Dissimilarity of species interaction networks: quantifying the effect of turnover and rewiring

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Despite having established its usefulness in the last ten years, the decomposition of ecological networks in components allowing to measure their β-diversity retains some methodological ambiguities. Notably, how to quantify the relative effect of mechanisms tied to interaction rewiring *vs.* species turnover has been interpreted differently by different authors. In this contribution, I present mathematical arguments and numerical experiments that should (i) establish that the decomposition of networks as it is currently done is indeed fit for purpose, and (ii) provide guidelines to interpret the values of the components tied to turnover and rewiring.

Ecological networks are variable both in time and space (Poisot *et al.* 2015; Trøjelsgaard & Olesen 2016) - this variability motivated the emergence of methodology to compare ecological networks, including in a way that meshes with the core concept for the comparison of ecological communities, namely β-diversity (Poisot *et al.* 2012). The need to understand network variability through partitioning in components equivalent to α, β, and γ diversities is motivated by the prospect to further integrate the analysis of species interactions to the analysis of species compositions. Because species that make up the networks do not react to their environment in the same way, and because interactions are only expressed in subsets of the environments in which species co-occurr, the β-diversity of networks may behave in complex ways, and its quantification is likely to be ecologically informative.

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 the number of shared and unique links among species within a pair of networks. Their approach differentiates this sharing of links between those established between species occurring in both networks, and those established with at least one unique species. This framework is expressed as the decomposition $\beta_{wn} = \beta_{os} + \beta_{st}$, namely the fact that 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 (β_{st}). Presumably, the value of these components for a pair of networks can generate insights about the mechanisms involved in dissimilarity.

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); the impact of environment gradients on multi-trophic metacommunities (**Ohlmann2018MapImp?**); 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 (Magrach *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 & De Cáceres 2013) approach to understand how environment changes drive network dissimilarity (Poisot *et al.* 2017).

[Figure 1 about here.]

Yet, the precise meaning of β_{st}, namely the importance of species turnover in the overall dissimilarity, has been difficult to capture, and a source of confusion for some practitioners. This is not particularly surprising, as this component of the decomposition responds to unique species introducing their unique interactions both between themselves, and with species that are common to both networks fig. 1. For this reason, it is important to come up with guidelines for the interpretation of this measure, and how to use it to extract ecological insights.

Furthermore, much like the definition of β-diversity in all its forms is a contentious topic amongst community ecologists (see *e.g.* Tuomisto 2010), the β-diversity of networks has been submitted to methodological scrutiny over the years. A synthesis of some criticisms, related to the correct denominator to use to express the proportion of different links, has recently been published (Fründ 2021). It argues that the calculation of network dissimilarity terms as originally 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. As mist-understanding either of these quantities can lead to biased inferences about the mechanisms generating network dissimilarity, it is important to assess how the values (notably of β_{os}, and therefore of β_{st}) react to methodological choices.

Here, I present a mathematical analysis of the Poisot *et al.* (2012) method, explain how information about species turnover and link rewiring can be extracted from its decomposition, and conduct numerical experiments to guide the interpretation of the β-diversity values thus obtained (with a specific focus on β_{st}). These numerical experiments establish three core facts. First, the decomposition adequately captures the relative roles of species turnover and interaction rewiring; second, the decomposition responds to differences in network structure (like connectance) as expected; finally, the decomposition more accurately captures rewiring than the proposed alternative using a different denominator put forth by Fründ (2021).

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 *et al.* (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 $|\cdot|$ is the cardinality of set $\cdot$ (the number of elements it contains), and $\setminus$ is the set substraction 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 *et al.* (2003) is that the overwheling majority of measures of β-diversity can be re-expressed as functions that operate on the cardinality of these sets – this allows to focus on the number of unique and common elements, as outlined in fig. 1.

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 (as is presented in fig. 1), this representation is not optimal to reach a robust 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 of $\mathcal{G}$, 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 $\mathcal{G}$. The adjancency matrix $\mathbf{A}$ of this network would therefore have a non-zero entry at A_{ij}.

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 common species, V_m and V_n are the species belonging only to network m and n (respectivly), E_c are the common edges, and E_{sm} and E_{um} are the interactions unique to k involving, respectively, only species in V_c, and at least one species from V_m (the same notation applies for the subscript $_n$).

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 entire 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} ("rewiring"), and β_{wn} (the overall dissimilarity including non-shared species). We can express the components a, b, and c of Koleff *et al.* (2003) as the cardinality of the following sets:

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

It is fundamental to note that these components can be measured entirely from the interactions, and that the number of species in either network are never directly involved.

In the following sections, I present a series of calculations aimed at expressing the values of β_{os}, β_{wn}, and therefore β_{st} as a function of species sharing probability (as a proxy for mechanisms generating turnover), and link rewiring probability (as a proxy for mechanisms generating differences in interactions among shared species). These calculations are done using `Symbolics.jl` (**Gowda2021HigSym?**), and subsequently transformed in executable code for *Julia* (**Bezanson2017JulFre?**), used to produce the figures.

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. We will use $\beta = (b+c)/(2a+b+c)$, which in the Koleff *et al.* (2003) framework is (Wilson & Shmida 1984). This measure 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 $C = |E_c|$ be the number of links that are identical between networks (as a mnemonic, C stands for "common"); $R = |E_{sn} \cup E_{sm}|$ 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 $\mathcal{M} \cap \mathcal{N}$; as a mnemonic, R stands for "rewired"); and $T = |E_{un} \cup E_{um}|$ the number of links that are not shared, and involve at least one unique species (as a mnemonic, T stands for "turnover").

There are two important points to note here. First, as mentionned earlier, 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; indeed, I present a numerical experiment where connectance varies independently later in this manuscript.

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 *et al.* (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 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 $0 \geq \beta_{st} \geq 1$; 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 $\beta_{st}/\beta wn$ (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 partitionned 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. 2.

[Figure 2 about here.]

The rewiring component β_{os} varies as a function of the proportion of shared links that are rewired; by contrast, β_{wn} varies *only* as a function of the proportion of links that are shared: that the unshared links are established between common or unique species has no effect on overall network dissimilarity. The quadratic nature of the denominator for β_{st} is clear here, with a maximum reach when there is no re-wiring, and a small number of shared links (*i.e.* the networks are almost entirely dissimilar except for the links between shared species). Althought the *raw* values of β_{st} may seem low, the normalization using β_{st}/β_{wn} magnifies this effect: its values are indeed maximized when the rewiring is lower, *i.e.* all of the network variation stems from turnover processes.

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. In this section, I present two numerical experiments showing (i) that the β_{os} component is in fact an accurate measure of rewiring, and (ii) that β_{st} captures the consequences of species turnover, and of the interactions brought by unique species.

Illustrations on arbitrarily 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 & 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: the decomposition captures the roles of rewiring and turnover accurately

Consider two bipartite networks, each with R species on either side, and each with the same connectance ρ. We will assume that these networks *share* a proportion p of their species from one side (and share all species from the other), and that the interactions between these species are undergo rewiring with at a rate q. This is sufficient information to calculate the values of A, S, and U required to get the values of β_{os} and β_{wn}. Note that the simplification of assuming that only species from one side can vary is merely for the sake of simplicity, but does not decrease the generality of the argument.

Each network will have $\rho(1-p)R^2$ interactions that are unique due to species turnover, and so

$$U = 2\rho(1-p)R^2\,.$$

The part of both networks composed of overlapping species has $\rho p R^2$ interactions, of which $\rho(1-q)pR^2$ are shared, and $\rho q p R^2$ underwent rewiring. This leads to

$$A = \rho(1-q)pR^2\,,$$

and

$$S = \rho p q R^2\,.$$

Note that we can drop the multiplicative constant R^2, making the result independent of the size of the network. Based on these components, we can get the values of β_{os} and β_{wn}, as presented in fig. 3.

[Figure 3 about here.]

The value of β_{os} is entirely unchanged by variations in p (species sharing), and responds *only* to changes in q (the probability of rewiring), whereas as expected, β_{wn} responded to changes in both of these parameters: the most dissimilar networks have low species sharing (interactions are dissimilar because brought by unique species), and high rewiring (shared species do not share interactions). The relative changes in β_{os} and β_{wn} lead to predictable changes in β_{st}: its value is maximized when both rewiring *and* species sharing are low. Increasing rewiring decreases the impact of species turnover (because, for an equal number of interactions, the dissimilarity of interactins in shared species contributes more to β_{wn}); increasing the chance of sharing species also does decrease β_{st}, trivially because there is no species turnover anymore. Note that when using the correction of β_{st}/β_{wn}, the effect of species turnover is magnified for low probabilities of re-wiring.

In conclusion, this numerical experiment shows that the decomposition as initially presented by Poisot *et al.* (2012), *i.e.* using denominators that make sense from a network composition point of view, succeeds at capturing the relative effect of turnover and rewiring.

Numerical experiment: the decomposition captures the roles of species turnover and connectance accurately

Consider now two bipartite networks, which still have R species on either side, but differ in their connectance (ρ_1 and ρ_2) – by maintaining the assumption that species on one side are shared with probability p, and that interactions between shared species are rewired at probability q, we can examine the effect of varying both connectance and turnover on the value of the β-diversity components. Note that, although not presented, we will drop the multiplicative constant R^2 from all calculations, as it is a common factor for all values; again, this implies that the results presented here are independant of network richness.

The number of unique links due to species turnover is

$$U = (1-p)(\rho_1 + \rho_2)\,,$$

which decreases with the proportion of shared species, but increases with connectance. The number of links between shared species takes a little more steps to calculate. First, amongst the pR^2 species in both sub-graphs, network 1 will have $\rho_1 pR^2$, and network 2 will have $\rho_2 pR^2$. Because $\rho_1 \neq \rho_2$, there are only $\min(\rho_1, \rho_2)pR^2$ links that can be shared, a proportion q of which will undergo re-wiring, and a proportion $(1-q)$ of which will be shared. This leads to the expression (after dropping R^2) for the number of shared links:

$$A = p(1-q)\min(\rho_1, \rho_2)\,.$$

The number of unique links due to shared species is the sum of all links in network 1 ($\rho_1 R^2$), minus the sum of the shared links (AR^2) and the unique links due to species turnover ($(1-p)\rho_1 R^2$); this same quantity is calculated in the same way for the second networks, leading to (after dropping the multiplicative constant R^2 and some simplifications)

$$S = p(\rho_1 + \rho_2) - 2A\,.$$

Note that as expected, this last quantity scales with the proportion of shared species (p) *and* with connectance (as shared species bring more of their interactions), but decreases with the size of the shared links components. The consequences of varying ρ_2 and p are presented in fig. 4.

[Figure 4 about here.]

Although β_{os} is only responding to changes in connectance (as is expected, seeing that the relative connectances of both networks appear in the expression for S and A), β_{wn} changes in response to both parameters. Specifically, increasing the difference in connectance between the two networks, especially when also increasing the species dissimilarity, results in more dissimilar networks – this is because unique species from both networks bring their own interactions (at rate ρ_1 and ρ_2), and therefore contribute to dissimilarity. It is particularly noteworthy that β_{st}, regardless of the differences in connectance, increases with the proportion of unique species. At an equal proportion of shared species, β_{st} *decreases* with differences in connectance: this is an equally expected result, which indicates that the difference between β_{os} and β_{wn} is in part explained by non-turnover mechanisms (here, changes in connectance). Relying on the β_{st}/β_{wn} correction again magnifies this effect, without changing their interpretation.

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 indeed, as shown in many places in this manuscript, the network richness), 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 & Poisot 2021), without creating circularities.

TK 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.

TK 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.

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 which starts to add the effect of relative richness; this later case warrants a thorough 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 essential 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. Based on the results presented in this contribution, I argue that the original partition of network β-diversity from Poisot *et al.* (2012) should remain the default.

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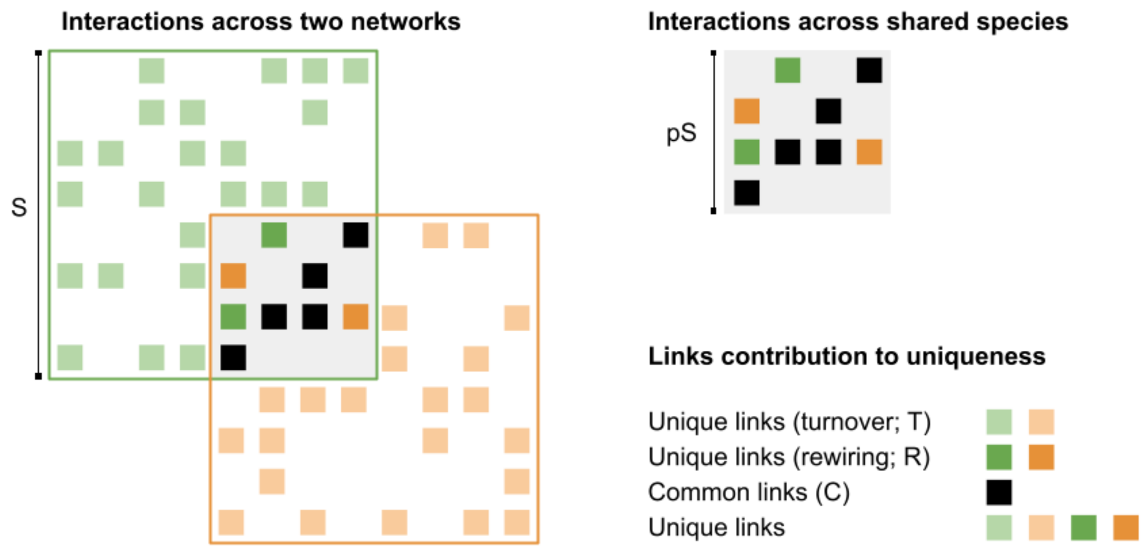

Figure 1: The dissimilarity of two networks (green and orange) of equal richness S (this also holds for unequal richness) depends on three families of interactions: those that are unique because of species turnover (in a pale color), those that are unique because of rewiring (in a saturated color), and those that are shared (in black). Assuming that the chance of sharing a species between the two networks is p, then there can be at most $p^2 \times S^2$ shared links – for this reason, overall network dissimilarity (β_{wn}) will have a component tied to species turnover, which is β_{st}.

figures/numexp1.png

Figure 2: 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.

figures/numexp2.png

Figure 3: Response of β_{os} and β_{wn}, and the consequences on β_{st}, to changes in rewiring probability (q) and probability of species sharing (p). As expected, β_{os} is not affected by species turnover, but increases with the rewiring probability. By contrast, β_{wn} increases when the rewiring probability is higher *and* when fewer species are shared. This has important consequences for β_{st}: its value is maximized for low species sharing, and decreases for high rewiring probability.

figures/numexp3.png

Figure 4: Effects of varying the connectance of the second network (ρ_2) and the proportion of shared species (p) on the values of the β-diversity components. As expected, β_{os} is still independent of species turnover, and β_{wn} increases when species turnover increases, or when the connectances become more dissimilar. These figures have been generated with $\rho_1 = 0.25$ and $q = 0.15$, and the results are qualitatively robust to changes in these parameters.