

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 (Magrach *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 $|x|$ is the cardinality of set x , and \setminus is the set

58 subtraction operation. In the perspective of species composition comparison, X_1 and X_2 are the sets of
 59 species in either community, so that if $X_1 = \{x, y, z\}$ and $X_2 = \{v, w, x, y\}$, we have $X_1 \cup X_2 = \{v, w, x, y, z\}$,
 60 $X_1 \cap X_2 = \{x, y\}$, $X_2 \setminus X_1 = \{v, w\}$, and $X_1 \setminus X_2 = \{z\}$. The core message of Koleff *et al.* (2003) is that the
 61 overwhelming majority of measures of β -diversity can be re-expressed as functions that operate on the
 62 cardinality (number of elements) of these sets.

63 **Re-expressing networks as sets**

64 Applying this framework to networks requires a few additional definitions. Although ecologists tend to
 65 think of networks as their adjacency matrix, this representation is far from optimal to get a solid
 66 understanding of which elements should be counted as part of which set when measuring network
 67 dissimilarity. For this reason, we need fall back on the definition of a graph as a pair of sets, wherein
 68 $\mathcal{G} = (V, E)$. These two components V and E represent vertices (nodes, species) and edges (interactions),
 69 where V is specifically a set containing the vertices \mathcal{G} , and E is a set of ordered pairs, in which every pair is
 70 composed of two elements of V ; an element $\{i, j\}$ in E indicates that there is an interaction *from* species i
 71 to species j in the network \mathcal{G} .

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

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

74 and

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

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

78 Defining the partitions from networks as sets

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

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

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

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

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

89 The decomposition of β -diversity from Poisot *et al.* (2012) uses these components to measure β_{os} (the
90 interaction dissimilarity between shared species, which Fründ (2021) terms “rewiring”), and β_{wn} (the
91 overall dissimilarity including non-shared species). We can express the components a , b , and c of Koleff *et*
92 *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	$E_{sn} \cup E_{un}$	$E_{sm} \cup E_{um}$

93 These decompositions are used to perform the calculations of β -diversity in the `EcologicalNetworks.jl`
94 package (Banville *et al.* 2021) for Julia, which I use for the following numerical experiments.

95 Quantifying the importance of species turnover

96 The difference between β_{os} and β_{wn} stems from the species dissimilarity between \mathcal{M} and \mathcal{N} , and it is
97 easier to understand the effect of turnover by picking a dissimilarity measure to work as an exemplar. At
98 this point, Fründ (2021) introduce a confusing terminology in their work, stating that Sørensen's and
99 Whittaker's measures of dissimilarity are the same in the Koleff *et al.* (2003) framework (they are not; in
100 practice, $\beta_{Sor} = 1 - \beta_w$), and (ii) noting Whittaker's measure as $(b + c)/(2a + b + c)$, which in the Koleff *et*
101 *al.* (2003) framework is, in fact, β_t (Wilson & Shmida 1984). This does not change the overall conclusions
102 as these measures can be re-expressed to converge to the same value. For the sake of consistency, I will use
103 β_t moving forward; it returns values in $[0, 1]$, with 0 meaning complete similarity, and 1 meaning complete
104 dissimilarity.

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

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

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

107 So as to simplify the notation of the following section, I will introduce a series of new variables. Let
108 $A = |E_c|$ be the number of links that are identical between networks; $S = |E_{sn} \cup E_{sm}|$ be the number of
109 links that are not shared, but only involve shared species (*i.e.* links from $\mathcal{M} \cup \mathcal{N}$ established between
110 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
111 one unique species. Adopting the perspective developed in the previous section, wherein networks are
112 sets and the measures of β -diversity operates on these sets, highlights the conceptual issue in the Fründ
113 (2021) alternative normalization: they are using components of the networks that are *not* part of the
114 networks being compared.

115 There are two important points to note here. First, the number or proportion of species that are shared is
116 not involved in the calculation. Second, the connectance of either network is not involved in the
117 calculation. That all links counted in *e.g.* U come from \mathcal{M} , or that they are evenly distributed between \mathcal{M}
118 and \mathcal{N} , has no impact on the result. This is a desirable property of the approach: whatever quantitative
119 value of the components of dissimilarity can be interpreted in the light of the connectance and species

120 turnover *without* any risk of circularity. Therefore the argument of Fründ (2021), whereby the β_{os}
 121 component should decrease with turnover, and be invariant to connectance, does not hold: the very point
 122 of the approach is to provide measures that can be interpreted in the light of connectance and species
 123 turnover.

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

127 The expression of β_{st} does not involve a partition into sets that can be plugged into the framework of
 128 Koleff *et al.* (2003), because the part of \mathcal{M} and \mathcal{N} that are composed of their unique species cannot, by
 129 definition, share interactions. One could, theoretically, express these as $\mathcal{M} \setminus \mathcal{N} = (V_m, E_{um})$ and
 130 $\mathcal{N} \setminus \mathcal{M} = (V_v, E_{vn})$ (note the non-commutativity here), but the dissimilarity between these networks is
 131 trivially maximal for the measures considered.

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

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

133 and

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

134 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
 135 $k = U$. 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
 136 cardinalities of sets, they are necessarily satisfying this condition.

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

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

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

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

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

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

144 which reduces to

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

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

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

149 To illustrate the behavior of β_{st} , I conducted a simple numerical experiment in which two networks have
 150 the same number of interactions L (recall from the previous section that we do not need to set a number of
 151 species yet), and these interactions are partitionned according to proportions p_s and p_r into shared (A),
 152 rewired (S), and unique (U) links, with $A = p_s \times L$, $S = (1 - p_s) \times p_r \times L$, and $U = (1 - p_s) \times (1 - p_r) \times L$.
 153 The results are represented in fig. 2.

154 [Figure 2 about here.]

155 The rewiring component β_{os} varies as a function of the proportion of shared links that are rewired; by
 156 contrast, β_{wn} varies *only* as a function of the proportion of links that are shared: that the unshared links
 157 are established between common or unique species has no effect on overall network dissimilarity. The
 158 quadratic nature of the denominator for β_{st} is clear here, with a maximum reach when there is no
 159 re-wiring, and a small number of shared links (*i.e.* the networks are almost entirely dissimilar except for

the links between shared species). Although 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 $\rho(1 - q)p R^2$ are shared, and $\rho q p R^2$ underwent rewiring. This leads to

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

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.

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

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

213 **Numerical experiment: the decomposition captures the roles of species turnover and** 214 **connectance accurately**

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

222 The number of unique links due to species turnover is

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

223 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.

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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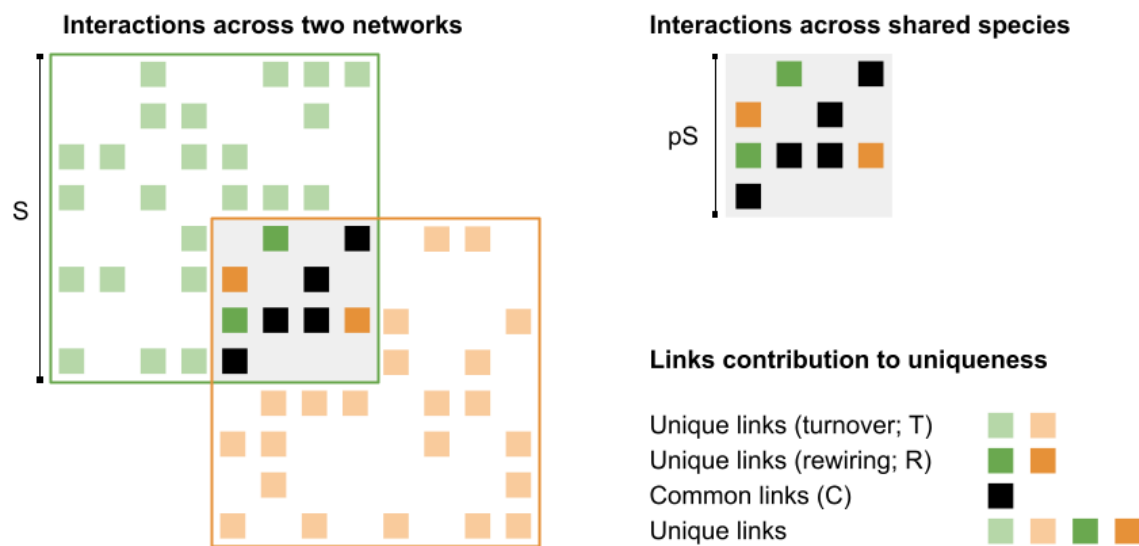


Figure 1: TK

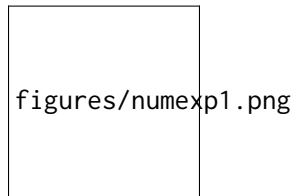


Figure 2: Values of β_{os} , β_{wn} , β_{st} , and β_{st}/β_{wn} as a function of the proportion of rewired links and the proportion of shared links.

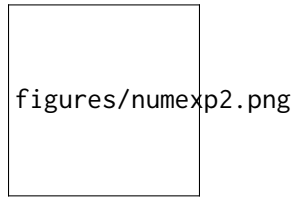


Figure 3: Response of β_{os} and β_{wn} , and the consequences on β_{st} , to changes in rewiring probability (q) and probability of species sharing (p). As expected, β_{os} is not affected by species turnover, but increases with the rewiring probability. By contrast, β_{wn} increases when the rewiring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

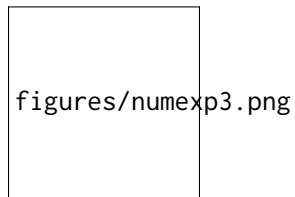


Figure 4: Effects of varying the connectance of the second network (ρ_2) and the proportion of shared species (p) on the values of the β -diversity components. As expected, β_{os} is still independent of species turnover, and β_{wn} increases when species turnover increases, or when the connectances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