

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

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Last revision: *October 26, 2021*

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**
4 **β -diversity (Poisot *et al.* 2012). The** need to understand network variability **through partitioning in**
5 **components equivalent to α , β , and γ diversities** is motivated by the **prospect to further integrate**
6 **the analysis of species interactions to the analysis of species compositions. Because** species that
7 make up the networks do not react to their environment in the same way, and **because interactions are**
8 **only expressed in subsets of the environments in which species co-occur**, the β -diversity of
9 networks may behave in complex ways, **and its 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**
13 **established between species occurring in both networks, and those established with at least one**
14 unique species. This framework **is expressed as the decomposition** $\beta_{wn} = \beta_{os} + \beta_{st}$, namely the fact
15 that network dissimilarity (β_{wn}) has a component that can be calculated directly from the dissimilarity of
16 interactions between shared species (β_{os}), and a component that cannot (β_{st}). **Presumably, the value of**
17 **these components for a pair of networks can generate insights about the mechanisms involved**
18 **in dissimilarity.**

19 This approach has been widely adopted since its publication, with recent examples using it to understand
20 the effect of fire on pollination systems (Baronio *et al.* 2021); the impact of rewiring on spatio-temporal
21 network dynamics (Campos-Moreno *et al.* 2021); the effects of farming on rural and urban landscapes on
22 species interactions (Olsson *et al.* 2021); **the impact of environment gradients on multi-trophic**
23 **metacommunities (Ohlmann *et al.* 2018)**; and as a tool to estimate the sampling completeness of
24 networks (Souza *et al.* 2021). It has, similarly, received a number of extensions, including the ability to
25 account for interaction strength (Magrach *et al.* 2017), the ability to handle probabilistic ecological
26 networks (Poisot *et al.* 2016), and the integration into the Local Contribution to Beta Diversity (Legendre
27 & De Cáceres 2013) approach to understand how environment changes drive network dissimilarity (Poisot
28 *et al.* 2017).

29

[Figure 1 about here.]

30 Yet, the precise meaning of β_{st} , namely the importance of species turnover in the overall
31 dissimilarity, has been difficult to capture, and a source of confusion for some practitioners.
32 This is not particularly surprising, as this component of the decomposition responds to unique
33 species introducing their unique interactions both between themselves, and with species that
34 are common to both networks fig. 1. For this reason, it is important to come up with guidelines
35 for the interpretation of this measure, and how to use it to extract ecological insights.

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

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

54 Partitioning network dissimilarity

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

58 $a = |X_1 \cup X_2|$, $b = |X_2 \setminus X_1|$, and $c = |X_1 \setminus X_2|$, where $|\cdot|$ is the cardinality of set \cdot (**the number of**
59 **elements it contains**), and \setminus is the set subtraction operation. In the perspective of species composition
60 comparison, X_1 and X_2 are the sets of species in either community, so that if $X_1 = \{x, y, z\}$ and
61 $X_2 = \{v, w, x, y\}$, 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 $X_1 \setminus X_2 = \{z\}$.
62 The core message of Koleff *et al.* (2003) is that the overwhelming majority of measures of β -diversity can be
63 re-expressed as functions that operate on the cardinality of these sets – **this allows to focus on the**
64 **number of unique and common elements, as outlined in fig. 1.**

65 **Re-expressing networks as sets**

66 Applying this framework to networks requires a few additional definitions. Although ecologists tend to
67 think of networks as their adjacency matrix (**as is presented in fig. 1**), this representation is **not optimal**
68 **to reach a robust** understanding of which elements should be counted as part of which set when
69 measuring network dissimilarity. For this reason, we need fall back on the definition of a graph as a pair of
70 sets, wherein $\mathcal{G} = (V, E)$. These two components V and E represent vertices (nodes, species) and edges
71 (interactions), where V is specifically a set containing the vertices **of** \mathcal{G} , and E is a set of ordered pairs, in
72 which every pair is composed of two elements of V ; an element $\{i, j\}$ in E indicates that there is an
73 interaction *from* species i to species j in the network \mathcal{G} . **The adjacency matrix A of this network**
74 **would therefore have a non-zero entry at A_{ij} .**

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

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

77 and

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

78
79 where V_c is the set of **common species**, V_m and V_n are the species belonging only to network m and n
80 (**respectively**), E_c are the **common** edges, and E_{sm} and E_{um} are the interactions unique to k involving,

81 respectively, only species in V_c , and at least one species from V_m (the same notation applies for the
 82 subscript n).

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

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

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

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

93 We can similarly define the intersection (**also** commutative) of two networks:

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

94 The decomposition of β -diversity from Poisot *et al.* (2012) uses these components to measure β_{os}
 95 (“rewiring”), and β_{wn} (the overall dissimilarity including non-shared species). We can express the
 96 components a , b , and c of Koleff *et al.* (2003) as the cardinality of the following sets:

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

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

99 **In the following sections, I present a series of calculations aimed at expressing the values of β_{os} ,**
100 **β_{wn} , and therefore β_{st} as a function of species sharing probability (as a proxy for mechanisms**
101 **generating turnover), and link rewiring probability (as a proxy for mechanisms generating**
102 **differences in interactions among shared species). These calculations are done using**
103 **Symbolics.jl (Gowda *et al.* 2021), and subsequently transformed in executable code for Julia**
104 **(Bezanson2017JulFre?), used to produce the figures.**

105 **Quantifying the importance of species turnover**

106 The difference between β_{os} and β_{wn} stems from the species dissimilarity between \mathcal{M} and \mathcal{N} , and it is
107 easier to understand the effect of turnover by picking a dissimilarity measure to work as an exemplar. **We**
108 **will use $\beta = (b + c)/(2a + b + c)$, which in the Koleff *et al.* (2003) framework is (Wilson & Shmida 1984).**
109 This **measure** returns values in $[0, 1]$, with 0 meaning complete similarity, and 1 meaning complete
110 dissimilarity.

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

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

112 So as to simplify the notation of the following section, I will introduce a series of new variables. Let
113 $C = |E_c|$ be the number of links that are identical between networks (**as a mnemonic, C stands for**
114 **“common”**); $R = |E_{sn} \cup E_{sm}|$ be the number of links that are not shared, but only involve shared species
115 (*i.e.* links from $\mathcal{M} \cup \mathcal{N}$ established between species from $\mathcal{M} \cap \mathcal{N}$; **as a mnemonic, R stands for**
116 **“rewired”**); and $T = |E_{un} \cup E_{um}|$ the number of links that are not shared, and involve at least one unique
117 species (**as a mnemonic, T stands for “turnover”**).

118 There are two important points to note here. First, **as mentionned earlier**, the number or proportion of
119 species that are shared is not involved in the calculation. Second, the connectance of either network is not
120 involved in the calculation. That all links counted in *e.g.* U come from \mathcal{M} , or that they are evenly
121 distributed between \mathcal{M} and \mathcal{N} , has no impact on the result. This is a desirable property of the approach:
122 whatever quantitative value of the components of dissimilarity can be interpreted in the light of the
123 connectance and species turnover *without* any risk of circularity; **indeed, I present a numerical**

124 **experiment where connectance varies independently later in this manuscript, reinforcing this**
125 **point.**

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

129 The expression of β_{st} does not involve a partition into sets that can be plugged into the framework of
130 Koleff *et al.* (2003), because the part of \mathcal{M} and \mathcal{N} that are composed of their unique species cannot, by
131 definition, share interactions. One could, theoretically, express these as $\mathcal{M} \setminus \mathcal{N} = (V_m, E_{um})$ and
132 $\mathcal{N} \setminus \mathcal{M} = (V_v, E_{vn})$ (note the non-commutativity here), but the dissimilarity between these networks is
133 trivially maximal for the measures considered.

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

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

135

136 and

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

137

138 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
139 $k = U$. As long as $k \geq 0$, it is guaranteed that $\beta_{wn} \geq \beta_{os}$, and therefore that $0 \geq \beta_{st} \geq 1$; as \mathbf{C} , \mathbf{T} , and \mathbf{R} are
140 cardinalities of sets, they are necessarily satisfying this condition.

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

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

143

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

146 $4C^2 + R^2 + 4CR + 2CT + RT$. As such, we expect that the value of β_{st} will vary in a hump-shaped way with
147 the proportion of shared interactions. For this reason, Poisot *et al.* (2012) suggest that β_{st}/β_{wn} (alt.
148 $1 - \beta_{os}/\beta_{wn}$) is a better indicator of the *relative* importance of turnover processes on network dissimilarity.
149 This can be calculated as

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

150

151 which reduces to

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

152

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

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

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

158 **As the decomposition of beta diversity into sets presented above reveals, the value of the**
159 **components β_{os} and β_{st} will respond to two family of mechanisms: the probability of sharing a**
160 **species between the two networks, noted p , which will impose bounds on the value of T ; and the**
161 **probability of an interactions between shared species *not* being rewired, noted q , which will**
162 **impose bounds on the value of C . These two probabilities represent, respectively, mechanisms**

163 involved in species turnover and link turnover, as per Poisot *et al.* (2015), and the aim of this
164 numerical experiment is to describe how these families of processes drive network
165 dissimilarity.

166 In order to simplify the calculations, I make the assumptions that the networks have equal
167 species richness (noted S), so that $S_1 = S_2 = S$, and the same connectance (noted ρ), so that
168 $\rho_1 = \rho_2 = \rho$. As a consequence, the two networks have the same number of links
169 $L = \rho \times S_1^2 = \rho \times S_2^2$. The assumption of equal connectance will be relaxed in a subsequent
170 numerical experiment. These simplifications allow to express the size of C , R , and T only as
171 functions of p and q , as they would all be multiplied by L , which can therefore be dropped from
172 the calculation.

173 [Figure 2 about here.]

174 The value of C is the proportion of shared species p^2 , as per fig. 1, times the proportion of shared
175 links, q , giving $C = qp^2$. Each network has $r = p^2 - (qp^2)$ rewired links, which leads to
176 $R = 2r = 2p^2(1 - q)$. Finally, we can get the number of unique links in each network t by
177 subtracting $C + r$ from the total number of links (which, since we scale everything by L , is 1),
178 yielding $t = 1 - qp^2 - p^2 + qp^2$, which is $t = 1 - p^2$. The total number of unique links due to
179 turnover is $T = 2t = 2(1 - p^2)$. It is important to note that C and R , namely the number of links
180 that are kept or rewired, depends on species sharing (p), as the possible size of the overlap
181 between the two networks does, but the quantity of links that are different due to turnover does
182 not depends on rewiring.

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

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

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

187 Similarly, we can write

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

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

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

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

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

198 **Sensibility of the decomposition to differences in connectance**

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

209 **The maximal number of links that can be shared is ap^2 (i.e. $\min(p^2, ap^2)$), as we cannot share**
 210 **more links than are in the sparsest of the two networks. Of these, q are not rewired, leading to**

211 $C = aqp^2$. The number of links that are rewired in network 1 is the number of its links between
 212 shared species minus C , i.e. $r_1 = ap^2 - aqp^2 = ap^2(1 - q)$, and similarly $r_2 = p^2 - aqp^2 = p^2(1 - aq)$,
 213 leading to $R = r_1 + r_2 = p^2[a(1 - q) + 1]$. Using the same approach, we can get $t_1 = a(1 - p^2)$ and
 214 $t_2 = (1 - p^2)$, leading to $T = t_1 + t_2 = (1 - p^2)(1 + a)$.

215 As in the previous section, we can use these values to write

$$\beta_{os} = 1 - 2\frac{aq}{1 + a},$$

$$\beta_{wn} = 1 - 2\frac{ap^2q}{1 + a},$$

216 and

$$\beta_{st} = 2aq\frac{(1 - p^2)(1 + a)}{a^2 + 2a + 1}.$$

217 [Figure 3 about here.]

218 The values of these components are visualized in fig. 3. The introduction of the connectance
 219 ratio makes these expressions marginally more complex than in the case without differences in
 220 connectance, but the noteworthy result remains that in the presence of differences of
 221 connectance, the value of β_{os} is still independent from species turnover. In fact, there is an
 222 important conclusion to be drawn from this expression. The shared species component is by
 223 definition square, meaning that from an actual measurement of β_{os} between two networks for
 224 which we know the connectance, noted b_{os} , we can get the probability of rewiring by
 225 reorganizing the terms of $b_{os} = 1 - 2aq/(1 + a)$ as

$$q \approx \frac{(1 - b_{os})(a + 1)}{2a},$$

226 which gives the probability of rewiring as $1 - q$; note that this is an *approximation*, as it assumes
 227 that the connectances of the entire network and the connectances of the shared components
 228 are the same.

229 Does the partition of network dissimilarity needs a new normalization?

230 One of the arguments put forth **in a recent paper** by Fründ (2021) is that the decomposition outlined
231 above will overestimate the effect of rewiring; I argue that this is based on a misunderstanding of what β_{st}
232 achieves. It is paramount to clarify that β_{st} is not a direct measure of the importance of turnover: it is a
233 quantification of the relative impact of rewiring to overall dissimilarity, which, all non-turnover
234 mechanisms being accounted for in the decomposition, can be explained by turnover mechanisms. In this
235 section, I present two numerical experiments showing (i) that the β_{os} component is in fact an accurate
236 measure of rewiring, and (ii) that β_{st} captures the consequences of species turnover, and of the
237 interactions brought by unique species.

238 Illustrations on arbitrarily small networks are biased

239 We can re-calculate the illustration of Fründ (2021), wherein a pair of networks with two shared
240 interactions ($C = 2$) receive either an interaction in T , **in** R , or in both:

C	T	R	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

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

250 effect of rewiring.

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

260 **Therefore the argument of Fründ (2021), whereby the β_{os} component should decrease with**
261 **turnover, and be invariant to connectance, does not hold: the very point of the approach is to**
262 **provide measures that can be interpreted in the light of connectance and species turnover.**
263 **Adopting the perspective developed in the previous section, wherein networks are sets and the**

264 **measures of β -diversity operates on these sets, highlights the conceptual issue in the Fründ (2021)**
265 **alternative normalization: they are using components (namely, interactions) of the networks**
266 **that are *not* directly part of the two networks being compared.**

267 **Using an alternative normalization trivializes the results**

268 **In this numerical experiment, we reproduce the results in fig. 2, but using the alternative**
269 **normalization described above. The results are presented in fig. 4. Producing the analytical**
270 **solutions for the various components, following the expressions for C , T , and R given for fig. 2,**
271 **yields a similar value for β_{wn} (*i.e.* the two approaches estimate the same value for total**
272 **dissimilarity), but different values for β_{st} and β_{os}**

273 **. Specifically, β_{os} becomes $p^2(1 - q)$, which becomes dependent on species turnover. This, from**
274 **an ecological point of view, makes no sense: the quantification of how much shared species**
275 **interact in a similar way should not depend on how much species actually overlap. The opposite**
276 **problem arises for β_{st} , which becomes $1 - p^2$. In short, the relative importance of species**
277 **turnover is simply species turnover itself, and has no information on interaction dissimilarity.**
278 **Therefore the core issue of the Fründ (2021) alternative is that, by attempting to fix a non-issue**
279 **(namely the over-estimate of the importance of re-wiring, which is only true in trivially small**
280 **networks), it blurs the meaning of β_{os} , and renders β_{st} useless as it is a re-expression of species**
281 **beta-diversity.**

282 [Figure 4 about here.]

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

284 **Based on the numerical experiments and the derivations presented in this paper, we can establish**
285 **a number of recommendations for the measurement and analysis of network dissimilarity.**
286 **First, β_{os} allows to estimate the rate of rewiring, which is an important ecological information to**
287 **have; quantifying it properly can give insights as to how networks differ. Second, β_{st} captures**
288 **both turnover and rewiring mechanisms, but its interpretation is easier to accomplish in the**
289 **context of total network dissimilarity, and therefore β_{st}/β_{wn} should be interpreted more**

290 **thoroughly. Finally, because the alternative denominator from Fründ (2021) removes the**
291 **interesting property of β_{os} (independent estimate of rewiring rate), and trivializes the meaning**
292 **of β_{st} (by turning it into species dissimilarity), there seems to be no valid reason to use it.**

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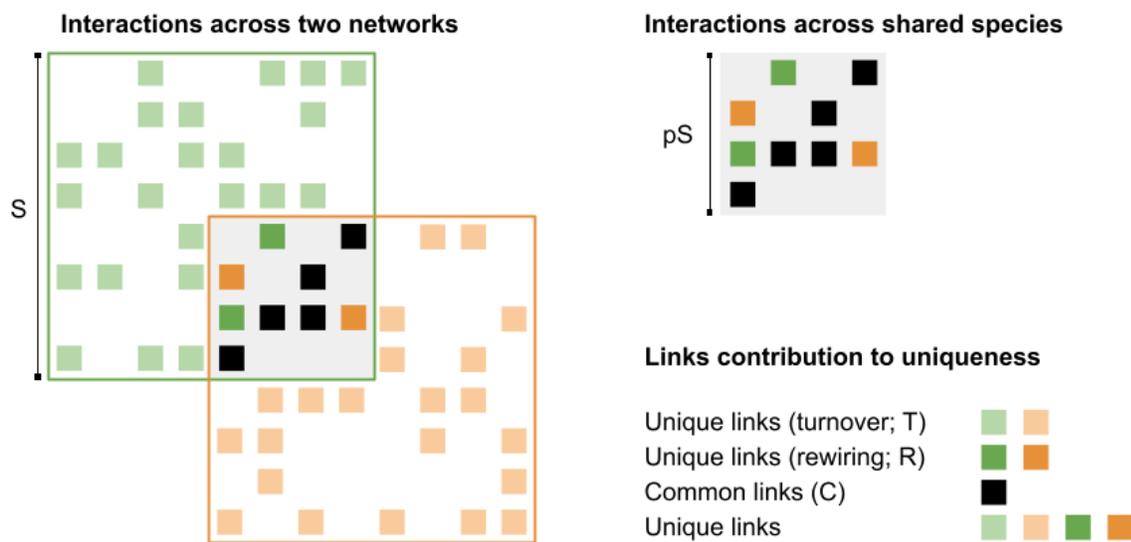


Figure 1: The dissimilarity of two networks (green and orange) of equal richness S (this also holds for unequal richness) depends on three families of interactions: those that are unique because of species turnover (in a pale color), those that are unique because of rewiring (in a saturated color), and those that are shared (in black). Assuming that the chance of sharing a species between the two networks is p , then there can be at most $p^2 \times S^2$ shared links – for this reason, overall network dissimilarity (β_{un}) will have a component tied to species turnover, which is β_{st} .

□

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

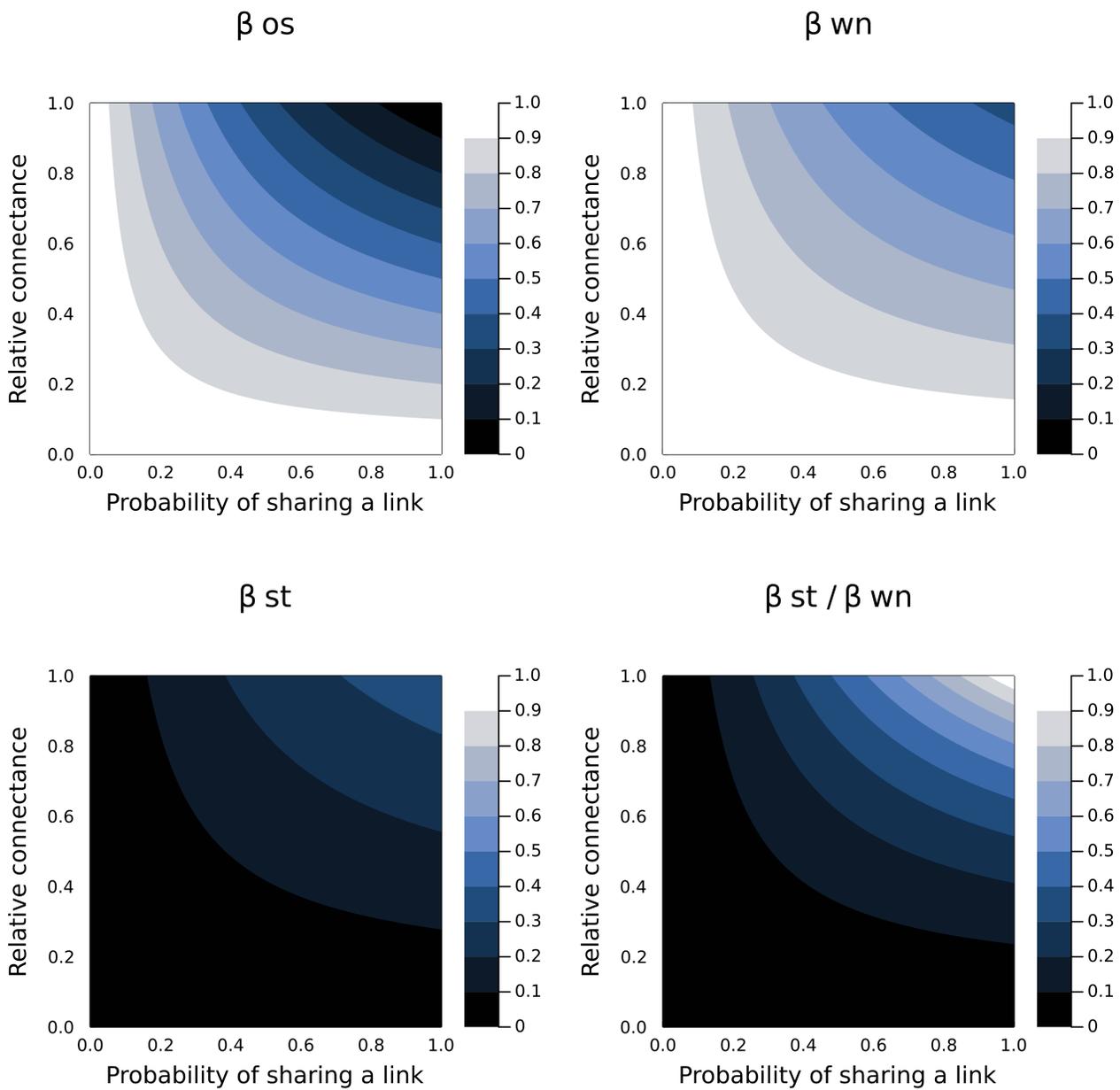


Figure 3: Consequences of changing the ratio of connectances between two equally species-rich networks on the decomposition of network beta-diversity, assuming $p = 0.8$. Networks with stronger differences in connectance will tend to be more similar, because the differences in number of links becomes extreme enough that the chances of all the links in the sparser network being in the denser network increases.

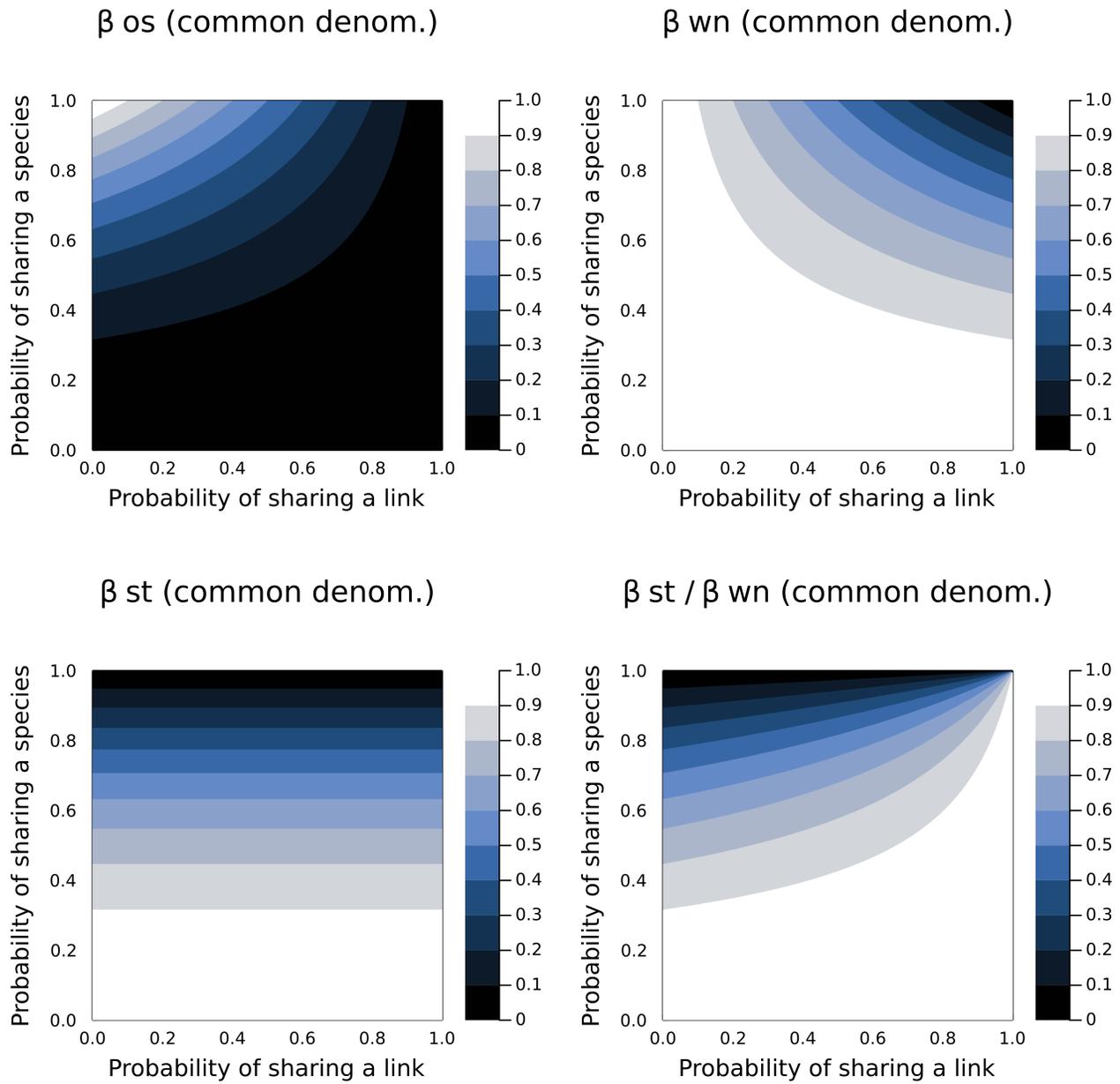


Figure 4: Reproduction of fig. 2 with the alternative denominators proposed by Fründ (2021).