Dissimilarity of species interaction networks: how to measure the effect of species turnover

Timothée Poisot

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In a recent contribution, Fründ (2021) argues that the calculation of network dissimilarity terms first introduced by Poisot et al. (2012) is incorrect, as it can lead to over-estimating the role of interactions between shared species in a network, and therefore under-estimate the importance of species turnover across network. Here, I present an argument for why this is not the case, and urge network ecologists to exercise greater caution when attempting to "normalize" the effect of species turnover in network dissimilarity, as it may invalidate the calculation.

Partitioning network dissimilarity

The approach to quantifying the difference between pairs of networks suggested by Poisot et al. (2012) is a simple extension of the overall method by Koleff, Gaston, and Lennon (2003) for species dissimilarity baed on presence-absence data. The objects to compare, X_1 and X_2, are partitioned into three sets, $a = |X_1 \cup X_2|$, $b = |X_2 \setminus X_1|$, and $c = |X_1 \setminus X_2|$, where $|x|$ is the cardinality of set x, and $\setminus$ is the set substraction operation.

In order to apply this framework to networks, we first need to establish a few definitions. Although ecologists tend to think of networks as their adjacency matrix, this representation muddies what the terms used in calculation of dissimilarity ought to be. For this reason, we will use the definition of networks as a pair of sets, whereing $\mathcal{G} = (V, E)$, where V is a set containing the vertices (species) of $\mathcal{G}$, and E is a set of ordered pairs, in which every pair is two elemenets of V, which representes the edges (interactions). In the context of networks comparison (assuming the networks to compare are $\mathcal{M}$ and $\mathcal{N}$), we can further decompose the contents of these sets as

$$\mathcal{M} = (V_c \cup V_m, E_c \cup E_{sm} \cup E_{um}),$$

and

$$\mathcal{M} = (V_c \cup V_n, E_c \cup E_{sn} \cup E_{un}) \,,$$

where V_c is the set of shared species, V_k are the species belonging only to network k, E_c are the shared edges, and $E_s k$ and $E_u k$ are the interactions unique to k involving, respectively, only species in V_c, and at least one species from V_k.

The metaweb (Dunne 2006), which is to say the entire regional species pool and their interaction, can be defined as $\mathcal{M} \cup \mathcal{N}$ (this operation is commutative), which is to say

$$\mathcal{M} \cup \mathcal{N} = (V_c \cup V_m \cup V_n, E_c \cup E_{sm} \cup E_{um} \cup E_{sn} \cup E_{un}) \,.$$

Making the usual assumption that only species with at least one interaction are present in the set of vertices, all elements of the set of vertices are used at least once in the set of edges.

We can similarly define the intersection (similarly commutative) of two networks:

$$\mathcal{M} \cap \mathcal{N} = (V_c, E_c \cup E_{sm} \cup E_{sn}) \,,$$

namely all interactions that are established between species that are shared by both networks.

The decomposition of β-diversity from Poisot et al. (2012) uses these components to measure β_{os} (the interaction dissimilarity between shared species, which Fründ (2021) terms "rewiring"), and β_{wn} (the overall dissimilarity including non-shared species). We can express the components a, b, and c of Koleff, Gaston, and Lennon (2003) as follows:

Component	a	b	c
β_{os}	$|E_c|$	$|E_{sn}|$	$|E_{sm}|$
β_{wn}	$|E_c|$	$|E_{sn} \cup E_{un}|$	$|E_{sm} \cup E_{um}|$

Note that in *all* instances $a + b + c$ is equal to the total number of links in either $\mathcal{M} \cup \mathcal{N}$ (for β_{wn}) or $\mathcal{M} \cap \mathcal{N}$ (for β_{os}), and that the nodes of the networks can correctly be induced from the edgelist.

Quantifying the importance of species turnover

The difference between β_{os} and β_{wn} stems from the species dissimilarity between $\mathcal{M}$ and $\mathcal{N}$, and it is easier to understand the effect of turnover by picking a dissimilarity measure to work as an exemplar. At this point, Fründ (2021) introduce a substantial mistake in their manuscript by (i) stating that Sørensen's and Whittaker's measures of dissimilarity are the same in the Koleff, Gaston, and

Lennon (2003) framework (they are not), and (ii) noting Whittaker's measure as $(b + c)/(2a + b + c)$, which in the Koleff, Gaston, and Lennon (2003) framework is, in fact, β_t (Wilson and Shmida 1984). This error, although serious, does not change the overall conclusions as these measures behave in the same monotonously increasing way with regard to dissimilarity, with a minimum of 0 and a maximum of 1. For the sake of comparison, I will use β_t moving forward, as Koleff, Gaston, and Lennon (2003) also recommend it as a default measure.

Based on a partition between three sets of cardinality a, b, and c,

$$\beta_t = \frac{b + c}{2a + b + c} \, .$$

So as to simplify the notation of the following section, we will introduce a series of new variables. Let $A = |E_c|$ be the number of links that are identical between networks; $S = |E_{sn} \cup E_{sm}|$ be the number of links that are not shared, but only involve shared species; and $U = |E_{un} \cup E_{um}|$ the number of links that are not shared, and involve at least one unique species. Adopting the perspective developed in the previous section, wherein networks are sets and the measure of β-diversity operates on this sets, highlights the conceptual issue in the Fründ (2021) alternative normalization: they are using components of the networks that are *not* in the networks being compared.

There are two important points to note here. First, the number or proportion of species that are shared is not involved in the calculation. Second, the connectance of either network is not involved in the calculation. That all links counted in *e.g.* U come from $\mathcal{M}$, or that they are evenly distributed between $\mathcal{M}$ and $\mathcal{N}$, has no impact on the result. This is a desirable property of the approach: whatever quantitative value on the components of dissimilarity can be interpreted in the light of the connectance and species turnover *without* any risk of circularity. Therefore the argument of Fründ (2021), whereby the β_{os} component should decrease with turnover, and be invariant to connectance, does not hold: the point of the approach is to provide measures that can be interpreted in the light of connectance and species turnover.

The final component of network dissimilarity in Poisot et al. (2012; which is itself an extension of the initial approach by Canard et al. 2014) is β_{st}, *i.e.* the part of β_{wn} that is not explained by changes in interactions between shared species (β_{os}), and therefore stems from species turnover. This fraction is defined as $\beta_{st} = \beta_{wn} - \beta_{os}$.

The expression of β_{st} does not involve a partition into sets that can be plugged into the framework of Koleff, Gaston, and Lennon (2003), because the part of $\mathcal{M}$ and $\mathcal{N}$ that are composed of their unique species cannot, by definition, share interactions. One could, theoretically, express these as $\mathcal{M} \setminus \mathcal{N} = (V_m, E_{um})$ and $\mathcal{N} \setminus \mathcal{M} = (V_v, E_{un})$ (note the non-commutativity here), but the dissimilarity between these networks is trivially maximal for the measure considered.

Using the β_w measure of dissimilarity, we can write

$$\beta_{os} = \frac{S}{2A+S} ,$$

and

$$\beta_{wn} = \frac{S+U}{2A+S+U} .$$

As β_{os} has the form x/y, and β_{wn} has the form $(x+k)/(y+k)$, with $x = S$, $y = 2A + S$, and $k = U$, as long as $k \geq 0$, it is guaranteed that $\beta_{wn} \geq \beta_{os}$, and therefore that $0 \geq \beta_{st} \geq 1$.

Although it holds little information, we can get an expression for β_{st}, by bringing β_{os} and β_{wn} to a common denominator:

$$\beta_{st} = \frac{2AU}{(2A+S)(2A+S+U)} .$$

Note that this measure varies in a non-monotonic way with regards to the number of shared interactions – this is obvious when developing the denominator into

$$4A^2 + 2AS + 2AU + 2AS + S^2 + SU = 4A^2 + S^2 + 4AS + 2AU + SU ,$$

which reveals why this value tends towards 0 whenever one component (β_{wn} or β_{os}) explains the entire dissimilarity (*i.e.* its value tends towards 1). Note further that for this reason, Poisot et al. (2012) suggest that $\beta_{st}/\beta wn$ is a better indicator of the *relative* importance of turnover processes on network dissimilarity. This can be calculated as

$$\frac{\beta_{st}}{\beta_{wn}} = \frac{2AU}{(2A+S)(2A+S+U)} \times \frac{S+U}{2A+S+U} ,$$

which reduces to

$$\frac{\beta_{st}}{\beta_{wn}} = \frac{2AU}{(2A+S)(S+U)} .$$

This expression admits roots for $A = 0$ (the turnover of species has no contribution to the difference between β_{wn} and β_{os} if there are no shared species), and for $U = 0$ (the turnover of species has no contribution if all species are shared).

4

Is this decomposition over-estimating the effect of "rewiring"?

One of the arguments put forth by Fründ (2021) is that the decomposition outlined above will overestimate the effect of rewiring; I argue that this is based on a misunderstanding of what β_{st} achieves. It is paramount to clarify that β_{st} is not a direct measure of the importance of turnover: it is a quantification of the relative impact of rewiring to overall dissimilarity, which, all non-turnover mechanisms being accounted for in the decomposition, can be explained by turnover mechanisms.

We can re-calculate the illustration of Fründ (2021), wherein a pair of networks with two shared interactions ($A = 2$) receive either an interaction in S, in U, or in both:

A	S	U	β_{os}	β_{wn}	β_{st}	β_{st}/β_{wn}
2	0	0	0	0	0	
2	1	0	1/5	1/5	0	0
2	0	1	0	1/5	1/5	0
2	1	1	1/5	1/3	2/15	2/5

The over-estimation argument hinges on the fact that $\beta_{st} < \beta_{os}$ in the last situation (one interaction as rewiring, one as turnover). Reaching the conclusion of an overestimation from this is based on a mis-interpretation of what β_{st} means. The correct interpretation is that, out of the entire network dissimilarity, only three-fifths are explained by re-wiring. The fact that this fraction is not exactly one-half comes from the fact that the Wilson and Shmida (1984) measure counts shared interactions *twice* (*i.e.* it has a $2A$ term), which over-amplifies the effect of shared interactions as the network is really small. Running the same calculations with $A = 10$ gives a relative importance of the turnover processes of 47%, and β_{st} goes to $1/2$ as $A/(S+U)$ increases. As an additional caveat, the value of β_{st} will depend on the measure of beta-diversity used. Measures that do not count the shared interaction twice are not going to amplify the effect of rewiring.

Does the partition of network dissimilarity needs a new normalization?

Based on the arguments presented above, I do not think the suggestion of Fründ (2021) to change the denominator of β_{os} makes sense as a default; the strength of the original approach by Poisot et al. (2012) is indeed that the effect of turnover is based on a rigorous definition of networks as graphs (as opposed to networks as matrices), in which the induction of vertices from the edgelist being compared gives rise to biologically meaningful denominators. The advantage of this approach is that at no time does the turnover of species itself, or the

connectance of the network, enter into the calculation. As such, it is possible to use β_{os} and β_{wn} in relationship to these terms, calculated externally (as was recently done by *e.g.* Higino and Poisot 2021) without creating circularities.

The choice of changing the denominator hinges on what one admits as a definition for β_{st}. If the point of β_{st} is to be a component of overall β-diversity as advocated by Fründ (2021) and Novotny (2009), a change of numerator *might* be acceptable. Nevertheless, this change of numerator contributes to blurring the frontier between a measure of interaction dissimilarity and a measure of community dissimilarity, and may warrant a full methodological assessment. Conversely, if as we argue in Poisot et al. (2012), β_{st} is to be meant as a *guide* to the interpretation of β_{wn} and β_{os}, and related to actual measures of species turnover and network connectance, one must not change the denominator. It is central to recognize that there are multiple reasons to calculate network dissimilarity, and it is our opinion that the arguments levied by Fründ (2021) against the original partition stem from a misunderstanding of what it intends to do (and does, indeed, do well), not from intrinsic methodological issues in the partition itself.

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