along environmental gradients, which is general enough to work on any type of network and accomodate any β-diversity measure. This framework can be expanded to assess multiple-network dissimilarity. We assess through simulations the robustness of the framework to sampling effort. By applying this framework on a robust dataset of host and ectoparasites networks, we report no correlation between species β-diversity and interactions β-diversity, suggesting that species and interactions can be locally sorted through different mechanisms. We provide guidelines for the interpretation of the results, and recommendations for the sampling and reconstruction of networks through space or time.

THE DISSIMILARITY OF NETWORKS

Additive partitioning

Table 1 synthesises our partitioning of diversity. Differences in interactions between networks (β_{WN}) originate from differences in species composition (β_{ST}, dissimilarity in interaction structure introduced by dissimilarity in species composition), and because shared species between the two realisations may interact differently (β_{OS},

Table 1 Synthetic view of the components of network dissimilarity. The contribution of species dissimilarity to the dissimilarity of networks is determined indirectly from the fraction of network dissimilarity explained by species dissimilarity alone (β_{ST})

Measure	Definition	Items	Ref.
β_S	Dissimilarity in the species composition of communities	Species identity	e.g. Koleff *et al.* (2003)
β_{OS}	Dissimilarity of interactions established between species common to both realisations	Interactions of shared species	Canard (2011)
β_{WN}	Dissimilarity of interactions	All interactions	Canard (2011)
β_{ST}	Dissimilarity of interactions due to species turnover	Eqn 1	This study
β'_{OS}	Dissimilarity between a local network and its counterpart in the metaweb		This study
β_{ST}/β_{WN}	Contribution of species dissimilarity to network dissimilarity		This study

dissimilarity of interactions in co-occuring species). This leads to an additive view of network dissimilarity, wherein:

$$\beta_{WN} = \beta_{ST} + \beta_{OS}. \tag{1}$$

By definition, β_{WN} and β_{ST}, but not β_{OS}, will covary with the species composition dissimilarity between networks (β_S). Given that β_{OS} (dissimilarity of interactions between shared species) is a component of β_{WN}, the inequality $\beta_{OS} \le \beta_{WN}$ is always satisfied, and β_{ST} takes values between 0 (dissimilarity between two networks is entirely explained by shared species interacting differently), and β_{WN} (the shared species interact in the same way, and all the difference between the two networks is explained by species turnover). Because differences in network structure can arise either through changes in species compositions or realised interactions, there is no obvious analytical solution for β_{ST}, which is found by removing the impact of dissimilarity of interactions on the total dissimilarity between networks as indicated above.

Indices of network dissimilarity

We follow the widespread approach put forth by Koleff *et al.* (2003) to measure network dissimilarity, which consists in a re-expression of classical measures of disimilarity based on a partition of shared and total items. Items (species, interactions etc.) found in two realised networks A and B, are divided into three sets (c, b and a) for which we measure the cardinality (number of members). This information is summed up in a vector termed the 'realisation membership' M, which takes the following form:

$$M = [c = \|A \notin B\|, b = \|B \notin A\|, a = \|A \cap B\|] \tag{2}$$

With this notation, c is the number of items (e.g. number of species, or number of interactions) unique to realisation A, b the count of items unique to realisation B and a the count of shared items, meaning that $c + b + a$ sums to the number of species (or interactions) in the aggregation of the two networks. The definition of 'items' varies for each partition (Table 1). For β_S, items are species identity of the metaweb. For β_{OS}, all species found only at realisations A or B are removed, so that the resulting A and B networks have all their species in common; in this case, items are the remaining interactions. For β_{WN}, we do not remove remove unique species at each realisation, so all interactions are taken into account (the a component will have the same size as that in β_{OS}, as shared interactions necessitate shared species – thus, β_{OS} is always a subset of β_{WN}). We will illustrate this procedure using β_w (Whittaker 1960) as the measure of dissimilarity. With a realisation membership M as defined in eqn 2, dissimilarity is then measured by:

$$\beta_w(M) = \frac{a + b + c}{(2a + b + c)/2} - 1 \tag{3}$$

Extension to multisite dissimilarity

Although different measures can be used to calculate dissimilarity (including different ones for species and interactions dissimilarity, or quantitative β-diversity measures like Bray–Curtis), the use of β_w seems desirable in the context of networks: this measure takes the value of 1 when sets are perfectly non-overlapping, and a value of 0 in case of perfect overlap, which is a useful property to guide interpretation (Faith *et al.* 1987) as it translates directly into a pairwise distance between networks. In addition, this measure is easily transposed into a multisite approach. Diserud & Odegaard (2007) showed that the Sørensen measure of dissimilarity, expanded to T sites having a regional richness (or number of interactions) S_T, and each site having a local richness n, is defined by

$$C_S^T = \frac{T}{T-1}\left(1 - \frac{S_T}{\sum_i n_i}\right), \tag{4}$$

and that it is possible to go back to β_w through the simple transformation

$$\beta_w = T - C_S^T(T-1) - 1 \tag{5}$$

To stay coherent with the notation of eqn 3, we express this last result as $\beta_w - 1 = (T-1) \times (1 - C_S^T)$. When all species are found at all sites, this takes the value of 0. When no species are in common, this takes the value of $T-1$. We thus range this measure, so that the value we report is $\beta_w - 1 = 1 - C_S^T$.

It is thus possible to measure a β_{WN}^T and a β_S^T by counting, respectively, the number of interactions and the number of species. However, how to obtain β_{OS}^T under this framework will require mathematical developments much beyond the conceptual framework presented in this study. Pairwise, β_{OS} requires to only look at interactions between shared species. As the turnover of taxonomic diversity will increase, we expect that the number of species common to all realisations will decrease, and using the interactions between them to calculate the β_{OS}^T will result in much loss of resolution. To circumvent this problem, we propose a different approach to the across-site dissimilarity in multiple species interaction networks in Appendix S1.

Theoretical examples

We use three simple realisations of the metaweb depicted in Fig. 1 to illustrate our framework. Despite their apparent simplicity, they encompass all of the building blocks needed to construct the more complex scenarios found in nature: networks can differs either because species composition differ across samples, because shared species interact in different ways or because of a combination of the above; we illustrate these three cases in turn. Networks 1 and 2 differ in that network 1 has one more species than network 2, while the interactions between shared species are similar. This configuration results in $\beta_{OS(1 \leftrightarrow 2)} = \beta_w([a = 2, b = 0, c = 0]) = 0$, and $\beta_{WN(1 \leftrightarrow 2)} = \beta_w([a = 2, b = 1, c = 0]) = 0.2$: there is no interaction dissimilarity for shared species, but the loss of the top predator in network 2 triggers a difference in the whole-network dissimilarity. Following eqn 1, we have $\beta_{ST(1 \leftrightarrow 2)} = 0.2$, meaning that the whole-network dissimilarity (β_{WN}) is explained by the difference in species composition. Networks 2 and 3 differ in that, despite sharing all of their species, network 3 has one supplementary interaction. This results in $\beta_{OS(2 \leftrightarrow 3)} = \beta_w([a = 2, b = 1, c = 0]) = 0.2$, and $\beta_{WN(2 \leftrightarrow 3)} = \beta_w([a = 2, b = 1, c = 0]) = 0.2$. The network dissimilarity is fully explained by different interactions between the two realisations.

The difference between networks 1 and 3 is perhaps the most likely situation to occur in nature, as it incorporates both causes of dissimilarity (i.e. species and interactions turnover). Network 1 has one more interaction than network 3 due to the presence of the top predator, whereas network 3 has one more interaction than network 1 due to the interaction between some shared species. This

results in $\beta_{OS(1\leftrightarrow3)} = \beta_w([a = 2, b = 1, c = 0]) = 0.2$, and $\beta_{WN(1\leftrightarrow3)} = \beta_w([a = 2, b = 1, c = 1]) \approx 0.33$. From this, it comes that $\beta_{ST(1\leftrightarrow3)} \approx 0.11$: the dissimilarity of network structure has both a compositional and an interactive component. The relative influence of these components can be expressed in a more intuitive way, by stating that the relative impact of compositional difference is given by $(\beta_{ST}/\beta_{WN}) \times 100 = 33\%$. This relatively low value is explained by the fact that the unique species is a specialist (i.e. establishes only one interaction), and thus has a small impact on the overall network structure. In addition, given that β_{ST} is indirectly affected by β_S, the relative importance of a variation in the identity of species and interactions will differ in networks of different sizes and heterogeneity. As the networks in these examples are unrealistically small, it is not worth reading too much into the values of the different components; these examples are intended to highlight how the framework functions.

These theoretical examples are easy to make sense of. Networks 2 and 3 are similar in terms of species composition, but not in terms of interaction composition. Networks 1 and 2 are somehow similar in terms of species compositon (and species compositions between them are nested, Krasnov *et al.* 2011), and share all their interactions between shared species. Their only difference stems from one species being only present in network 1. Finally, networks 1 and 3 are the most dissimilar, with interactions differing between shared species, and species composition differing. These simple examples show how, by decomposing the dissimilarity of whole-network structure (β_{WN}) into two additive components, one compositional (β_{ST}) and one interactive (β_{OS}), we are able to not only express how much two networks are different, but also to pinpoint the source of this variation.

We can measure the multisite dissimilarity of these three example networks, using our adaptation of the Diserud & Odegaard (2007) method. The multisite species diversity is $\beta_S^T = 0.075$. The multi-site whole-network dissimilarity is $\beta_{WN}^T = 0.25$. This result indicates that, at the scale of the three sites, interactions experience more turnover than species (which is intuited, given that the overlap between the three patches is strong). Given that there is only one species which is not shared between the three sites (the top predator unique to patch 1), it is possible to calculate β_{OS}^T without loosing too much information. To do so, we calculate the network dissimilarity by removing the top predator and its single interaction both from patch 1 and from the total count of species/interactions. This yields a value of $\beta_{OS}^T = 0.14$, which indicates that the structure of interactions is rather well conserved, regionally. As for the pairwise case, β_{ST}^T is found by substraction, with $\beta_{ST}^T = 0.11$. The last step of calculating β_{OS}^T can only be done if there are enough species common to all realisations. Nonetheless, this simple example shows how we can approach the multiple-site dissimilarity of species interactions networks. We detail in Appendix S1 a method for all situations, which additionally allows comparing multiple-site dissimilarity between metawebs.

ROBUSTNESS TO SAMPLING EFFORT

One traditional obstacle in network studies is that accurately sampling all interactions can be a daunting task: it is possible that some interactions will not be detected because they are unfrequently established, or because the species establishing them are rare, thus more difficult to detect. An important number of methodological advances were made to either come up with recommendations about how to design the study (e.g. Berlow *et al.* 2004), or to conceive metrics robust to sampling effort (e.g. Blüthgen *et al.* 2006; Poisot *et al.* 2012). In addition to common issues related to the sampling of interaction networks, working in the metaweb introduces the need to account for two novel features: the size of local realisations relative to the metaweb, and the exhaustivity with which interactions were sampled in each realisation. Here, we test the robustness of our new metrics of network dissimilarity to these two issues. We do so by conducting simulations with a theoretical reference metaweb of 50 species and connectance (the ratio of the number of established interactions over the number of potential interactions – with S species and L interactions, connectance is L/S^2) of 0.3, generated using the classical niche model algorithm (Williams & Martinez 2000).

The ratio of the realisation size compared to the metaweb is a contingency that could affect network dissimilarity: just by chance alone, two small realisations of a large metaweb are expected to have much less species and interactions in common than large realisations. This effect will be stronger for species-composition components than for interaction components, provided that the consistency of interactions between realisations is high. We therefore conducted a simple simulation to assess the effect of the relative sizes of two realised networks on the components of network turnover. We did so by varying the ratio of sizes between one large realisation of the metaweb of fixed size S_1 and one smaller realisation of varying size S_2. We express this ratio as $\Delta_S = \log_{10}(S_1/S_2)$. A Δ_S of 0 means that the two networks have the same size. We first draw from the metaweb one random realisation of 40 species, with no unconnected species. We then draw 1000 random realisations for each number of species ranging from 4 to 40. We find that changes in relative realisation size do not affect the behavior of β_{OS}, which is focused on overlapping species (Fig. 2a). As β_{ST} is found by removing β_{OS} from β_{WN}, it is as robust as these two measures are, and as such exhibits the same reaction to the networks having different sizes.

A second issue with sampling networks is missing interactions due to insufficient efforts (Martinez *et al.* 1999; Vázquez *et al.* 2007; Dormann *et al.* 2009; Poisot *et al.* 2012). If interactions are unequally sampled in different realisations, we would expect an inflated β_{OS} component, as networks will appear artificially more dissimilar than they actually are. We simulated decreasing sampling effort by randomly extracting two realisations from the metaweb described above. For each of them, we removed a fixed number of interactions at random, and measured the absolute error on estimating the dissimilarity of interactions based on the partial sampling. The error is expressed as $\varepsilon = (X - X')^2$, where X and X' are respectively the values of the dissimilarity component on the completely and partially sampled realisations. The situations ranged from all interactions correctly sampled to 99% of the interactions missed. For each probability of missing an interaction, 1000 replicates were conducted. The results of this analysis are presented in Fig. 2b. We find that our framework is robust to incomplete sampling as, even when half of the interactions are missed (which is in itself an already extreme scenario), β_{OS} accumulates a total error equal to 5×10^{-2}. In Appendix S2, we conduct simulations showing that our framework performs equally well when both species and interactions are not correctly sampled, provided that the sampling of species is not too sparse (i.e. not sparser than the sampling of interactions).
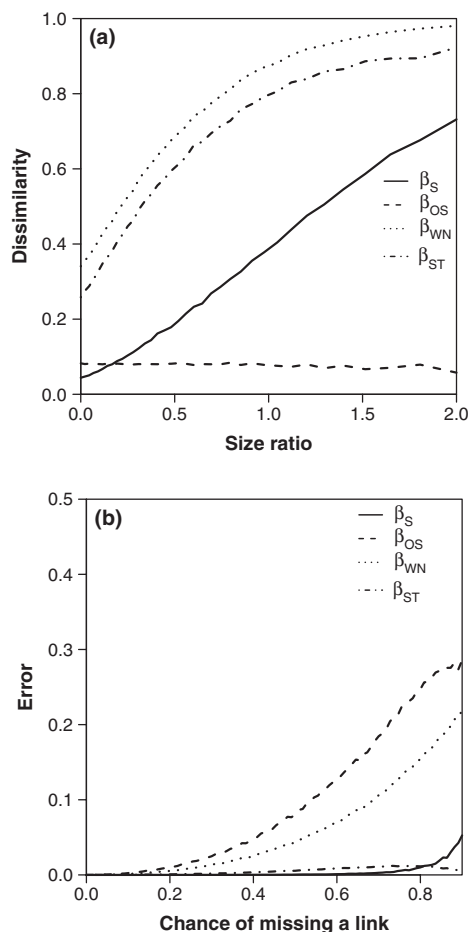
Figure 2 Results of the simulations. (a) Consequences of working on realisations of different sizes. Changes in network size resulted in metrics interacted to species composition dissimilarity increasing, but β_{OS} is insensitive to this effect. (b) Consequences of missing interactions during sampling. Both β_{OS} and β_{WN} are extremely robust, and β_S and β_{ST} are largely unaffected. After 1000 realisations, the standard deviation is extremely small, and for this reason is not presented here.

DISSIMILARITY OF EMPIRICAL NETWORKS

### Patterns of dissimilarity between parasitic communities

We analyse the spatial patterns of dissimilarity in parasitic interactions obtained from 113 communities of small rodents from central Europe (Stanko *et al.* 2002). These data are bipartite networks, but our method can work indiscriminately on all types of networks. Data were collected in central Europe over a period of 15 years. A high proportion of species are found at several locations but experience high spatial turnover, thus making β-diversity analyses meaningful between them. The metaweb is constructed by aggregating all of the observed interactions, that is, whenever two species are found to interact in at least one realisation, they are assigned one interaction in the metaweb. Given that all networks were thoroughly sampled at several times, we confidently assume that the metaweb is a correct image of the interactions in the system (see the second application). However, some pairs of species may potentially interact given their traits, but as their environmental niches do not overlap, they do not realise any interaction (Olesen *et al.* 2011).

We partition β-diversity between all pairs of sites. The results are presented in Fig. 3. As expected, β_{WN} increases with β_S, e.g. when the communities were increasingly dissimilar in terms of species composition, the whole-network dissimilarity follows the same trend. However, there is no clear pattern linking β_S to β_{OS}, which is expected as this later component is focusing only on shared species, and consequently eliminates compositional differences. This result also shows that β_{OS} conveys unique information to our understanding of community structure. The contribution of species turnover to network turnover, β_{ST}, increases strongly and linearly with β_S, which reinforces the importance of why species and interactions turnover should be decomposed. This result should be expected, as the more networks will become dissimilar in term of species composition, the less differences in interactions between shared species will be important. Finally, we observe that values of β_{OS} are consistently lower than values of β_{WN}, as is intuitive given that β_{WN} is the total turnover in the network. These results emphasise that when attempting to compare networks in the light of how a shared set of species interact, β_{OS} carries more unique information than β_{WN}. Confronting panels a and b of Fig. 3 is convincingly telling us why we should integrates species interactions into our understanding of classical biogeography. Although the dissimilarity in the whole-network structure (β_{WN}) increases with the dissimilarity in the species compositions (β_S), the same is not true for the dissimilarity of interactions established by shared species (β_{OS}). This suggests that environmental filtering of species and interactions are different, and the degree to which two networks vary with regard to their species compositions is not a reliable predictor of the dissimilarity of interactions between shared species.

Test for the completeness of sampling

As previously mentioned, sampling all the species and interactions in the metaweb is perhaps the core methodological issue. We use an approach based on rarefaction curves (Gotelli & Colwell 2001; Ricotta *et al.* 2012) to illustrate how a better understanding of network dissimilarity can help to evaluate the completeness of sampling. Each realisation of the metaweb is an independent sample. We use a bootstrap approach to estimate how many interactions and species were recovered at a given sampling effort (i.e. number of realisations – 500 random draws were made per level of sampling effort), by resampling the Stanko *et al.* (2002) dataset. For each level of sampling effort *n*, we draw at random *n* realisations from the pool of 113 realisations, and reconstruct a partial metaweb $\mathbf{M}'_n$. We then measure the different components of networks dissimilarity between the empirical metaweb (i.e. as reconstructed from the integration of all the realisations) and the bootstrapped one, yielding an indication of the degree of sampling completeness. We observe that while the species rarefaction curve is reaching the saturation point for species richness (Fig. 4a), meaning that most of the taxonomic diversity was sampled, the number of interactions is still far from the plateau (Fig. 4b). This last result indicates that some realised interactions were not sampled, and that metaweb may not be entirely exhaustive.

The evaluation of average network dissimilarity among realisations is also useful to assess metaweb sampling quality. We evaluate two important metrics of network structure, the connectance (number of interactions relative to the size of the network) and nestedness (the tendency of specialists to exploit a subset of the niche of more
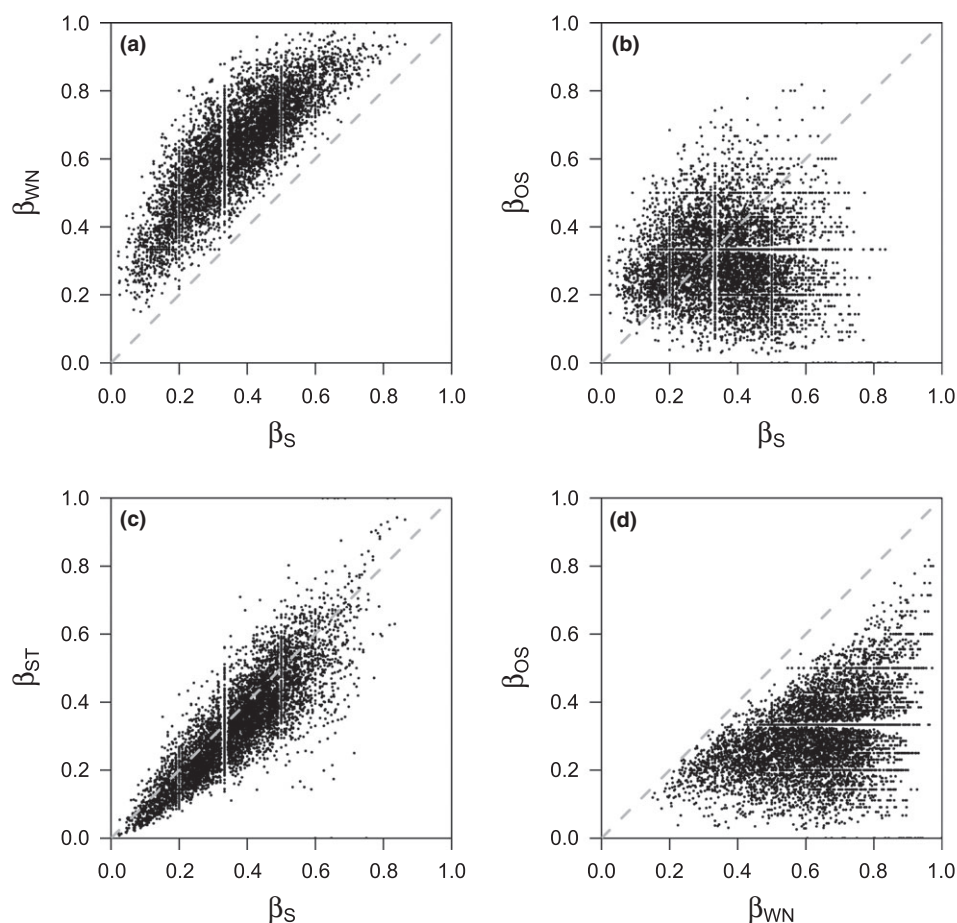
Figure 3 Relationships between the partitions of diversity on all possible pairs between 113 networks. The dashed grey line indicates the 1:1 relationship.

generalist species, Almeida-Neto *et al.* 2008), at the scale of the metaweb, with increasing sampling effort. We find that while the species and interactions are not all entirely sampled, the value of these two metrics are correctly estimated when *c.* 30 realisations are sampled (Fig. 4c). This result indicates that, although perfectly sampling the metaweb can be an extremely daunting task, a satisfying approximation of it structural properties can be quite easily obtained. We propose that the metrics of dissimilarity described in this article can directly be used to assess the completeness of metaweb sampling. For each of the 500 replicates conducted for each sampling effort, we reconstruct the metaweb and compare it to the metaweb reconstructed with the 113 realisations (i.e. what is assumed to be the most exhaustive knowledge of the metaweb). If sampling is complete, we expect that all components of dissimilarity will become asymptotically close to 0 as *n* increases. Indeed, if all the interactions are correctly sampled, bringing in a new network will not add to our knowledge of either species or interactions, and the metaweb aggregated from a random pool of $n - 1$, $n - 2, \ldots$ networks will not be different from the complete one aggregated over the *n* samples. Should all the species and interactions have been entirely sampled, the values of all the dissimilarity components should be at 0 for high sampling efforts. As we show in Fig. 4d, we find that whereas it is nearly the case for β_S and β_{ST}, thus confirming the results of Fig. 4a, the values of β_{OS}, and thus β_{WN}, are still steadily decreasing with each new sampled realisation, confirming that not all the interactions are known.

POTENTIAL APPLICATIONS

Network structure is a key theme for numerous ecological topics, including ecosystem stability (May 1972; Allesina & Pascual 2007; Rooney & McCann 2012), functioning (Duffy 2002) and resilience to exploitation or species extinction (Worm & Duffy 2003; Worm *et al.* 2006). It is therefore crucial to (1) understand how dissimilar interaction networks are across environments, time and space (Link 2002), and (2) predict how the structure of interactions will be affected by global changes (Gilman *et al.* 2010), a task which is often overlooked in favour of predicting species or traits loss (Bellard *et al.* 2012). Meynard *et al.* (2011) highlighted the need to integrate the multiple axes of biodiversity (α, β and γ on one hand, and phylogenetic, taxonomic and functional on the other), to optimise conservation strategies. We propose that the same reasoning should be held for species interactions, which would represent an additional level (i.e. in addition to species themselves) at which diversity should be measured. The use of β-diversity measures can, and should, go well beyond descriptive or comparative objectives (Tuomisto 2011). For instance, recent research showed that the combination of several diversity indices offers deeper insights on community assembly dynamics and processes (Münkemüller *et al.* 2012). Defining measures of network dissimilarity would allow the same type of work to be carried out for ecological networks. With such metrics in hand, one could investigate drivers of variation in network structure: What is the role of phenology in regulating network structure? How sensitive are interactions
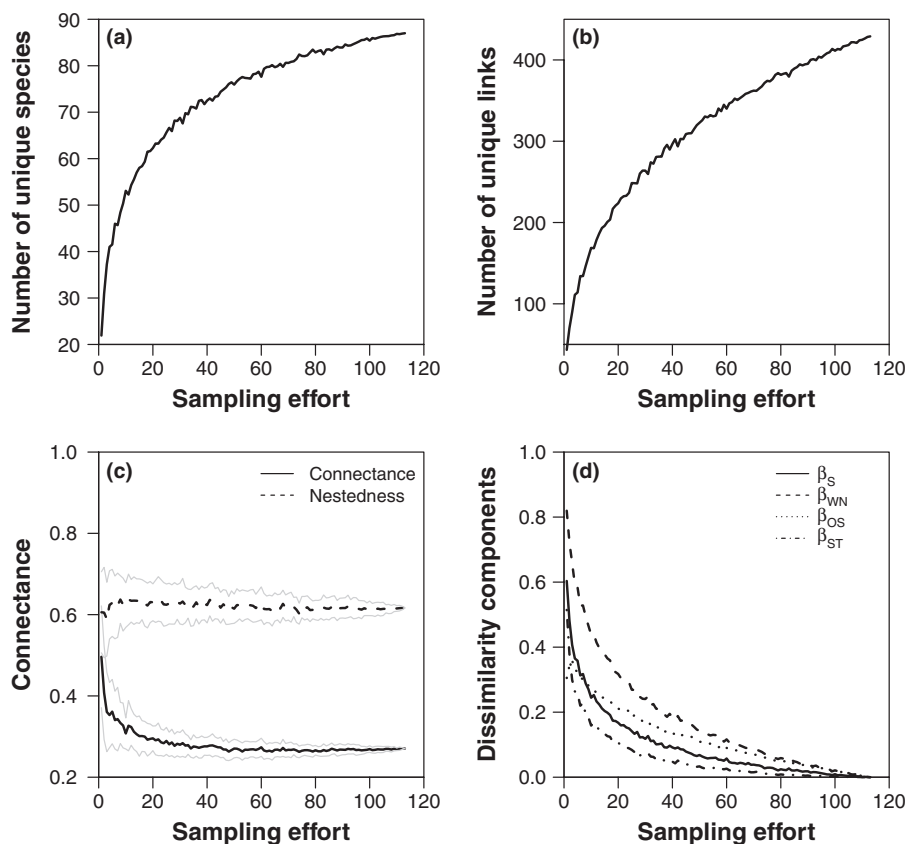
Figure 4 Rarefaction curve-like approach to investigate the thoroughness of the metaweb sampling, using the Stanko *et al.* (2002) data. In all panels, the *x*-axis is the number of networks used to reconstruct the metaweb (500 replicates for each level of sampling effort). (a) Number of unique species, both hosts and parasites, present in the metaweb. (b) Number of unique interactions in the metaweb (number of interactions). (c) Mean, and standard deviation (grey lines), for nestedness (NODF/100) and connectance of the metaweb. (d) Values of the dissimilarity components.

to particular environmental conditions? Is species turnover a good predictor of network turnover?

Our framework offers the new opportunity to understand *why* networks vary through space and time. We expect that the connectance of the metaweb will be lower than the connectance of each local network (realisation), as even a single occurrence of one interaction will be reported into the metaweb (Gravel *et al.* 2011b). We thus expect that as the proportion of rare interactions (interactions occuring only in a few realisations) increases, local realisations will become increasingly dissimilar to the metaweb (high β'_{OS}; Table 1). If the distribution of β'_{OS} values for all the realisations is biased towards high dissimilarities, then the proportion of rare interactions would be high and species interactions strongly regulated by local conditions. This would result in population dynamics and selective pressure stemming for species interactions being geographically structured, which bears important consequences for evolutionary dynamics (Thompson 2005).

The distribution of β'_{OS} can further be investigated for example, spatial or temporal autocorrelation through an analysis of distance decay (Nekola & White 1999; Morlon *et al.* 2008; Canard 2011). Finally, understanding network variability can lead to an increased understanding of ecosystem functioning. Several theoretical studies highlighted that the structure of biotic interactions bears important consequences for functioning (Thébault & Loreau 2003; Thébault *et al.* 2007), and being able to compare interaction networks between sites will offer the ability to understand why they differ in

functioning. This requires an expansion of our framework, from pairwise comparisons to multiple-networks comparisons. In Appendix S1, we propose a way to measure the variability across multiple networks using their relative differences from the metaweb, and provide ways to standardise these differences in a way allowing for comparison across multiple systems.

CONCLUSIONS & FUTURE DIRECTIONS

A theoretical understanding of the biogeography of species interactions will only be reached if we are able to generate sufficient data, and analyse them with appropriate tools. The methodological toolbox for assessing species β diversity is well developed, and we show that translating it to networks is a relatively easy task, and one which will yield promising results. The usefulness of these methods will increase with a refinement of our understanding of the different levels at which β diversity of species interactions networks should be analysed.

As in the case of species diversity (Reiss *et al.* 2009), interaction diversity can be qualified by its phylogenetic, functional and taxonomical components. In this article, we only covered the taxonomical side. It is our intuition that most of the groundwork to describe phylogenetic and functional β diversity with respect to interactions is already laid out. In a taxonomical perspective, as presented in this study, all species contribute equally to network dissimilarity, because there is no way to rank them according to their biological distinctiv-

ness. By accounting for functional traits, or phylogenetic related-ness, species with rare functions or representing a unique evolutionary history should count more toward dissimilarity than common species. Only some minor extrapolation seems to be needed to come up with such measures for species interactions. Robust and well-described measures of phylogenetic spatial diversity (Ives & Helmus 2010; Morlon *et al.* 2011) have been developed in the recent years. Similarly, studies focusing on the replacement of taxonomically distinct species by functionally equivalent species (Dupont *et al.* 2009; Díaz-Castelazo *et al.* 2010) hint at the fact that functional β diversity may be lower than its taxonomic counterpart. This effect can be accentuated in community assembly following a disturbance, as species traits matter more than species identity in the filling of niche space (Helsen *et al.* 2012).

The need to integrate different measures of diversity to accurately characterise ecological patterns is emphasised in several domains (Münkemüller *et al.* 2012; Tuomisto 2012) and our framework is a significant step forward in that direction. Although we laid out the methodological work with this study, further understanding of the processes acting on network structure through space is contingent upon our ability to gather sufficient high-quality data. While it is now easy, and tempting, to build on recent theoretical studies to speculate about what a biogeographical theory of species interaction would look like, it is our opinion that this reasoning would be better grounded in data. As we show in Fig. 4, gathering enough networks to adequately describe the metaweb is a difficult task, and assuming that species co-occurence is enough for an interaction to happen is not a sufficient sampling strategy. For this reason, we think it is time for the community of ecologists interested in interaction networks to engage in a discussion about the best way to gather data from the field, as this will pave the way to a biogeographical theory of species interactions.

AUTHORSHIP

TP and DG conceived the study, TP and EC analysed the data, TP and DG wrote the first draft of the manuscript and all authors contributed substantially to revisions.

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SUPPORTING INFORMATION