

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

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

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

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

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

34 **Partitioning network dissimilarity**

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

44 **Re-expressing networks as sets**

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

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

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

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

55 and

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

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

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

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

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

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

67 β -diversity operate on interactions (not species), this property is maintained at every decomposition we
 68 will describe next.

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

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

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

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

74 Quantifying the importance of species turnover

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

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

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

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

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

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

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

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

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

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

112 and

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

113 Note that β_{os} has the form x/y with $x = S$ and $y = 2A + S$, and β_{wn} has the form $(x + k)/(y + k)$, with
 114 $k = U$. As long as $k \geq 0$, it is guaranteed that $\beta_{wn} \geq \beta_{os}$, and therefore that $0 \leq \beta_{st} \leq 1$; as A , S , and
 115 U are cardinalities of sets, they are necessarily satisfying this condition.

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

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

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

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

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

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

124 which reduces to

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

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

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

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

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

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

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

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

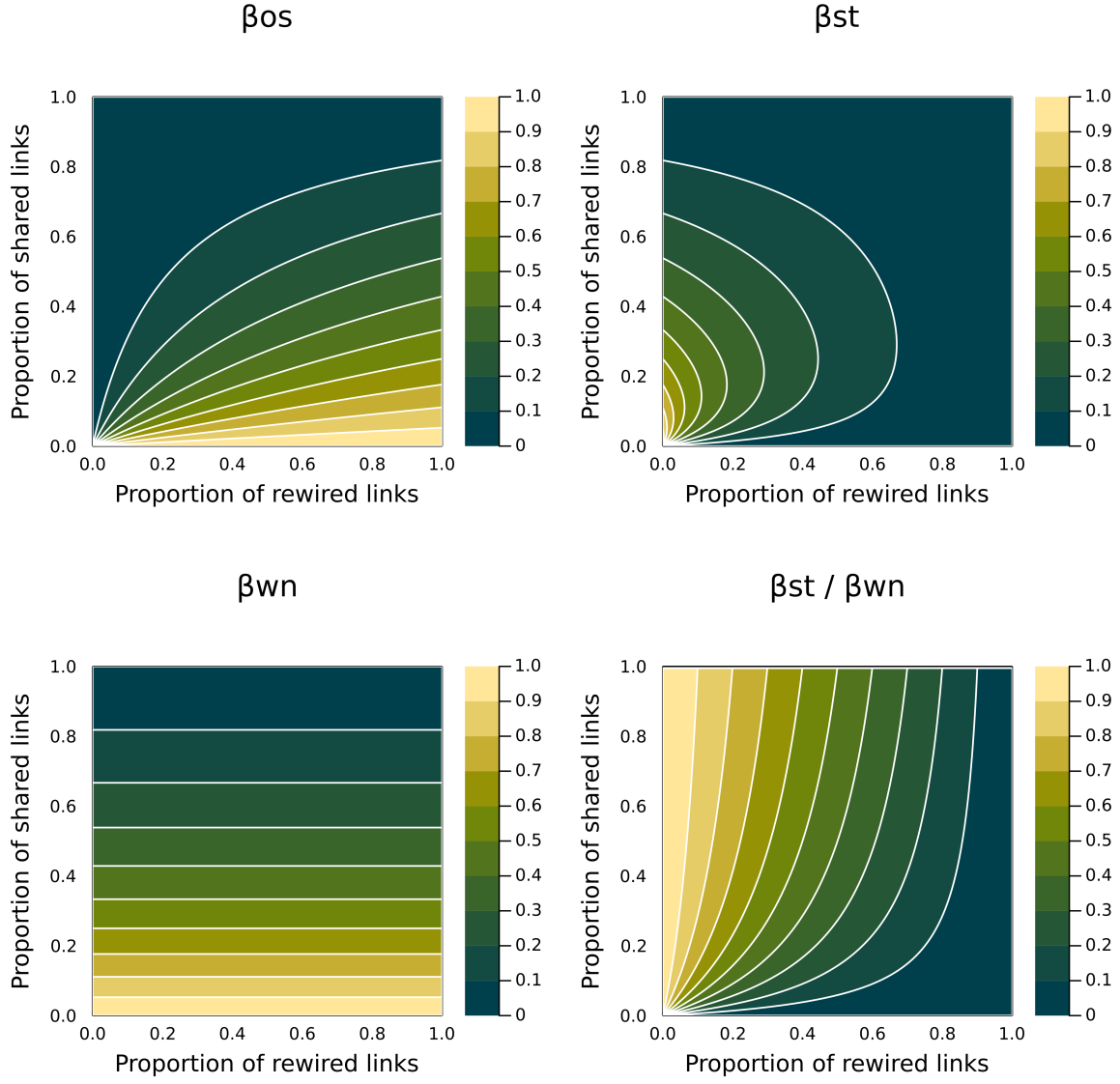


Figure 1: Values of β_{os} , β_{wn} , β_{st} , and β_{st}/β_{wn} as a function of the proportion of rewired links and the proportion of shared links.

A	S	U	β_{os}	β_{wn}	β_{st}	β_{st}/β_{wn}
2	0	0	0	0	0	
2	1	0	1/5	1/5	0	0
2	0	1	0	1/5	1/5	0
2	1	1	1/5	1/3	2/15	2/5

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

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

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

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

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

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

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

166 and

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

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

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

178 **Numerical experiment: the decomposition captures the roles of species turnover and connectance**
 179 **accurately**

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

181 Based on the arguments presented above, I do not think the suggestion of Fründ (2021) to change the
 182 denominator of β_{os} makes sense as a default; the strength of the original approach by Poisot et al. (2012)
 183 is indeed that the effect of turnover is based on a rigorous definition of networks as graphs (as opposed

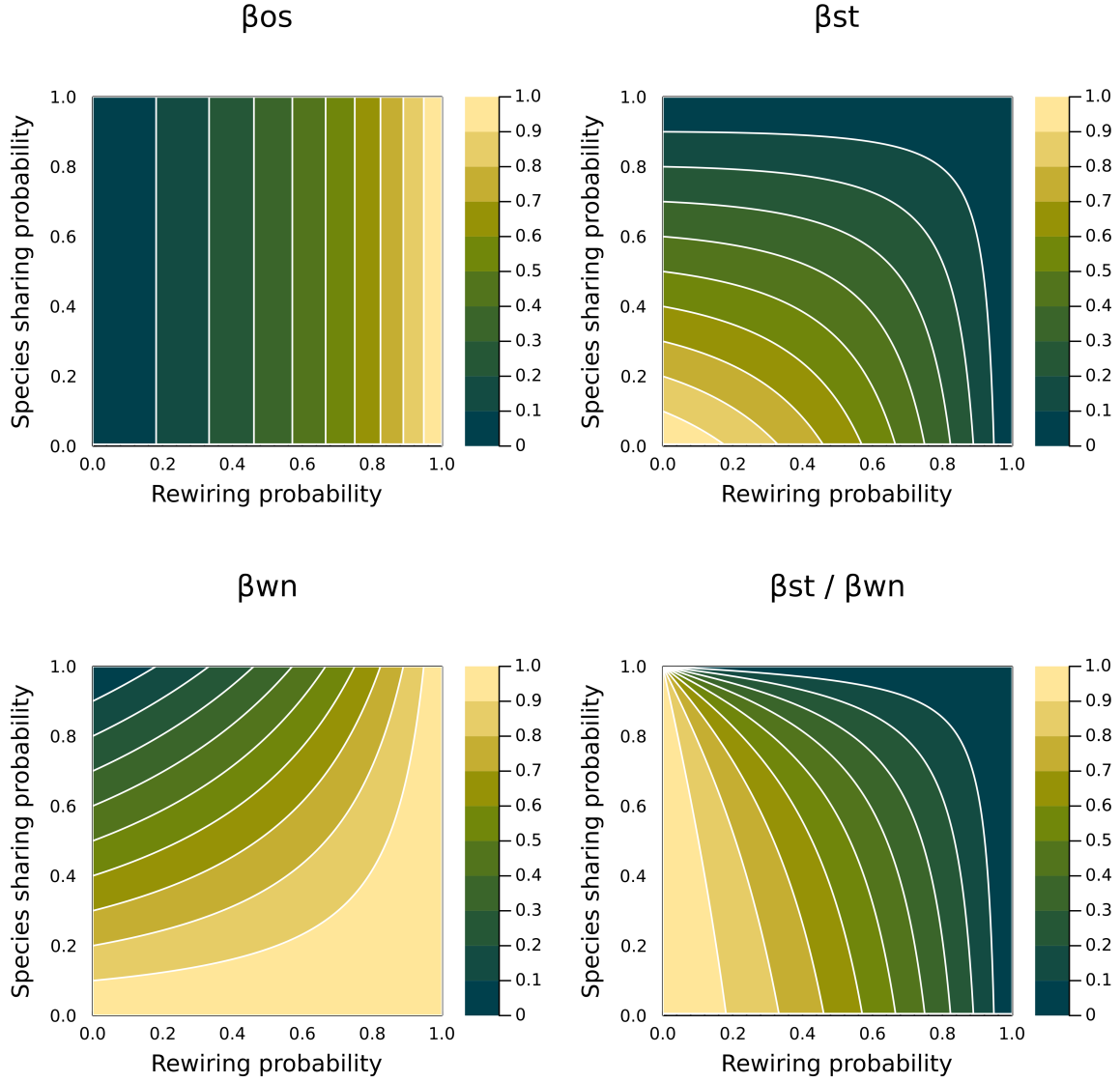


Figure 2: Response of β_{os} and β_{wn} , and the consequences on β_{st} , to changes in rewiring probability (q) and probability of species sharing (p). As expected, β_{os} is not affected by species turnover, but increases with the rewiring probability. By contrast, β_{wn} increases when the rewiring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

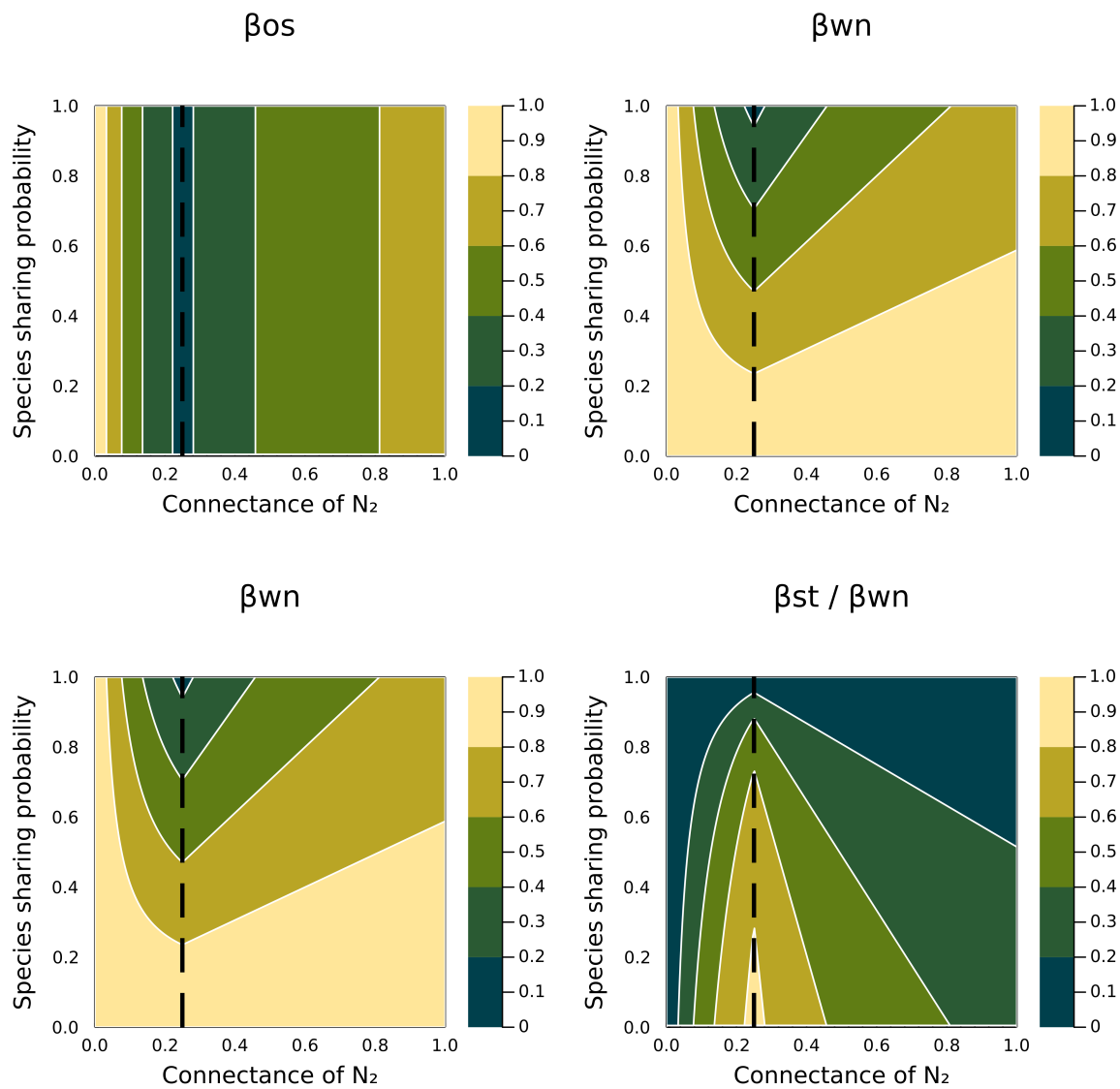


Figure 3: dsds

to networks as matrices), in which the induction of vertices from the edgelist being compared gives rise to biologically meaningful denominators. The advantage of this approach is that at no time does the turnover of species itself, or the connectance of the network, enter into the calculation. As such, it is possible to use β_{os} and β_{wn} in relationship to these terms, calculated externally (as was recently done by *e.g.* Higino and Poisot 2021) without creating circularities.

The choice of changing the denominator hinges on what one admits as a definition for β_{st} . If the point of β_{st} is to be a component of overall β -diversity as advocated by Fründ (2021) and Novotny (2009), a change of numerator *might* be acceptable. Nevertheless, this change of numerator contributes to blurring the frontier between a measure of interaction dissimilarity and a measure of community dissimilarity, and may warrant a full methodological assessment. Conversely, if as we argue in Poisot et al. (2012), β_{st} is to be meant as a *guide* to the interpretation of β_{wn} and β_{os} , and related to actual measures of species turnover and network connectance, one must not change the denominator. It is central to recognize that 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.

References

- Baronio, Gudryan J., Camila S. Souza, Pietro K. Maruyama, Josué Raizer, Maria Rosângela Sigrist, and Camila Aoki. 2021. “Natural Fire Does Not Affect the Structure and Beta Diversity of Plant-Pollinator Networks, but Diminishes Floral-Visitor Specialization in Cerrado.” *Flora* 281 (August): 151869. <https://doi.org/10.1016/j.flora.2021.151869>.
- Campos-Moreno, Diego F., Lee A. Dyer, Danielle Salcido, Tara Joy Massad, Gabriela Pérez-Lachaud, Eric J. Tepe, James B. Whitfield, and Carmen Pozo. 2021. “Importance of Interaction Rewiring in Determining Spatial and Temporal Turnover of Tritrophic (Piper-Caterpillar-Parasitoid) Metanetworks in the Yucatán Península, México.” *Biotropica* 53 (4): 1071–81. <https://doi.org/10.1111/btp.12946>.
- Canard, E. F., N. Mouquet, D. Mouillot, M. Stanko, D. Miklisova, and D. Gravel. 2014. “Empirical

- 210 Evaluation of Neutral Interactions in Host-Parasite Networks.” *The American Naturalist* 183 (4):
211 468–79. <https://doi.org/10.1086/675363>.
- 212 Dunne, Jennifer A. 2006. “The Network Structure of Food Webs.” In *Ecological Networks: Linking*
213 *Structure and Dynamics*, edited by Jennifer A Dunne and Mercedes Pascual, 27–86. Oxford
214 University Press.
- 215 Fründ, Jochen. 2021. “Dissimilarity of Species Interaction Networks: How to Partition Rewiring and
216 Species Turnover Components.” *Ecosphere* 12 (7): e03653. <https://doi.org/10.1002/ecs2.3653>.
- 217 Higino, Gracielle T., and Timothée Poisot. 2021. “Beta and Phylogenetic Diversities Tell Comple-
218 mentary Stories About Ecological Networks Biogeography.” *Parasitology*, March, 1–23. <https://doi.org/10.1017/S0031182021000391>.
- 220 Koleff, Patricia, Kevin J. Gaston, and Jack J. Lennon. 2003. “Measuring Beta Diversity for Presence–
221 Absence Data.” *Journal of Animal Ecology* 72 (3): 367–82. <https://doi.org/10.1046/j.1365-2656.2003.00710.x>.
- 223 Legendre, Pierre, and Miquel De Cáceres. 2013. “Beta Diversity as the Variance of Community Data:
224 Dissimilarity Coefficients and Partitioning.” Edited by Hélène Morlon. *Ecology Letters* 16 (8):
225 951–63. <https://doi.org/10.1111/ele.12141>.
- 226 Magrach, Ainhoa, Andrea Holzschuh, Ignasi Bartomeus, Verena Riedinger, Stuart P. M. Roberts, Maj
227 Rundlöf, Ante Vujić, et al. 2017. “Plant-Pollinator Networks in Semi-Natural Grasslands Are
228 Resistant to the Loss of Pollinators During Blooming of Mass-Flowering Crops.” *Ecography*,
229 February, n/a–n/a. <https://doi.org/10.1111/ecog.02847>.
- 230 Novotny, Vojtech. 2009. “Beta Diversity of Plant–Insect Food Webs in Tropical Forests: A Conceptual
231 Framework.” *Insect Conservation and Diversity* 2 (1): 5–9. <https://doi.org/10.1111/j.1752-4598.2008.00035.x>.
- 233 Olsson, Rachel L., Matthew R. Brousil, Robert E. Clark, Quinlyn Baine, and David W. Crowder. 2021.
234 “Interactions Between Plants and Pollinators Across Urban and Rural Farming Landscapes.” *Food*
235 *Webs* 27 (June): e00194. <https://doi.org/10.1016/j.fooweb.2021.e00194>.

- 236 Poisot, Timothee, Cynthia Gueveneux-Julien, Marie-Josée Fortin, Dominique Gravel, and Pierre
237 Legendre. 2017. “Hosts, Parasites and Their Interactions Respond to Different Climatic Variables.”
238 *Global Ecology and Biogeography*, n/a–n/a. <https://doi.org/10.1111/geb.12602>.
- 239 Poisot, Timothée, Elsa Canard, David Mouillot, Nicolas Mouquet, and Dominique Gravel. 2012.
240 “The Dissimilarity of Species Interaction Networks.” *Ecology Letters* 15 (12): 1353–61. <https://doi.org/10.1111/ele.12002>.
241
- 242 Poisot, Timothée, Alyssa R. Cirtwill, Kévin Cazelles, Dominique Gravel, Marie-Josée Fortin, and
243 Daniel B. Stouffer. 2016. “The Structure of Probabilistic Networks.” Edited by Jana Vamosi.
244 *Methods in Ecology and Evolution* 7 (3): 303–12. <https://doi.org/10.1111/2041-210X.12468>.
- 245 Poisot, Timothée, Daniel B. Stouffer, and Dominique Gravel. 2015. “Beyond Species: Why Ecological
246 Interaction Networks Vary Through Space and Time.” *Oikos* 124 (3): 243–51. <https://doi.org/10.1111/oik.01719>.
247
- 248 Souza, Camila S., Pietro K. Maruyama, Karen C. B. S. Santos, Isabela G. Varassin, Caroline L.
249 Gross, and Andréa C. Araujo. 2021. “Plant-Centred Sampling Estimates Higher Beta Diversity of
250 Interactions Than Pollinator-Based Sampling Across Habitats.” *New Phytologist* 230 (6): 2501–12.
251 <https://doi.org/10.1111/nph.17334>.
- 252 Trøjelsgaard, Kristian, and Jens M. Olesen. 2016. “Ecological Networks in Motion: Micro- and
253 Macroscopic Variability Across Scales.” *Functional Ecology* 30 (12): 1926–35. <https://doi.org/10.1111/1365-2435.12710>.
254
- 255 Tuomisto, Hanna. 2010. “A Diversity of Beta Diversities: Straightening up a Concept Gone Awry. Part
256 1. Defining Beta Diversity as a Function of Alpha and Gamma Diversity.” *Ecography* 33 (1): 2–22.
257 <https://doi.org/10.1111/j.1600-0587.2009.05880.x>.
- 258 Wilson, M. V., and A. Shmida. 1984. “Measuring Beta Diversity with Presence-Absence Data.” *Journal*
259 *of Ecology* 72 (3): 1055–64. <https://doi.org/10.2307/2259551>.