

1 Dissimilarity of species interaction networks: how to quantify the 2 impact of species turnover?

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

12 Poisot et al. (2012) and Canard et al. (2014) have suggested an approach to β -diversity for ecological
13 networks which is based on the comparison of shared and unique links among species, and differentiate
14 this sharing of links between common and unique species. This framework can be summarized as
15 $\beta_{wn} = \beta_{os} + \beta_{st}$, namely the fact that overall network dissimilarity (β_{wn}) has a component that can be
16 calculated directly from the dissimilarity of interactions between shared species (β_{os}), and a component
17 that cannot, the later originating in unique species introducing their unique interactions (β_{st}). This
18 approach has been widely adopted since its publication, with recent examples using it to understand the
19 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
21 on species interactions (Olsson et al. 2021); and as a tool to estimate the sampling completeness of
22 networks (Souza et al. 2021). It has, similarly, received a number of extensions, including the ability to

23 account for interaction strength (Magrath et al. 2017), the ability to handle probabilistic ecological
24 networks (Poisot et al. 2016), and the integration into the Local Contribution to Beta Diversity (Legendre
25 and De Cáceres 2013) approach to understand how environment changes drive network dissimilarity
26 (Poisot et al. 2017).

27 In a recent contribution, Fründ (2021) argues that the calculation of network dissimilarity terms as
28 outlined by Poisot et al. (2012) is incorrect, as it can lead to over-estimating the role of interactions
29 between shared species in a network (“rewiring”), and therefore underestimate the importance of species
30 turnover across networks. Here, I present a more thorough justification of the methodological choices
31 for the Poisot et al. (2012) method, explain how information about species turnover can be extracted
32 from its decomposition, and conduct numerical experiments to guide the interpretation of the β -diversity
33 values thus obtained.

34 **Partitioning network dissimilarity**

35 The approach to quantifying the difference between pairs of networks established in Poisot et al. (2012) is
36 a simple extension of the overall method by Koleff, Gaston, and Lennon (2003) for species dissimilarity
37 based on presence-absence data. The objects to compare, X_1 and X_2 , are partitioned into three values,
38 $a = |X_1 \cup X_2|$, $b = |X_2 \setminus X_1|$, and $c = |X_1 \setminus X_2|$, where $|x|$ is the cardinality of set x , and \setminus is
39 the set subtraction operation. In the perspective of species composition comparison, X_1 and X_2 are
40 the sets of species in either community, so that if $X_1 = \{x, y, z\}$ and $X_2 = \{v, w, x, y\}$, we have
41 $X_1 \cup X_2 = \{v, w, x, y, z\}$, $X_1 \cap X_2 = \{x, y\}$, $X_2 \setminus X_1 = \{v, w\}$, and $X_1 \setminus X_2 = \{z\}$. The core message
42 of Koleff, Gaston, and Lennon (2003) is that the overwhelming majority of measures of β -diversity can
43 be re-expressed as functions that operate on the cardinality (number of elements) of these sets.

44 **Re-expressing networks as sets**

45 Applying this framework to networks requires a few additional definitions. Although ecologists tend
46 to think of networks as their adjacency matrix, this representation is far from optimal to get a solid
47 understanding of which elements should be counted as part of which set when measuring network
48 dissimilarity. For this reason, we need fall back on the definition of a graph as a pair of sets, wherein

49 $\mathcal{G} = (V, E)$. These two components V and E represent vertices (nodes, species) and edges (interactions),
 50 where V is specifically a set containing the vertices \mathcal{G} , and E is a set of ordered pairs, in which every
 51 pair is composed of two elements of V ; an element $\{i, j\}$ in E indicates that there is an interaction *from*
 52 species i to species j in the network \mathcal{G} .

53 In the context of networks comparison (assuming the networks to compare are \mathcal{M} and \mathcal{N}), we can
 54 further decompose the contents of these sets as

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

55 and

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

56 where V_c is the set of shared species, V_k are the species belonging only to network k , E_c are the shared
 57 edges, and E_{sk} and E_{uk} are the interactions unique to k involving, respectively, only species in V_c , and
 58 at least one species from V_k .

59 **Defining the partitions from networks as sets**

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

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

62 This operation gives us an equivalent to γ -diversity for networks, in that the set of vertices contains *all*
 63 species from the two networks, and the set of edges contains *all* the interactions between these species.
 64 If, further, we make the usual assumption that only species with at least one interaction are present in
 65 the set of vertices, then all elements of the set of vertices are present at least once in the set of edges,
 66 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} (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 ,

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

86 So as to simplify the notation of the following section, I will introduce a series of new variables. Let
 87 $A = |E_c|$ be the number of links that are identical between networks; $S = |E_{sn} \cup E_{sm}|$ be the number
 88 of links that are not shared, but only involve shared species (*i.e.* links from $\mathcal{M} \cup \mathcal{N}$ established between
 89 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
 90 least one unique species. Adopting the perspective developed in the previous section, wherein networks
 91 are sets and the measures of β -diversity operates on these sets, highlights the conceptual issue in the
 92 Fründ (2021) alternative normalization: they are using components of the networks that are *not* part of
 93 the networks being compared.

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

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

106 The expression of β_{st} does not involve a partition into sets that can be plugged into the framework
 107 of Koleff, Gaston, and Lennon (2003), because the part of \mathcal{M} and \mathcal{N} that are composed of their
 108 unique species cannot, by definition, share interactions. One could, theoretically, express these as
 109 $\mathcal{M} \setminus \mathcal{N} = (V_m, E_{um})$ and $\mathcal{N} \setminus \mathcal{M} = (V_v, E_{vn})$ (note the non-commutativity here), but the dissimilarity
 110 between these networks is trivially maximal for the measures considered.

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

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

112 and

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

113 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
 114 $k = U$. 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
 115 U are cardinalities of sets, they are necessarily satisfying this condition.

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

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

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

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

120 As such, we expect that the value of β_{st} will vary in a hump-shaped way with the proportion of
 121 shared interactions. For this reason, Poisot et al. (2012) suggest that β_{st}/β_{wn} (alt. $1 - \beta_{os}/\beta_{wn}$) is a
 122 better indicator of the *relative* importance of turnover processes on network dissimilarity. This can be
 123 calculated as

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

124 which reduces to

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

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

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

129 To illustrate the behavior of β_{st} , I conducted a simple numerical experiment in which two networks
130 have the same number of interactions L (recall from the previous section that we do not need to set
131 a number of species yet), and these interactions are partitionned according to proportions p_s and p_r
132 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
133 $U = (1 - p_s) \times (1 - p_r) \times L$. The results are represented in fig. 1.

134 **Is this decomposition over-estimating the effect of “rewiring”?**

135 One of the arguments put forth by Fründ (2021) is that the decomposition outlined above will overesti-
136 mate the effect of rewiring; I argue that this is based on a misunderstanding of what β_{st} achieves. It is
137 paramount to clarify that β_{st} is not a direct measure of the importance of turnover: it is a quantification
138 of the relative impact of rewiring to overall dissimilarity, which, all non-turnover mechanisms being
139 accounted for in the decomposition, can be explained by turnover mechanisms. In this section, I present
140 two numerical experiments showing (i) that the β_{os} component is in fact an accurate measure of rewiring,
141 and (ii) that β_{st} captures the consequences of species turnover, and of the interactions brought by unique
142 species.

143 **Illustrations on arbitrarily small networks are biased**

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

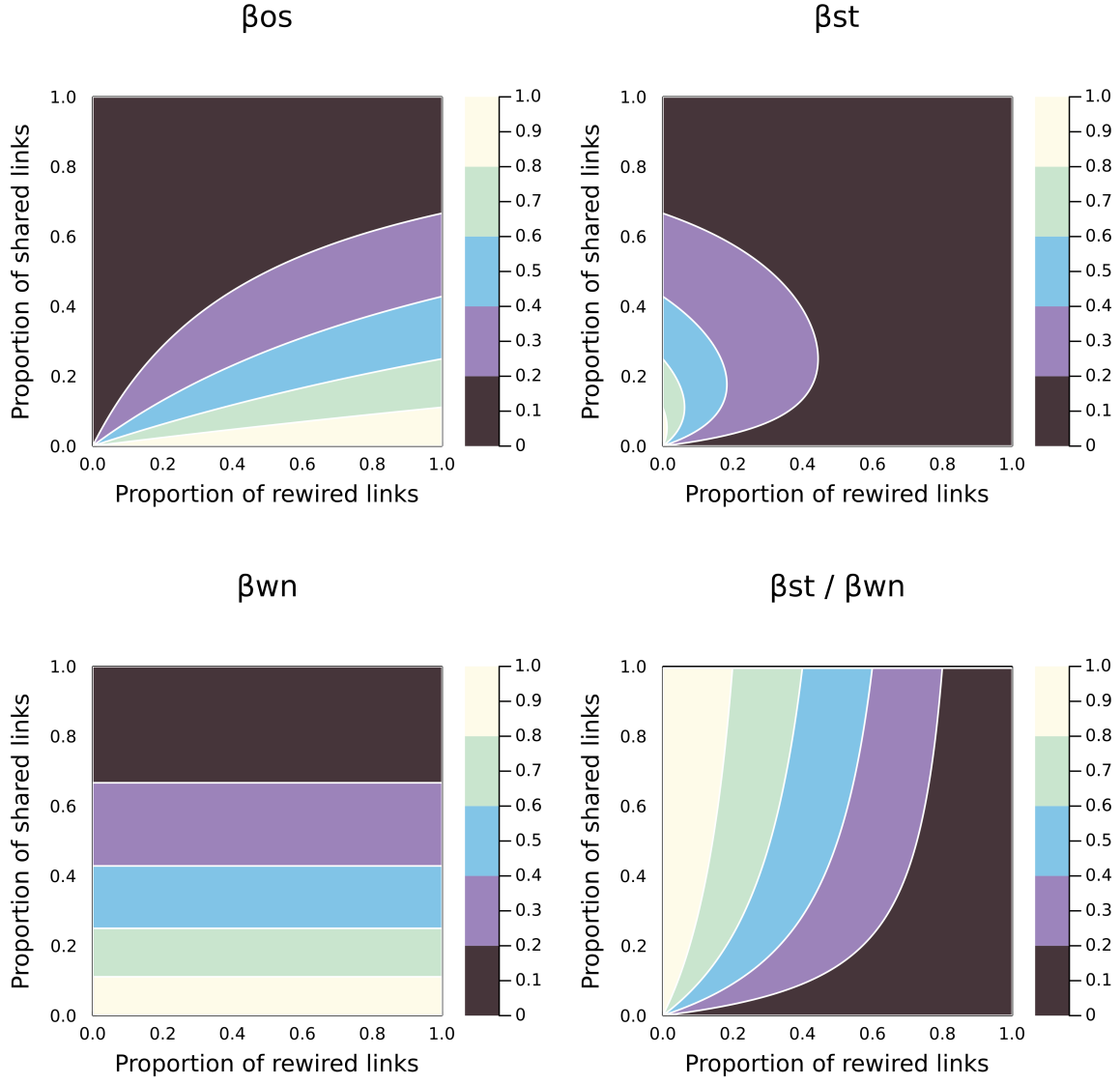


Figure 1: Values of β_{os} , β_{wn} , β_{st} , and β_{st}/β_{wn} as a function of the proportion of rewired links and the proportion of shared links.

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

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

156 **Numerical experiment: the decomposition captures the roles of rewiring and turnover accurately**

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

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

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

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

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

166 and

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

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

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

179 In conclusion, this numerical experiment shows that the decomposition as initially presented by Poisot et
 180 al. (2012), *i.e.* using denominators that make sense from a network composition point of view, succeeds
 181 at capturing the relative effect of turnover and rewiring. ### Numerical experiment: the decomposition
 182 captures the roles of species turnover and connectance accurately

183 Consider now two bipartite networks, which still have R species on either side, but differ in their
 184 connectance (ρ_1 and ρ_2) – by maintaining the assumption that species on one side are shared with

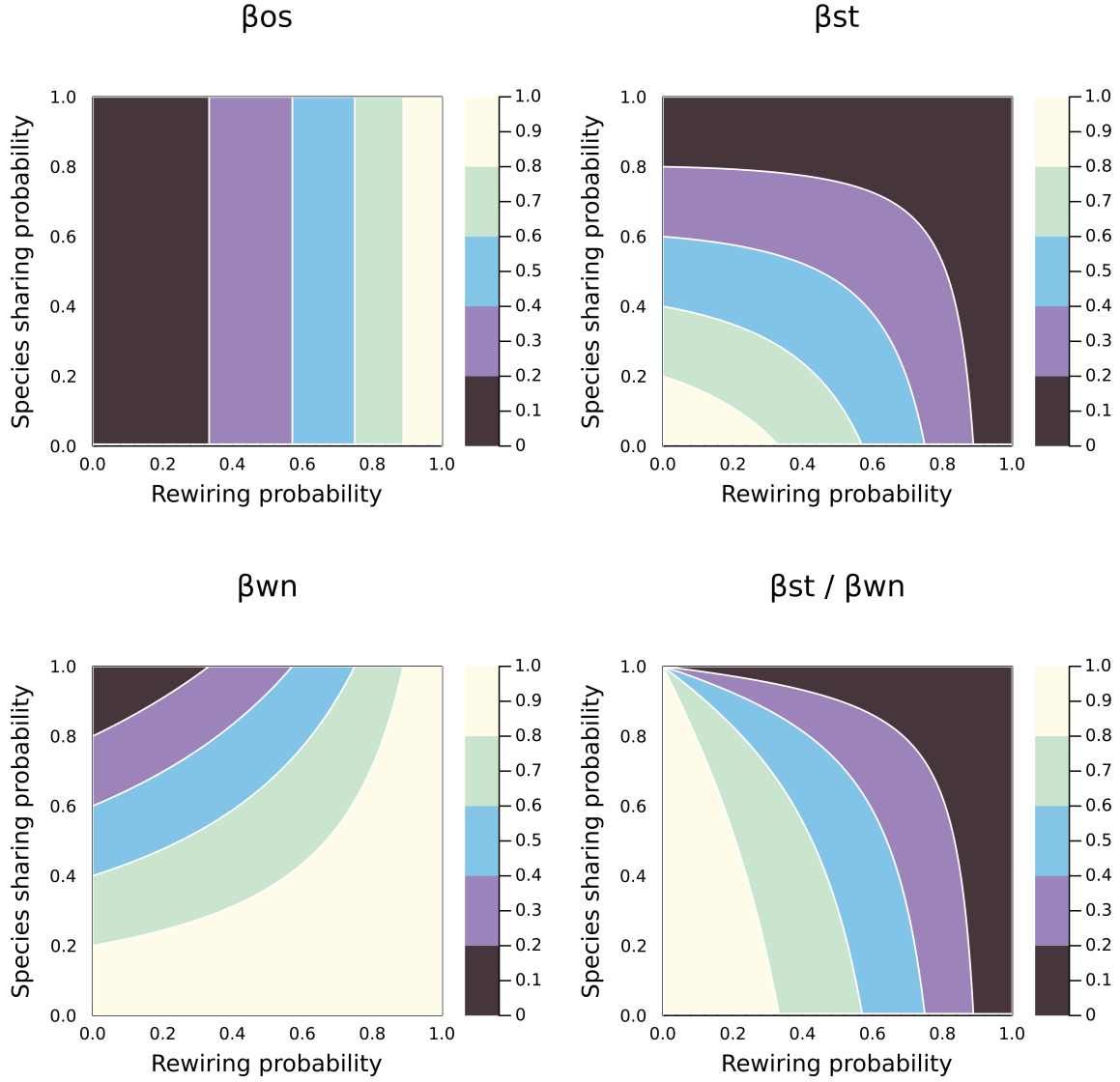


Figure 2: Response of β_{os} and β_{wn} , and the consequences on β_{st} , to changes in rewiring probability (q) and probability of species sharing (p). As expected, β_{os} is not affected by species turnover, but increases with the rewiring probability. By contrast, β_{wn} increases when the rewiring 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.

185 probability p , and that interactions between shared species are rewired at probability q , we can examine
 186 the effect of varying both connectance and turnover on the value of the β -diversity components. Note
 187 that, although not presented, we will drop the multiplicative constant R^2 from all calculations, as it is
 188 a common factor for all values; again, this implies that the results presented here are independent of
 189 network richness.

190 The number of unique links due to species turnover is

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

191 which decreases with the proportion of shared species, but increases with connectance. The number of
 192 links between shared species takes a little more steps to calculate. First, amongst the pR^2 species in
 193 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
 194 are only $\min(\rho_1, \rho_2)pR^2$ links that can be shared, a proportion q of which will undergo re-wiring, and
 195 a proportion $(1 - q)$ of which will be shared. This leads to the expression (after dropping R^2) for the
 196 number of shared links:

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

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

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

201 Note that as expected, this last quantity scales with the proportion of shared species (p) and with
 202 connectance (as shared species bring more of their interactions), but decreases with the size of the
 203 shared links components. The consequences of varying ρ_2 and p are presented in fig. 3.

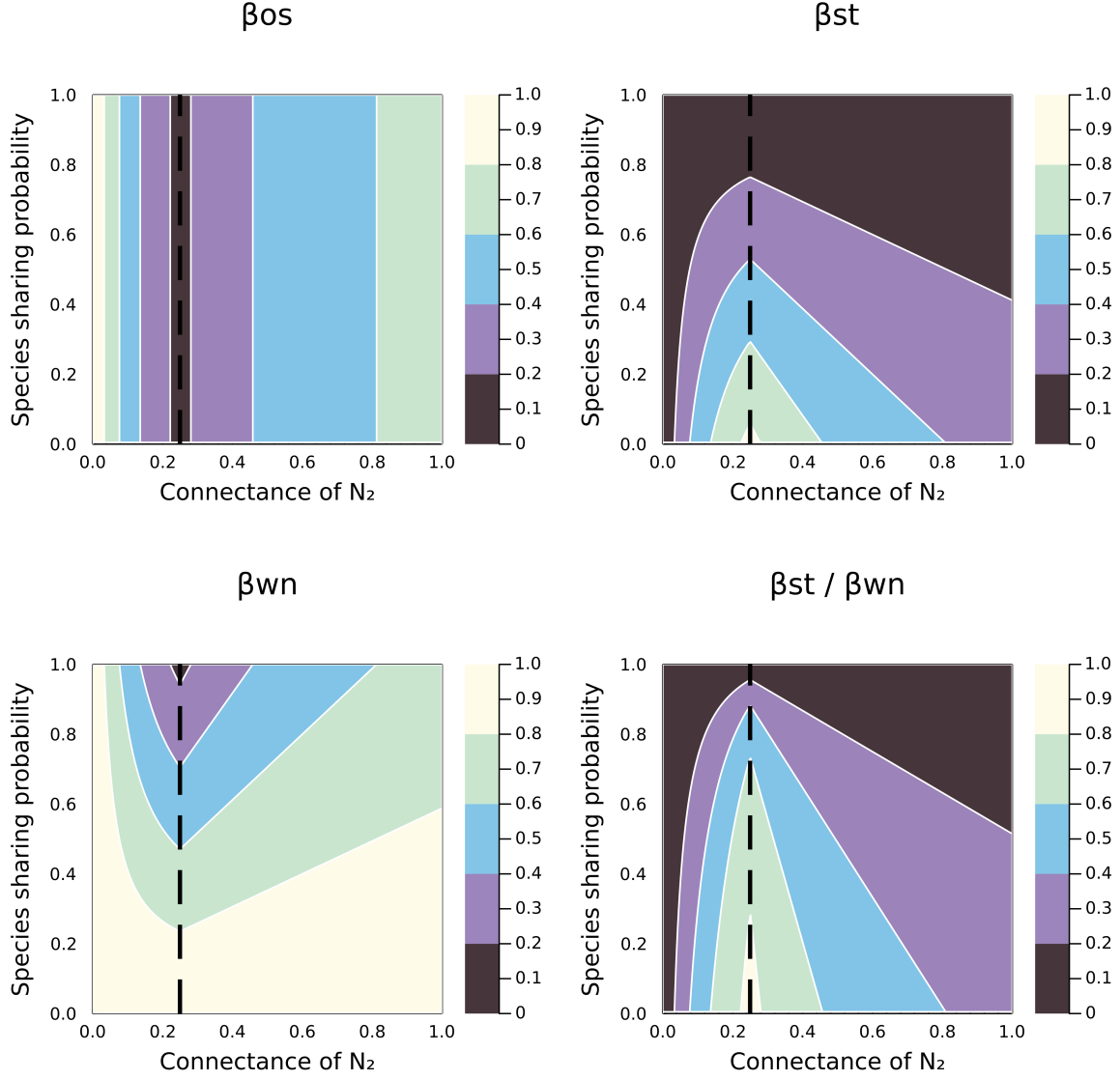


Figure 3: Effects of varying the connectance of the second network (ρ_2) and the proportion of shared species (p) on the values of the β -diversity components. As expected, β_{os} is still independent of species turnover, and β_{wn} increases when species turnover increases, or when the connectances 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.

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 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

231 there are multiple reasons to calculate network dissimilarity, and it is our opinion that the arguments
232 levied by Fründ (2021) against the original partition stem from a misunderstanding of what it intends to
233 do (and does, indeed, do well), not from intrinsic methodological issues in the partition itself.

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