

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

Timothée Poisot<sup>1,2,‡</sup>

<sup>1</sup> Université de Montréal   <sup>2</sup> Québec Centre for Biodiversity Sciences

‡ These authors contributed equally to the work

## Correspondance to:

Timothée Poisot — [timothee.poisot@umontreal.ca](mailto:timothee.poisot@umontreal.ca)

Despite having established its usefulness in the last ten years, the decomposition of ecological networks in components allowing to measure their  $\beta$ -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, in a way that  
3 meshes with the usual approaches of comparison of ecological communities, *i.e.*  $\beta$ -diversity; although the  
4 definition of  $\beta$ -diversity is a contentious topic amongst community ecologists (see *e.g.* Tuomisto 2010), the  
5 need to understand network variability is motivated by the fact that species that make up the networks do  
6 not react to their environment in the same way, and therefore the  $\beta$ -diversity of networks may behave in  
7 complex ways.

8 Poisot *et al.* (2012) and Canard *et al.* (2014) have suggested an approach to  $\beta$ -diversity for ecological  
9 networks which is based on the comparison of shared and unique links among species, and differentiate  
10 this sharing of links between common and unique species. This framework can be summarized as  
11  $\beta_{wn} = \beta_{os} + \beta_{st}$ , namely the fact that overall network dissimilarity ( $\beta_{wn}$ ) has a component that can be  
12 calculated directly from the dissimilarity of interactions between shared species ( $\beta_{os}$ ), and a component  
13 that cannot, the later originating in unique species introducing their unique interactions ( $\beta_{st}$ ). This  
14 approach has been widely adopted since its publication, with recent examples using it to understand the  
15 effect of fire on pollination systems (Baronio *et al.* 2021); the impact of rewiring on spatio-temporal  
16 network dynamics (Campos-Moreno *et al.* 2021); the effects of farming on rural and urban landscapes on  
17 species interactions (Olsson *et al.* 2021); and as a tool to estimate the sampling completeness of networks  
18 (Souza *et al.* 2021). It has, similarly, received a number of extensions, including the ability to account for  
19 interaction strength (Magrath *et al.* 2017), the ability to handle probabilistic ecological networks (Poisot *et al.*  
20 2016), and the integration into the Local Contribution to Beta Diversity (Legendre & De Cáceres 2013)  
21 approach to understand how environment changes drive network dissimilarity (Poisot *et al.* 2017).

22 In a recent contribution, Fründ (2021) argues that the calculation of network dissimilarity terms as  
23 outlined by Poisot *et al.* (2012) is incorrect, as it can lead to over-estimating the role of interactions  
24 between shared species in a network (“rewiring”), and therefore underestimate the importance of species  
25 turnover across networks. Here, I present a more thorough justification of the methodological choices for  
26 the Poisot *et al.* (2012) method, explain how information about species turnover can be extracted from its  
27 decomposition, and conduct numerical experiments to guide the interpretation of the  $\beta$ -diversity values  
28 thus obtained. These numerical experiments establish three core facts. First, the decomposition responds  
29 to the correct sources of network variation; second, the decomposition adequately captures the relative  
30 roles of species turnover and interaction rewiring; finally, the decomposition adequately captures the role

of turnover vs. non-turnover (like changes in connectance) processes. Although the alternative normalization suggested by Fründ (2021) is not without its uses, which I discuss in conclusion, it is inadequate as a network  $\beta$ -diversity measurement, as it introduces many confounding elements that make the interpretation of the results more difficult, and should likely not be used as a default.

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

## Re-expressing networks as sets

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

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

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

56 and

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

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

## 60 Defining the partitions from networks as sets

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

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

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

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

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

71 The decomposition of  $\beta$ -diversity from Poisot *et al.* (2012) uses these components to measure  $\beta_{os}$  (the  
72 interaction dissimilarity between shared species, which Fründ (2021) terms “rewiring”), and  $\beta_{wn}$  (the  
73 overall dissimilarity including non-shared species). We can express the components  $a$ ,  $b$ , and  $c$  of Koleff *et*  
74 *al.* (2003) as the cardinality of the following sets:

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

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

## 77 Quantifying the importance of species turnover

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

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

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

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

89 So as to simplify the notation of the following section, I will introduce a series of new variables. Let  
90  $A = |E_c|$  be the number of links that are identical between networks;  $S = |E_{sn} \cup E_{sm}|$  be the number of  
91 links that are not shared, but only involve shared species (*i.e.* links from  $\mathcal{M} \cup \mathcal{N}$  established between  
92 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  
93 one unique species. Adopting the perspective developed in the previous section, wherein networks are

94 sets and the measures of  $\beta$ -diversity operates on these sets, highlights the conceptual issue in the Fründ  
 95 (2021) alternative normalization: they are using components of the networks that are *not* part of the  
 96 networks being compared.

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

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

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

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

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

115 and

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

116 Note that  $\beta_{os}$  has the form  $x/y$  with  $x = S$  and  $y = 2A + S$ , and  $\beta_{wn}$  has the form  $(x + k)/(y + k)$ , with  
 117  $k = U$ . 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

118 cardinalities of sets, they are necessarily satisfying this condition.

119 We can get an expression for  $\beta_{st}$ , by bringing  $\beta_{os}$  and  $\beta_{wn}$  to a common denominator and simplifying the  
120 numerator:

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

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

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

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

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

126 which reduces to

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

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

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

131 To illustrate the behavior of  $\beta_{st}$ , I conducted a simple numerical experiment in which two networks have  
132 the same number of interactions  $L$  (recall from the previous section that we do not need to set a number of  
133 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. 1.

[Figure 1 about here.]

The rewiring component  $\beta_{os}$  varies as a function of the proportion of shared links that are rewired; by contrast,  $\beta_{wn}$  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  $\beta_{st}$  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). Although the *raw* values of  $\beta_{st}$  may seem low, the normalization using  $\beta_{st}/\beta_{wn}$  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  $\beta_{st}$  achieves. It is paramount to clarify that  $\beta_{st}$  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  $\beta_{os}$  component is in fact an accurate measure of rewiring, and (ii) that  $\beta_{st}$  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:

| $A$ | $S$ | $U$ | $\beta_{os}$ | $\beta_{wn}$ | $\beta_{st}$ | $\beta_{st}/\beta_{wn}$ |
|-----|-----|-----|--------------|--------------|--------------|-------------------------|
| 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                     |

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

### 167 **Numerical experiment: the decomposition captures the roles of rewiring and turnover** 168 **accurately**

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

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

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

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

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

178 and

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

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

181 [Figure 2 about here.]

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

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

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

197 Consider now two bipartite networks, which still have  $R$  species on either side, but differ in their  
198 connectance ( $\rho_1$  and  $\rho_2$ ) – by maintaining the assumption that species on one side are shared with  
199 probability  $p$ , and that interactions between shared species are rewired at probability  $q$ , we can examine  
200 the effect of varying both connectance and turnover on the value of the  $\beta$ -diversity components. Note that,  
201 although not presented, we will drop the multiplicative constant  $R^2$  from all calculations, as it is a  
202 common factor for all values; again, this implies that the results presented here are independent of  
203 network richness.

204 The number of unique links due to species turnover is

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

205 which decreases with the proportion of shared species, but increases with connectance. The number of  
206 links between shared species takes a little more steps to calculate. First, amongst the  $pR^2$  species in both  
207 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  
208  $\min(\rho_1, \rho_2)pR^2$  links that can be shared, a proportion  $q$  of which will undergo re-wiring, and a proportion  
209  $(1 - q)$  of which will be shared. This leads to the expression (after dropping  $R^2$ ) for the number of shared  
210 links:

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

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

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

215 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  $\rho_2$  and  $p$  are presented in fig. 3.

[Figure 3 about here.]

Although  $\beta_{os}$  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  $A$ ),  $\beta_{wn}$  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  $\rho_1$  and  $\rho_2$ ), and therefore contribute to dissimilarity. It is particularly noteworthy that  $\beta_{st}$ , regardless of the differences in connectance, increases with the proportion of unique species. At an equal proportion of shared species,  $\beta_{st}$  decreases with differences in connectance: this is an equally expected result, which indicates that the difference between  $\beta_{os}$  and  $\beta_{wn}$  is in part explained by non-turnover mechanisms (here, changes in connectance). Relying on the  $\beta_{st}/\beta_{wn}$  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  $\beta_{os}$  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  $\beta_{os}$  and  $\beta_{wn}$  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  $\beta_{st}$ . If the point of  $\beta_{st}$  is to be a component of overall  $\beta$ -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

243 starts to add the effect of relative richness; this later case warrants a thorough methodological assessment.  
244 Conversely, if as we argue in Poisot *et al.* (2012),  $\beta_{st}$  is to be meant as a *guide* to the interpretation of  $\beta_{wn}$   
245 and  $\beta_{os}$ , and related to actual measures of species turnover and network connectance, one must not  
246 change the denominator.

247 It is essential to recognize that there are multiple reasons to calculate network dissimilarity, and it is our  
248 opinion that the arguments levied by Fründ (2021) against the original partition stem from a  
249 misunderstanding of what it intends to do (and does, indeed, do well), not from intrinsic methodological  
250 issues in the partition itself. Based on the results presented in this contribution, I argue that the original  
251 partition of network  $\beta$ -diversity from Poisot *et al.* (2012) should remain the default.

## 252 References

- 253 Banville, F., Vissault, S. & Poisot, T. (2021). Mangal.jl and EcologicalNetworks.jl: Two complementary  
254 packages for analyzing ecological networks in Julia. *Journal of Open Source Software*, 6, 2721.
- 255 Baronio, G.J., Souza, C.S., Maruyama, P.K., Raizer, J., Sigrist, M.R. & Aoki, C. (2021). Natural fire does not  
256 affect the structure and beta diversity of plant-pollinator networks, but diminishes floral-visitor  
257 specialization in Cerrado. *Flora*, 281, 151869.
- 258 Campos-Moreno, D.F., Dyer, L.A., Salcido, D., Massad, T.J., Pérez-Lachaud, G., Tepe, E.J., *et al.* (2021).  
259 Importance of interaction rewiring in determining spatial and temporal turnover of tritrophic  
260 (Piper-caterpillar-parasitoid) metanetworks in the Yucatán Península, México. *Biotropica*, 53,  
261 1071–1081.
- 262 Canard, E.F., Mouquet, N., Mouillot, D., Stanko, M., Miklisova, D. & Gravel, D. (2014). Empirical  
263 evaluation of neutral interactions in host-parasite networks. *The American Naturalist*, 183, 468–479.
- 264 Dunne, J.A. (2006). The Network Structure of Food Webs. In: *Ecological networks: Linking structure and*  
265 *dynamics* (eds. Dunne, J.A. & Pascual, M.). Oxford University Press, pp. 27–86.
- 266 Fründ, J. (2021). Dissimilarity of species interaction networks: How to partition rewiring and species  
267 turnover components. *Ecosphere*, 12, e03653.
- 268 Higino, G.T. & Poisot, T. (2021). Beta and phylogenetic diversities tell complementary stories about  
269 ecological networks biogeography. *Parasitology*, 1–23.

270 Koleff, P., Gaston, K.J. & Lennon, J.J. (2003). Measuring beta diversity for presence–absence data. *Journal*  
 271 *of Animal Ecology*, 72, 367–382.

272 Legendre, P. & De Cáceres, M. (2013). Beta diversity as the variance of community data: Dissimilarity  
 273 coefficients and partitioning. *Ecology Letters*, 16, 951–963.

274 Magrach, A., Holzschuh, A., Bartomeus, I., Riedinger, V., Roberts, S.P.M., Rundlöf, M., *et al.* (2017).  
 275 Plant-pollinator networks in semi-natural grasslands are resistant to the loss of pollinators during  
 276 blooming of mass-flowering crops. *Ecography*, n/a–n/a.

277 Novotny, V. (2009). Beta diversity of plant–insect food webs in tropical forests: A conceptual framework.  
 278 *Insect Conservation and Diversity*, 2, 5–9.

279 Olsson, R.L., Brousil, M.R., Clark, R.E., Baine, Q. & Crowder, D.W. (2021). Interactions between plants  
 280 and pollinators across urban and rural farming landscapes. *Food Webs*, 27, e00194.

281 Poisot, T., Canard, E., Mouillot, D., Mouquet, N. & Gravel, D. (2012). The dissimilarity of species  
 282 interaction networks. *Ecology Letters*, 15, 1353–1361.

283 Poisot, T., Cirtwill, A.R., Cazelles, K., Gravel, D., Fortin, M.-J. & Stouffer, D.B. (2016). The structure of  
 284 probabilistic networks. *Methods in Ecology and Evolution*, 7, 303–312.

285 Poisot, T., Gueveneux-Julien, C., Fortin, M.-J., Gravel, D. & Legendre, P. (2017). Hosts, parasites and their  
 286 interactions respond to different climatic variables. *Global Ecology and Biogeography*, n/a–n/a.

287 Poisot, T., Stouffer, D.B. & Gravel, D. (2015). Beyond species: Why ecological interaction networks vary  
 288 through space and time. *Oikos*, 124, 243–251.

289 Souza, C.S., Maruyama, P.K., Santos, K.C.B.S., Varassin, I.G., Gross, C.L. & Araujo, A.C. (2021).  
 290 Plant-centred sampling estimates higher beta diversity of interactions than pollinator-based sampling  
 291 across habitats. *New Phytologist*, 230, 2501–2512.

292 Trøjelsgaard, K. & Olesen, J.M. (2016). Ecological networks in motion: Micro- and macroscopic variability  
 293 across scales. *Functional Ecology*, 30, 1926–1935.

294 Tuomisto, H. (2010). A diversity of beta diversities: Straightening up a concept gone awry. Part 1. Defining  
 295 beta diversity as a function of alpha and gamma diversity. *Ecography*, 33, 2–22.

296 Wilson, M.V. & Shmida, A. (1984). Measuring Beta Diversity with Presence-Absence Data. *Journal of*  
 297 *Ecology*, 72, 1055–1064.

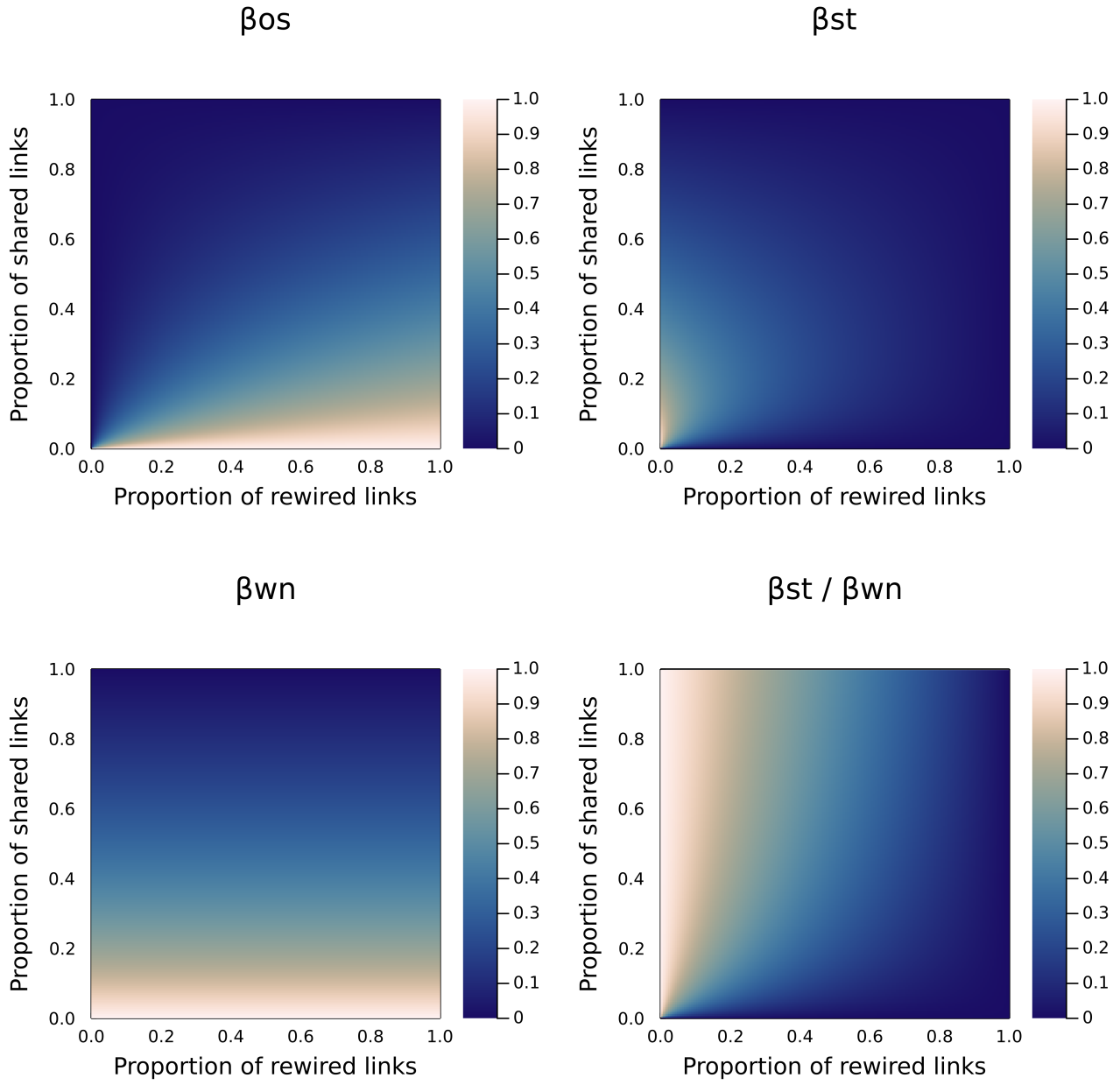


Figure 1: Values of  $\beta_{os}$ ,  $\beta_{wn}$ ,  $\beta_{st}$ , and  $\beta_{st}/\beta_{wn}$  as a function of the proportion of rewired links and the proportion of shared links.



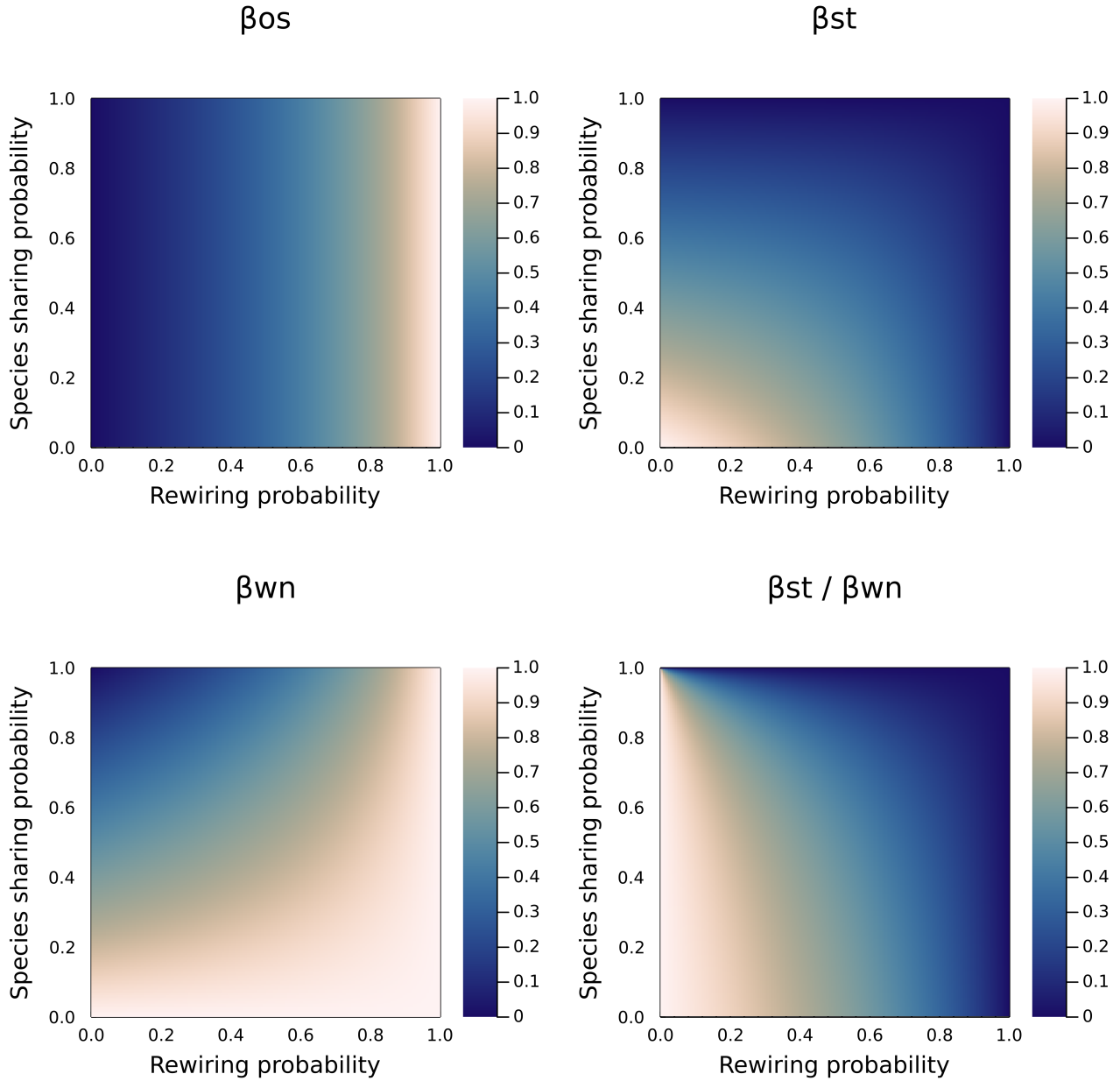


Figure 2: Response of  $\beta_{os}$  and  $\beta_{wn}$ , and the consequences on  $\beta_{st}$ , to changes in rewiring probability ( $q$ ) and probability of species sharing ( $p$ ). As expected,  $\beta_{os}$  is not affected by species turnover, but increases with the rewiring probability. By contrast,  $\beta_{wn}$  increases when the rewiring probability is higher *and* when fewer species are shared. This has important consequences for  $\beta_{st}$ : its value is maximized for low species sharing, and decreases for high rewiring probability.

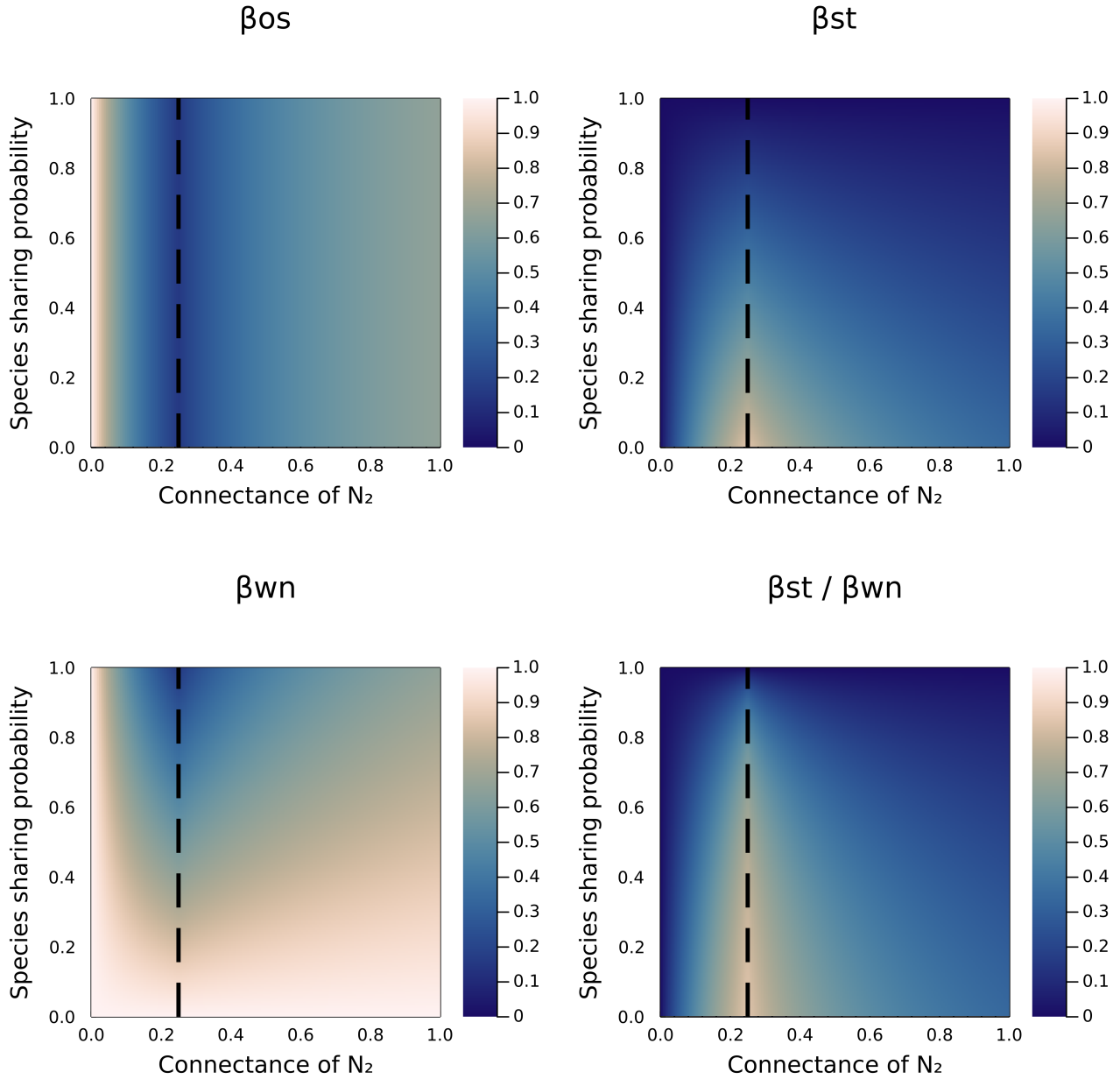


Figure 3: Effects of varying the connectance of the second network ( $\rho_2$ ) and the proportion of shared species ( $p$ ) on the values of the  $\beta$ -diversity components. As expected,  $\beta_{os}$  is still independent of species turnover, and  $\beta_{wn}$  increases when species turnover increases, 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.