

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.

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

10 Poisot *et al.* (2012) and Canard *et al.* (2014) have suggested an approach to β -diversity for ecological
11 networks which is based on the comparison of the number of shared and unique links among species
12 within a pair of networks. Their approach differentiates this sharing of links between those established
13 between species occurring in both networks, and those established with at least one unique species. This
14 framework is expressed as the decomposition $\beta_{wn} = \beta_{os} + \beta_{st}$, namely the fact that network dissimilarity
15 (β_{wn}) has a component that can be calculated directly from the dissimilarity of interactions between
16 shared species (β_{os}), and a component that cannot (β_{st}). Presumably, the value of these components for a
17 pair of networks can generate insights about the mechanisms involved in dissimilarity.

18 This approach has been widely adopted since its publication, with recent examples using it to understand
19 the effect of fire on pollination systems (Baronio *et al.* 2021); the impact of rewiring on spatio-temporal
20 network dynamics (Campos-Moreno *et al.* 2021); the effects of farming on rural and urban landscapes on
21 species interactions (Olsson *et al.* 2021); the impact of environment gradients on multi-trophic
22 metacommunities (Ohlmann2018MapImp?); and as a tool to estimate the sampling completeness of
23 networks (Souza *et al.* 2021). It has, similarly, received a number of extensions, including the ability to
24 account for interaction strength (Magrath *et al.* 2017), the ability to handle probabilistic ecological
25 networks (Poisot *et al.* 2016), and the integration into the Local Contribution to Beta Diversity (Legendre
26 & De Cáceres 2013) approach to understand how environment changes drive network dissimilarity (Poisot
27 *et al.* 2017).

28 [Figure 1 about here.]

29 Yet, the precise meaning of β_{st} , namely the importance of species turnover in the overall dissimilarity, has

30 been difficult to capture, and a source of confusion for some practitioners. This is not particularly
31 surprising, as this component of the decomposition responds to unique species introducing their unique
32 interactions both between themselves, and with species that are common to both networks fig. 1. For this
33 reason, it is important to come up with guidelines for the interpretation of this measure, and how to use it
34 to extract ecological insights.

35 Furthermore, much like the definition of β -diversity in all its forms is a contentious topic amongst
36 community ecologists (see *e.g.* Tuomisto 2010), the β -diversity of networks has been submitted to
37 methodological scrutiny over the years. A synthesis of some criticisms, related to the correct denominator
38 to use to express the proportion of different links, has recently been published (Fründ 2021). It argues that
39 the calculation of network dissimilarity terms as originally outlined by Poisot *et al.* (2012) is incorrect, as it
40 can lead to over-estimating the role of interactions between shared species in a network (“rewiring”), and
41 therefore underestimate the importance of species turnover across networks. As mist-understanding
42 either of these quantities can lead to biased inferences about the mechanisms generating network
43 dissimilarity, it is important to assess how the values (notably of β_{os} , and therefore of β_{st}) react to
44 methodological choices.

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

53 **Partitioning network dissimilarity**

54 The approach to quantifying the difference between pairs of networks established in Poisot *et al.* (2012) is
55 a simple extension of the overall method by Koleff *et al.* (2003) for species dissimilarity based on
56 presence-absence data. The objects to compare, X_1 and X_2 , are partitioned into three values,
57 $a = |X_1 \cup X_2|$, $b = |X_2 \setminus X_1|$, 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 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 *et al.* (2003) is that the overwhelming 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 adjacency 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 (respectively), 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).

81 Defining the partitions from networks as sets

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

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

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

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

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

92 The decomposition of β -diversity from Poisot *et al.* (2012) uses these components to measure β_{os}
 93 (“rewiring”), and β_{wn} (the overall dissimilarity including non-shared species). We can express the
 94 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	$E_{sn} \cup E_{un}$	$E_{sm} \cup E_{um}$

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

97 In the following sections, I present a series of calculations aimed at expressing the values of β_{os} , β_{wn} , and
 98 therefore β_{st} as a function of species sharing probability (as a proxy for mechanisms generating turnover),
 99 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.

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, reinforcing this point.

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

125 turnover. This fraction is defined as $\beta_{st} = \beta_{wn} - \beta_{os}$. The expression of β_{st} does not involve a partition into
 126 sets that can be plugged into the framework of Koleff *et al.* (2003), because the part of \mathcal{M} and \mathcal{N} that are
 127 composed of their unique species cannot, by definition, share interactions. One could, theoretically,
 128 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
 129 dissimilarity between these networks is trivially maximal for the measures considered.

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

$$\beta_{os} = \frac{R}{2C + R},$$

131 and

$$\beta_{wn} = \frac{R + T}{2C + R + T}.$$

132 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
 133 $k = U$. 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 C , T , and R are
 134 cardinalities of sets, they are necessarily satisfying this condition.

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

$$\beta_{st} = \frac{2CT}{(2C + R)(2C + R + T)}.$$

137 Note that this value varies in a non-monotonic way with regards to the number of interactions that are
 138 part of the common set of species – this is obvious when developing the denominator into
 139 $4C^2 + R^2 + 4CR + 2CT + RT$. As such, we expect that the value of β_{st} will vary in a hump-shaped way with
 140 the proportion of shared interactions. For this reason, Poisot *et al.* (2012) suggest that β_{st}/β_{wn} (alt.
 141 $1 - \beta_{os}/\beta_{wn}$) is a better indicator of the *relative* importance of turnover processes on network dissimilarity.
 142 This can be calculated as

$$\frac{\beta_{st}}{\beta_{wn}} = \frac{2CT}{(2C + S)(2C + R + T)} \times \frac{R + T}{2C + R + T},$$

143 which reduces to

$$\frac{\beta_{st}}{\beta_{wn}} = \frac{2CT}{(2C + R)(R + T)}.$$

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

147 **Quantifying the response of network beta-diversity to sources of variation**

148 **The relative effect of species turnover and link rewiring**

149 As the decomposition of beta diversity into sets presented above reveals, the value of the components β_{os}
150 and β_{st} will respond to two family of mechanisms: the probability of sharing a species between the two
151 networks, noted p , which will impose bounds on the value of T ; and the probability of an interactions
152 between shared species *not* being rewired, noted q , which will impose bounds on the value of C . These
153 two probabilities represent, respectively, mechanisms involved in species turnover and link turnover, as
154 per Poisot *et al.* (2015), and the aim of this numerical experiment is to describe how these families of
155 processes drive network dissimilarity.

156 In order to simplify the calculations, I make the assumptions that the networks have equal species
157 richness (noted S), so that $S_1 = S_2 = S$, and the same connectance (noted ρ), so that $\rho_1 = \rho_2 = \rho$. As a
158 consequence, the two networks have the same number of links $L = \rho \times S_1^2 = \rho \times S_2^2$. The assumption of
159 equal connectance will be relaxed in a subsequent numerical experiment. These simplifications allow to
160 express the size of C , R , and T only as functions of p and q , as they would all be multiplied by L , which can
161 therefore be dropped from the calculation.

162 [Figure 2 about here.]

163 The value of C is the proportion of shared species p^2 , as per fig. 1, times the proportion of shared links, q ,
164 giving $C = qp^2$. Each network has $r = p^2 - (qp^2)$ rewired links, which leads to $R = 2r = 2p^2(1 - q)$.
165 Finally, we can get the number of unique links in each network t by subtracting $C + r$ from the total
166 number of links (which, since we scale everything by L , is 1), yielding $t = 1 - qp^2 - p^2 + qp^2$, which is

167 $t = 1 - p^2$. The total number of unique links due to turnover is $T = 2t = 2(1 - p^2)$. It is important to note
 168 that C and R , namely the number of links that are kept or rewired, depends on species sharing (p), as the
 169 possible size of the overlap between the two networks does, but the quantity of links that are different due
 170 to turnover does not depends on rewiring.

171 With the values of C , R , and T , we can write

$$\beta_{os} = \frac{2p^2(1 - q)}{2p^2q + 2p^2(1 - q)} = \frac{1 - q}{q + 1 - q} = (1 - q).$$

172 This is a first noteworthy result: the value of β_{os} , in the ideal scenario of equal links and richness, is the
 173 probability of link re-wiring. Because this is true regardless of the value of p (species turnover), this makes
 174 β_{os} a strongly ecologically informative component.

175 Similarly, we can write

$$\beta_{wn} = \frac{2p^2(1 - q) + 2(1 - p^2)}{2p^2q + 2p^2(1 - q) + 2(1 - p^2)} = \frac{p^2(1 - q) + (1 - p^2)}{p^2q + p^2(1 - q) + (1 - p^2)} = 1 - qp^2.$$

176 The overall dissimilarity responds to q (rewiring) linearly, and to p quadratically (which is expected
 177 assuming unipartite networks, in which species are present on both sides).

178 Expressing β_{os} and β_{wn} as functions of p and q trivializes the search for the expression of β_{st} , which is

$$\beta_{st} = 1 - p^2q - 1 + q = q \times (1 - p^2).$$

179 It is worth examining this solution in some detail. β_{st} scales linearly with the probability that a link will
 180 *not* be rewired – in other words, in a pair of networks for which rewiring is important (q goes to 0), species
 181 turnover is going to be a *relatively* less important mechanism to dissimilarity. β_{st} increases when turnover
 182 is important (p goes to 0), and therefore β_{st} represents a *balance* between species turnover and link
 183 rewiring. These three values, as well as β_{st}/β_{wn} , are represented in fig. 2.

184 Sensibility of the decomposition to differences in connectance

185 The results presented in fig. 2 include the strong assumption that the two networks have equal
 186 connectance. Although the range of connectances in nature tends to be very strongly conserved within a
 187 system, we can relax this assumption, by letting one network have more interactions than the other. Note
 188 that for the sake of notation simplicity, I maintain the constraint that the two networks are equally species
 189 rich. Therefore, the sole variation in this numerical experiment is that one network has $L_1 = \rho \times a \times S^2$,
 190 and the other network has $L_2 = \rho \times S^2$; in other words, $L_1 = a \times L$ and $L_2 = L$. As one step of the
 191 components calculations involves a min operation, I will add the constraint that $L_1 \leq L_2$, which is to say
 192 $0 < a \leq 1$. The value of a is the *ratio* of connectances of the two networks, and the terms S^2 and ρ being
 193 shared across all factors, they will be dropped from the calculations.

194 The maximal number of links that can be shared is ap^2 (i.e. $\min(p^2, ap^2)$), as we cannot share more links
 195 than are in the sparsest of the two networks. Of these, q are not rewired, leading to $C = aqp^2$. The
 196 number of links that are rewired in network 1 is the number of its links between shared species minus C ,
 197 i.e. $r_1 = ap^2 - aqp^2 = ap^2(1 - q)$, and similarly $r_2 = p^2 - aqp^2 = p^2(1 - aq)$, leading to
 198 $R = r_1 + r_2 = p^2 [a(1 - q) + 1]$. Using the same approach, we can get $t_1 = a(1 - p^2)$ and $t_2 = (1 - p^2)$,
 199 leading to $T = t_1 + t_2 = (1 - p^2)(1 + a)$.

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

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

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

202 and

$$S = \rho pqR^2.$$

203 Note that we can drop the multiplicative constant R^2 , making the result independent of the size of the
 204 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 interactions 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. ## Does the partition of network dissimilarity needs a new normalization?

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

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

242 Based on the arguments presented above, I do not think the suggestion of Fründ (2021) to change the
 243 denominator of β_{os} makes sense as a default; the strength of the original approach by Poisot *et al.* (2012) is
 244 indeed that the effect of turnover is based on a rigorous definition of networks as graphs (as opposed to
 245 networks as matrices), in which the induction of vertices from the edgelist being compared gives rise to
 246 biologically meaningful denominators. The advantage of this approach is that at no time does the turnover
 247 of species itself (or indeed, as shown in many places in this manuscript, the network richness), or the
 248 connectance of the network, enter into the calculation. As such, it is possible to use β_{os} and β_{wn} in
 249 relationship to these terms, calculated externally (as was recently done by *e.g.* Higino & Poisot 2021),
 250 without creating circularities.

251 **TK** Therefore the argument of Fründ (2021), whereby the β_{os} component should decrease with turnover,
 252 and be invariant to connectance, does not hold: the very point of the approach is to provide measures that
 253 can be interpreted in the light of connectance and species turnover.

254 **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.

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 independent 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)

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

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

281 [Figure 4 about here.]

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

292 **Measuring network beta-diversity: recommendations**

293 The choice of changing the denominator hinges on what one admits as a definition for β_{st} . If the point of
 294 β_{st} is to be a component of overall β -diversity as advocated by Fründ (2021) and Novotny (2009), a change
 295 of numerator *might* be acceptable. Nevertheless, this change of numerator contributes to blurring the
 296 frontier between a measure of interaction dissimilarity and a measure of community dissimilarity which
 297 starts to add the effect of relative richness; this later case warrants a thorough methodological assessment.
 298 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}
 299 and β_{os} , and related to actual measures of species turnover and network connectance, one must not
 300 change the denominator.

301 It is essential to recognize that there are multiple reasons to calculate network dissimilarity, and it is our
 302 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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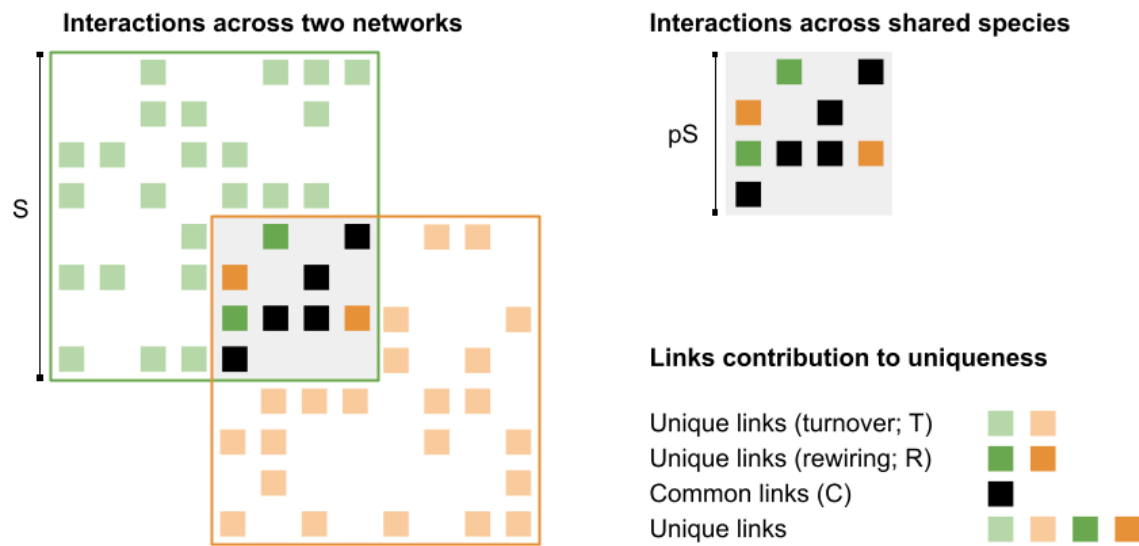


Figure 1: The dissimilarity of two networks (green and orange) of equal richness S (this also holds for unequal richness) depends on three families of interactions: those that are unique because of species turnover (in a pale color), those that are unique because of rewiring (in a saturated color), and 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_{un}) will have a component tied to species turnover, which is β_{st} .

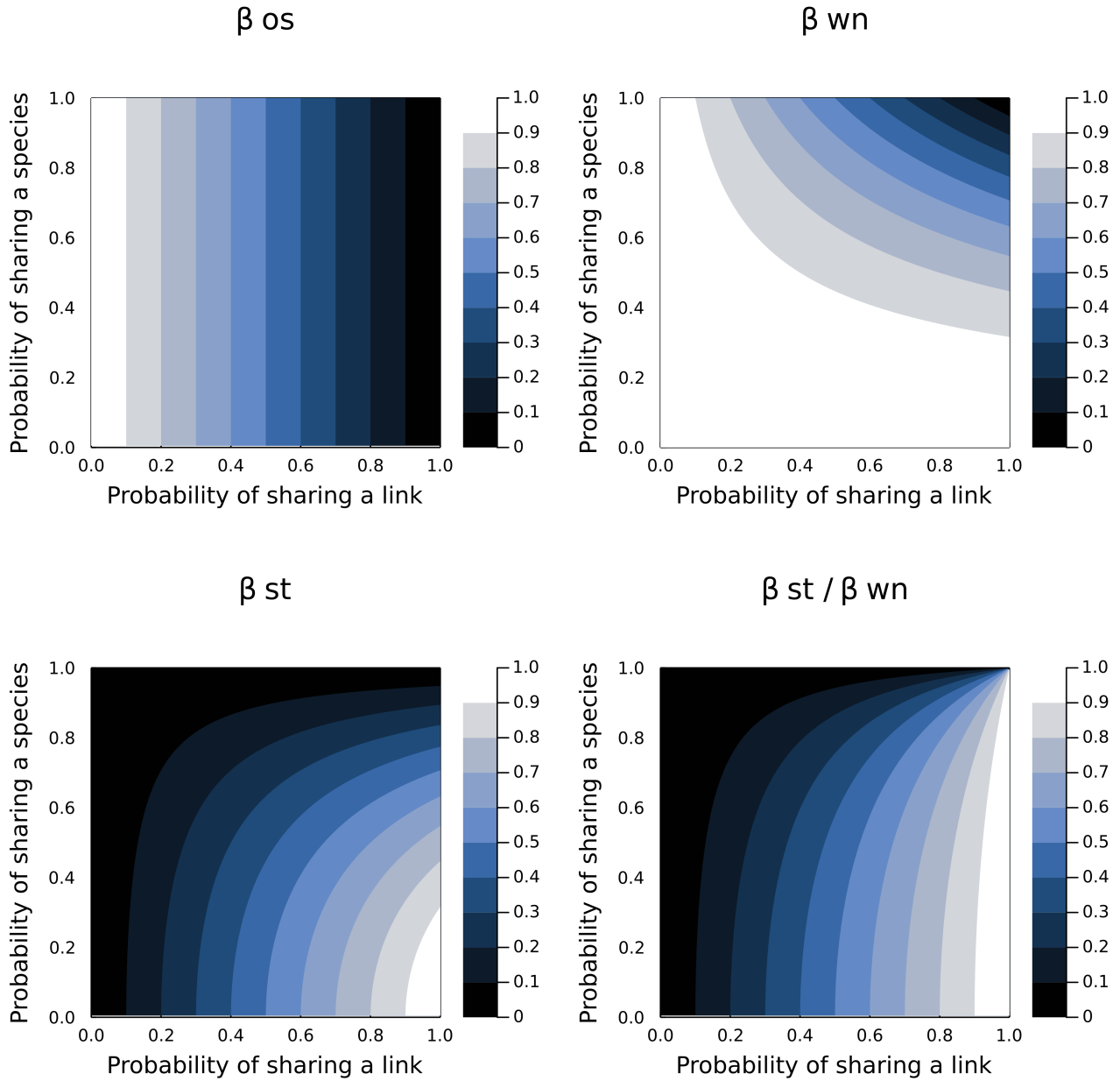


Figure 2: Values of β_{os} , β_{wn} , β_{st} , and β_{st}/β_{wn} as a function of the probability q or sharing a link (x -axis), and the probability p of sharing a species (y -axis). Larger values indicate *more* dissimilarity, such that for $p = q = 1$ the dissimilarity as measured by $\beta_{wn} = 0$, and for $p = q = 0$ the dissimilarity as measured by $\beta_{wn} = 1$. As expected, the relative importance of turnover (β_{st}) is maximal when there is no rewiring, and when turnover increases.

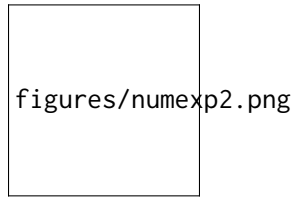


Figure 3: Response of β_{os} and β_{wn} , and the consequences on β_{st} , to changes in rewiring probability (q) and probability of species sharing (p). As expected, β_{os} is not affected by species turnover, but increases with the rewiring probability. By contrast, β_{wn} increases when the rewiring 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.

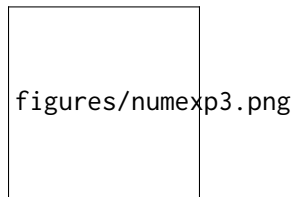


Figure 4: Effects of varying the connectance of the second network (ρ_2) and the proportion of shared species (p) on the values of the β -diversity components. As expected, β_{os} is still independent of species turnover, and β_{wn} increases when species turnover increases, or when the connectances 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.