

Dissimilarity of species interaction networks: how to quantify the impact of species turnover?

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Ecological networks are variable both in time and space (Poisot, Stouffer, and Gravel 2015; Trøjelsgaard and Olesen 2016) - this variability motivated the emergence of methodology to compare ecological networks, in a way that meshes with the usual approaches of comparison of ecological communities, *i.e.* β -diversity; although the definition of β -diversity is a contentious topic amongst community ecologists (see *e.g.* Tuomisto 2010), the need to understand network variability is motivated by the fact that species that make up the networks do not react to their environment in the same way, and therefore the β -diversity of networks may behave in complex ways.

Poisot et al. (2012) and Canard et al. (2014) have suggested an approach to β -diversity for ecological networks which is based on the comparison of shared and unique links among species, and differentiate this sharing of links between common and unique species. This framework can be summarized as $\beta_{wn} = \beta_{os} + \beta_{st}$, namely the fact that overall network dissimilarity (β_{wn}) has a component that can be calculated directly from the dissimilarity of interactions between shared species (β_{os}), and a component that cannot, the later originating in unique species introducing their unique interactions (β_{st}). This approach has been widely adopted since its publication, with recent examples using it to understand the effect of fire on pollination systems (Baronio et al. 2021); the impact of rewiring on spatio-temporal network dynamics (Campos-Moreno et al. 2021); the effects of farming on rural and urban landscapes on species interactions (Olsson et al. 2021); and as a tool to estimate the sampling completeness of networks (Souza et al. 2021). It has, similarly, received a number of extensions, including the ability to account for interaction strength (Magrath et al. 2017), the ability to handle probabilistic ecological networks (Poisot et al. 2016), and the integration into the Local Contribution to Beta Diversity (Legendre and De Cáceres 2013) approach to understand how environment changes drive network dissimilarity (Poisot et al. 2017).

In a recent contribution, Fründ (2021) argues that the calculation of network dissimilarity terms as outlined by Poisot et al. (2012) is incorrect, as it can lead to over-estimating the role of interactions between shared species in a

network (“rewiring”), and therefore underestimate the importance of species turnover across networks. Here, I present a more thorough justification of the methodological choices for the Poisot et al. (2012) method, explain how information about species turnover can be extracted from its decomposition, and conduct numerical experiments to guide the interpretation of the β -diversity values thus obtained.

Partitioning network dissimilarity

The approach to quantifying the difference between pairs of networks established in Poisot et al. (2012) is a simple extension of the overall method by Koleff, Gaston, and Lennon (2003) for species dissimilarity based on presence-absence data. The objects to compare, X_1 and X_2 , are partitioned into three values, $a = |X_1 \cup X_2|$, $b = |X_2 \setminus X_1|$, and $c = |X_1 \setminus X_2|$, where $|x|$ is the cardinality of set x , and \setminus is the set subtraction operation. In the perspective of species composition comparison, X_1 and X_2 are the sets of species in either community, so that if $X_1 = \{x, y, z\}$ and $X_2 = \{v, w, x, y\}$, we have $X_1 \cup X_2 = \{v, w, x, y, z\}$, $X_1 \cap X_2 = \{x, y\}$, $X_2 \setminus X_1 = \{v, w\}$, and $X_1 \setminus X_2 = \{z\}$. The core message of Koleff, Gaston, and Lennon (2003) is that the overwhelming majority of measures of β -diversity can be re-expressed as functions that operate on the cardinality (number of elements) of these sets.

Re-expressing networks as sets

Applying this framework to networks requires a few additional definitions. Although ecologists tend to think of networks as their adjacency matrix, this representation is far from optimal to get a solid understanding of which elements should be counted as part of which set when measuring network dissimilarity. For this reason, we need fall back on the definition of a graph as a pair of sets, wherein $\mathcal{G} = (V, E)$. These two components V and E represent vertices (nodes, species) and edges (interactions), where V is specifically a set containing the vertices \mathcal{G} , and E is a set of ordered pairs, in which every pair is composed of two elements of V ; an element $\{i, j\}$ in E indicates that there is an interaction from species i to species j in the network \mathcal{G} .

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

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

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_{sk} and E_{uk} are the interactions unique to k

involving, respectively, only species in V_c , and at least one species from V_k .

Defining the partitions from networks as sets

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

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

This operation gives us an equivalent to γ -diversity for networks, in that the set of vertices contains *all* species from the two networks, and the set of edges contains *all* the interactions between these species. If, further, we make the usual assumption that only species with at least one interaction are present in the set of vertices, then all elements of the set of vertices are present at least once in the set of edges, and the set of vertices can be entirely reconstructed from the set of edges. Although measures of network β -diversity operate on interactions (not species), this property is maintained at every decomposition we will describe next.

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

$$\mathcal{M} \cap \mathcal{N} = (V_c, E_c).$$

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 the cardinality of the following sets:

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

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 confusing terminology in their work, stating that Sørensen’s and Whittaker’s measures of dissimilarity are the same in the Koleff, Gaston, and Lennon (2003) framework (they are not; in practice, $\beta_{Sor} = 1 - \beta_w$), 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

does not change the overall conclusions as these measures can be re-expressed to converge to the same value. For the sake of consistency, I will use β_t moving forward; it returns values in $[0, 1]$, with 0 meaning complete similarity, and 1 meaning complete dissimilarity.

Establishing that $\beta_{wn} \geq \beta_{os}$

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, I 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 (*i.e.* links from $\mathcal{M} \cup \mathcal{N}$ established between species from $\mathcal{M} \cap \mathcal{N}$); 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 measures of β -diversity operates on these sets, highlights the conceptual issue in the Fründ (2021) alternative normalization: they are using components of the networks that are *not* part of 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 of 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 very 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) 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 $\mathcal{N} \setminus \mathcal{M} = (V_v, E_{vn})$ (note the non-commutativity here), but the dissimilarity between these networks is trivially maximal for the measures considered.

Using the β_t measure of dissimilarity, we can re-write (using the notation with A , S , and U)

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

and

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

Note that β_{os} has the form x/y with $x = S$ and $y = 2A + S$, and β_{wn} has the form $(x + k)/(y + k)$, with $k = U$. As long as $k \geq 0$, it is guaranteed that $\beta_{wn} \geq \beta_{os}$, and therefore that $0 \leq \beta_{st} \leq 1$; as A , S , and U are cardinalities of sets, they are necessarily satisfying this condition.

We can get an expression for β_{st} , by bringing β_{os} and β_{wn} to a common denominator and simplifying the numerator:

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

Note that this value varies in a non-monotonic way with regards to the number of interactions that are part of the common set of species – this is obvious when developing the denominator into

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

As such, we expect that the value of β_{st} will vary in a hump-shaped way with the proportion of shared interactions. For this reason, Poisot et al. (2012) suggest that β_{st}/β_{wn} (alt. $1 - \beta_{os}/\beta_{wn}$) 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

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

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

Numerical experiment: response of the components to different sources of network variation

To illustrate the behavior of β_{st} , I conducted a simple numerical experiment in which two networks have the same number of interactions L (recall from the previous section that we do not need to set a number of species yet), and these interactions are partitioned according to proportions p_s and p_r into shared (A), rewired (S), and unique (U) links, with $A = p_s \times L$, $S = (1 - p_s) \times p_r \times L$, and $U = (1 - p_s) \times (1 - p_r) \times L$. The results are represented in fig. 1.

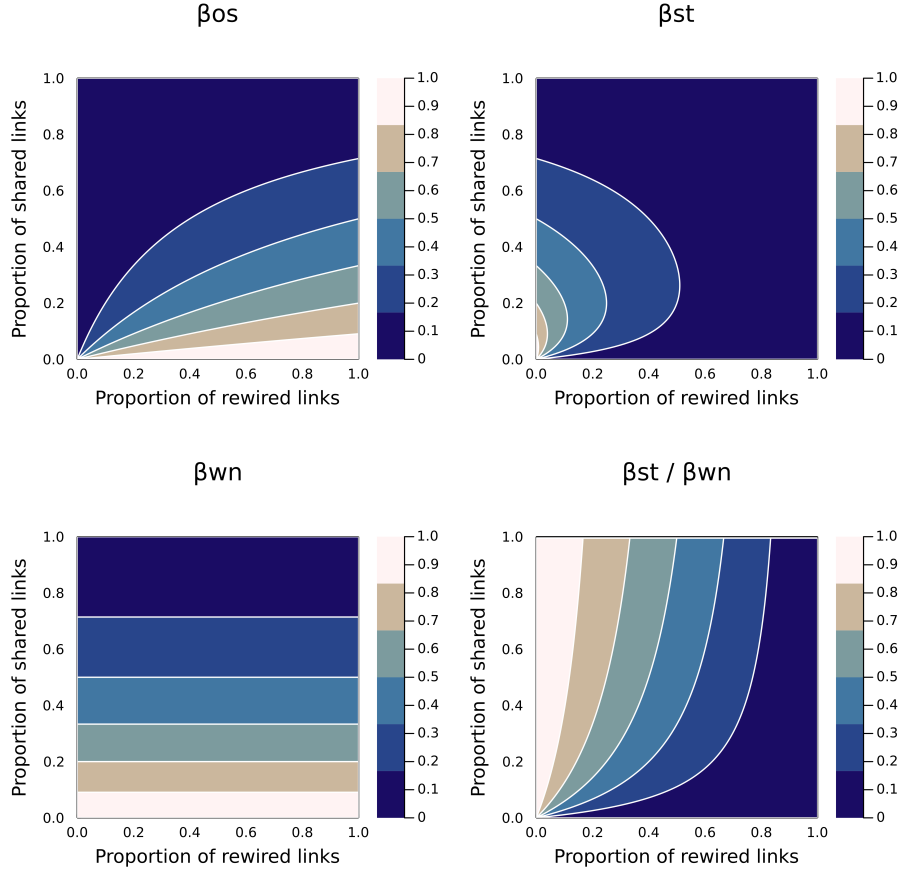


Figure 1: Values of β_{os} , β_{wn} , β_{st} , and β_{st}/β_{wn} as a function of the proportion of rewired links and the proportion of shared links.

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.

Illustration on irealistically small networks are biased

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.

Numerical experiment: β_{os} captures rewiring accurately

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

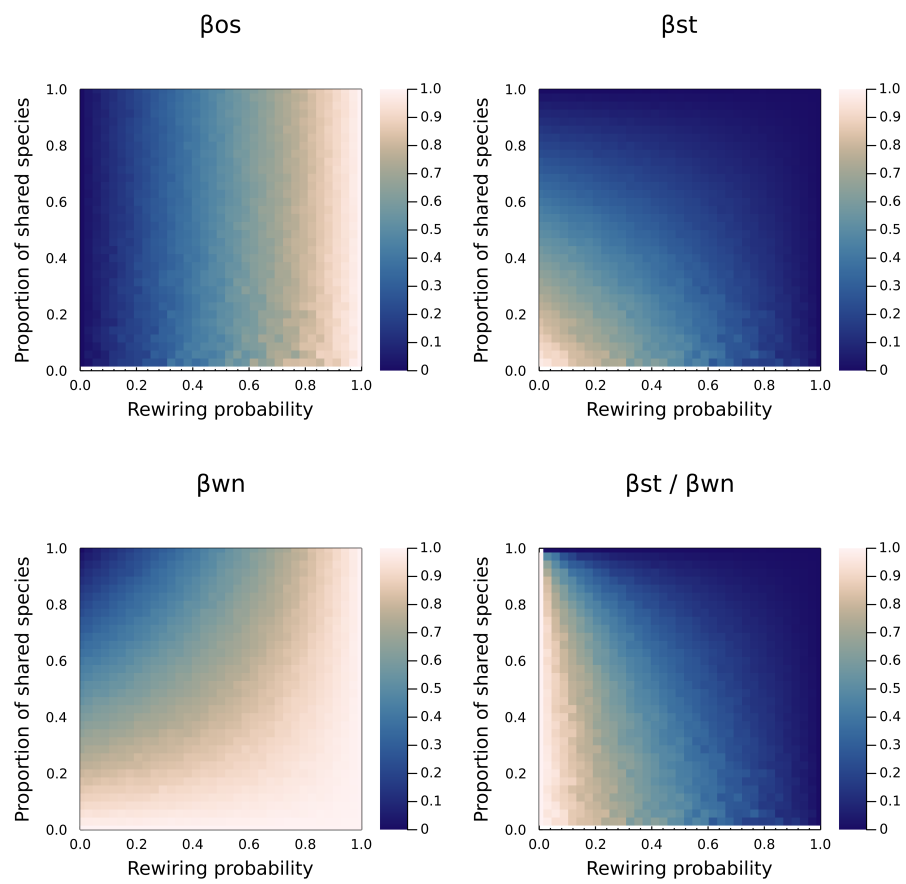


Figure 2: dsds

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.* Higinio 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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