

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

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4 July 29, 2021

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  $\beta$ -diversity; although the definition of  $\beta$ -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  $\beta$ -diversity of networks may behave in complex ways.

12 Poisot et al. (2012) and Canard et al. (2014) have suggested an approach to  $\beta$ -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 ( $\beta_{wn}$ ) has a component that can be  
16 calculated directly from the dissimilarity of interactions between shared species ( $\beta_{os}$ ), and a component  
17 that cannot, the later originating in unique species introducing their unique interactions ( $\beta_{st}$ ). 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  $\beta$ -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  $\beta$ -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  $\gamma$ -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

$\beta$ -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  $\beta$ -diversity from Poisot et al. (2012) uses these components to measure  $\beta_{os}$  (the interaction dissimilarity between shared species, which Fründ (2021) terms “rewiring”), and  $\beta_{wn}$  (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	$a$	$b$	$c$
$\beta_{os}$	$E_c$	$E_{sn}$	$E_{sm}$
$\beta_{wn}$	$E_c$	$E_{sn} \cup E_{un}$	$E_{sm} \cup E_{um}$

## Quantifying the importance of species turnover

The difference between  $\beta_{os}$  and  $\beta_{wn}$  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,  $\beta_t$  (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  $\beta_t$  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  $\beta$ -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  $\beta_{os}$  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  $\beta_{st}$ , *i.e.* the part of  $\beta_{wn}$  that is not  
 104 explained by changes in interactions between shared species ( $\beta_{os}$ ), and therefore stems from species  
 105 turnover. This fraction is defined as  $\beta_{st} = \beta_{wn} - \beta_{os}$ .

106 The expression of  $\beta_{st}$  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  $\beta_t$  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  $\beta_{os}$  has the form  $x/y$  with  $x = S$  and  $y = 2A + S$ , and  $\beta_{wn}$  has the form  $(x + k)/(y + k)$ , with  
 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  $\beta_{st}$ , by bringing  $\beta_{os}$  and  $\beta_{wn}$  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  $\beta_{st}$  will vary in a hump-shaped way with the proportion of  
 121 shared interactions. For this reason, Poisot et al. (2012) suggest that  $\beta_{st}/\beta_{wn}$  (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  $\beta_{wn}$  and  $\beta_{os}$  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  $\beta_{st}$ , 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  $\beta_{st}$  achieves. It is  
137 paramount to clarify that  $\beta_{st}$  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.

### 140 **Illustration on ireallistically small networks are biased**

141 We can re-calculate the illustration of Fründ (2021), wherein a pair of networks with two shared  
142 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	

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

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

153 **Numerical experiment:  $\beta_{os}$  captures rewiring accurately**

154 **Does the partition of network dissimilarity needs a new normalization?**

155 Based on the arguments presented above, I do not think the suggestion of Fründ (2021) to change the  
 156 denominator of  $\beta_{os}$  makes sense as a default; the strength of the original approach by Poisot et al. (2012)  
 157 is indeed that the effect of turnover is based on a rigorous definition of networks as graphs (as opposed  
 158 to networks as matrices), in which the induction of vertices from the edgelist being compared gives rise  
 159 to biologically meaningful denominators. The advantage of this approach is that at no time does the  
 160 turnover of species itself, or the connectance of the network, enter into the calculation. As such, it is  
 161 possible to use  $\beta_{os}$  and  $\beta_{wn}$  in relationship to these terms, calculated externally (as was recently done by  
 162 *e.g.* Higino and Poisot 2021) without creating circularities.

163 The choice of changing the denominator hinges on what one admits as a definition for  $\beta_{st}$ . If the point



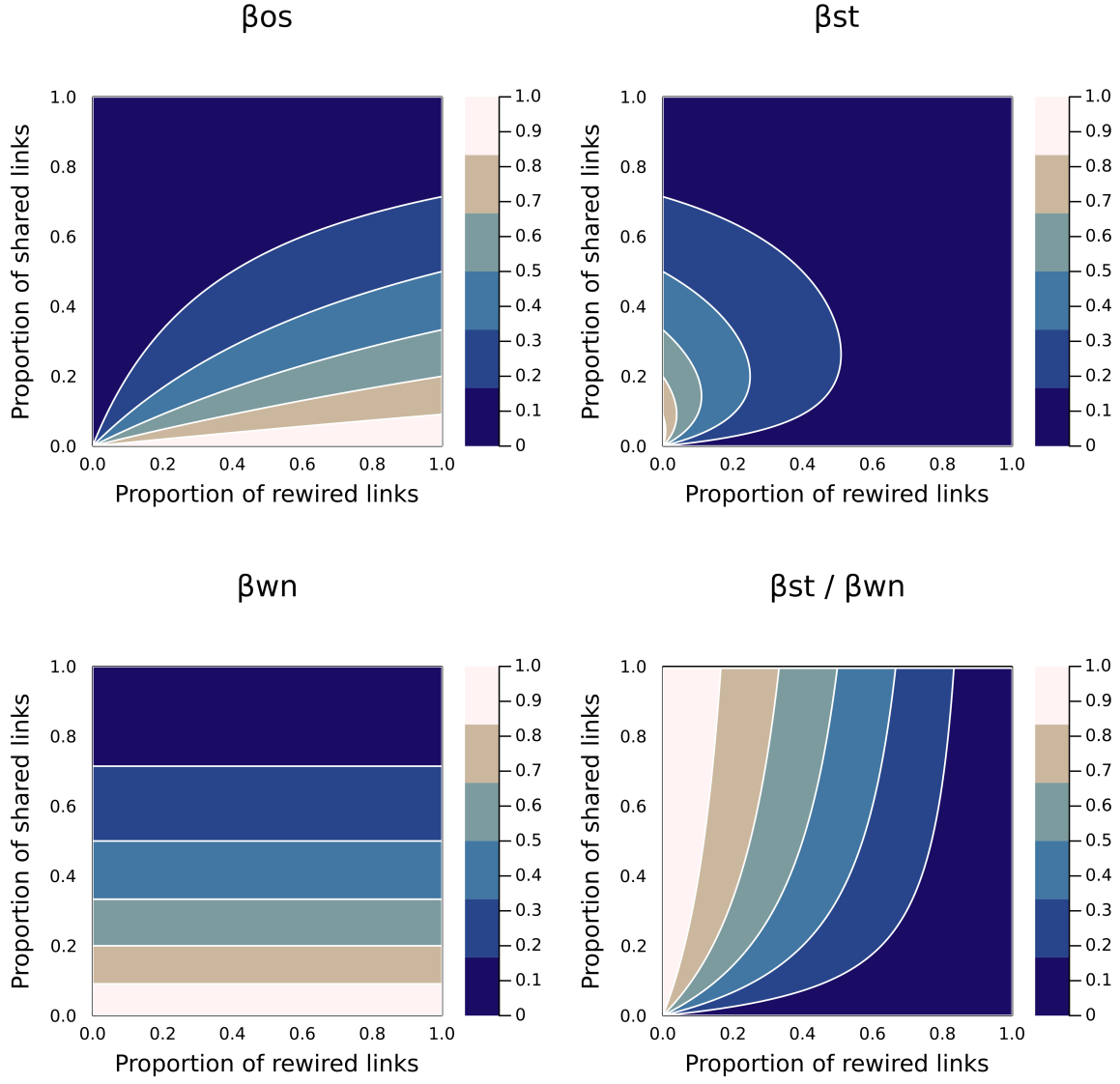


Figure 1: Values of  $\beta_{os}$ ,  $\beta_{wn}$ ,  $\beta_{st}$ , and  $\beta_{st}/\beta_{wn}$  as a function of the proportion of rewired links and the proportion of shared links.

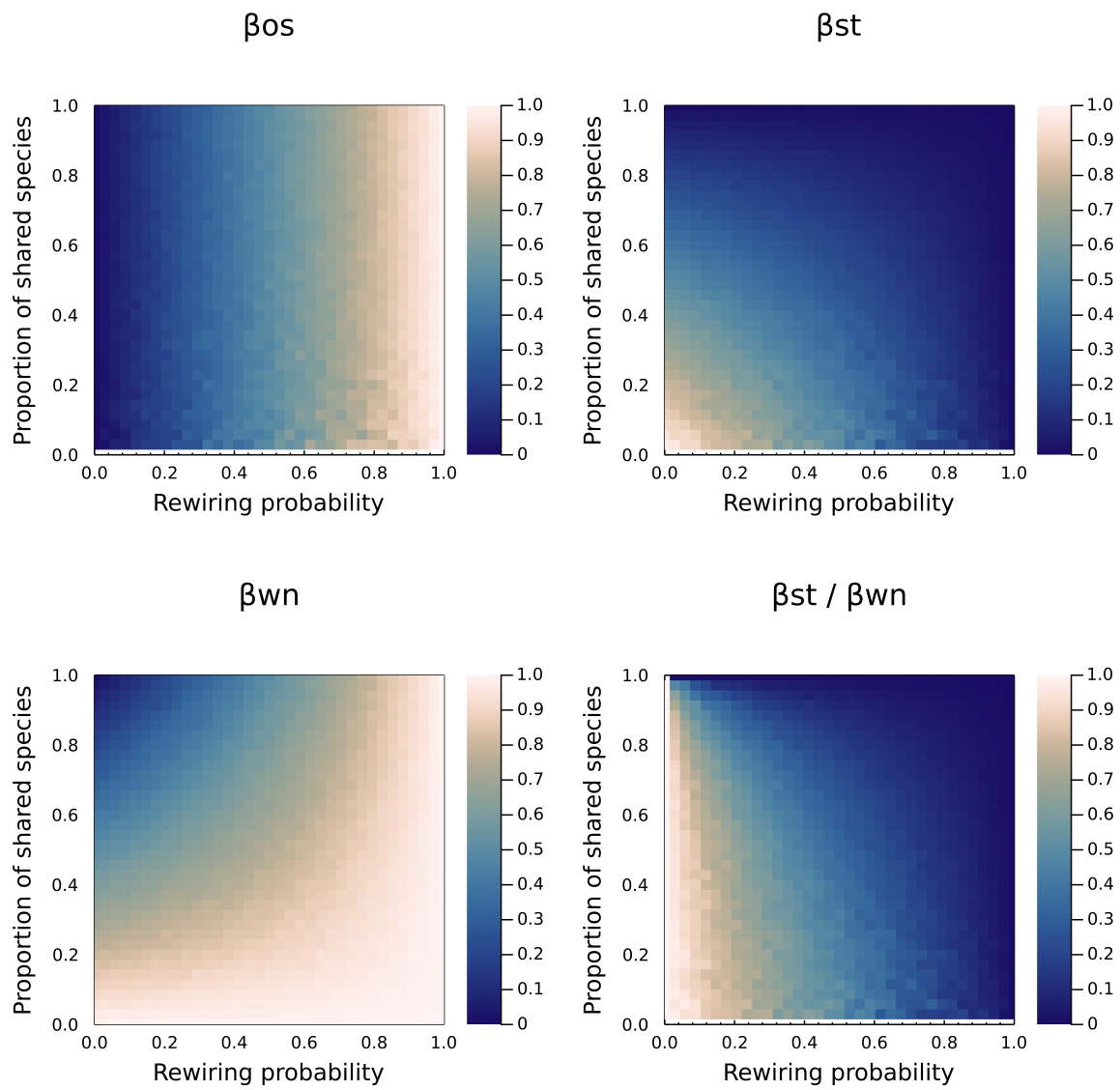


Figure 2: dsds

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, and may warrant a full methodological assessment. Conversely, if as we argue in Poisot et al. (2012),  $\beta_{st}$  is to be meant as a *guide* to the interpretation of  $\beta_{wn}$  and  $\beta_{os}$ , and related to actual measures of species turnover and network connectance, one must not change the denominator. It is central 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.

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