

Appendix C. Details on the analytical expression for D_{PW} and different competing hypotheses.

Deriving an analytical expression for D_{PW}

We start with two small subplots a and b which are located within an observation window W and separated by distance r . To measure their phylogenetic or functional dissimilarity we use the abundance weighted pairwise phylogenetic dissimilarity (Swenson et al. 2011):

$$D_{PW} = \left(\sum_{i=1}^{n_a} f_{i,a} \overline{\delta_{ib}} + \sum_{j=1}^{n_b} f_{j,b} \overline{\delta_{ja}} \right) / 2 \quad (\text{C.1})$$

where $f_{i,a}$ is the relative abundance of species i in subplot a , n_a is the number of species in subplot a , and $\overline{\delta_{ib}} = \frac{1}{n_b} \sum_{j=1}^{n_b} \delta_{ij}$ is the mean pairwise phylogenetic or functional distance between species i (in a) and all species present in b .

To obtain our final summary statistic $D_{PW}(r)$ that captures overall functional or phylogenetic dissimilarity as function of distance r between subplots we average the D_{PW} values of all pairs of subplots a, b within W which are distance r apart:

$$D_{PW}(r) = \frac{1}{N_a} \sum_a \frac{1}{N_{a,b}(r)} \sum_b \mathbf{1}(\|a-b\|=r) \left(\sum_{i=1}^{n_a} f_{i,a} \frac{1}{n_b} \sum_{j=1}^{n_b} \delta_{ij} \right) \quad (\text{C.2})$$

where the indicator function $\mathbf{1}(\|a-b\|=r)$ yields a value of one if the two subplots a, b are (approximately) distance r apart and zero otherwise, N_a is the number of focal plots a in W , and

$N_{a,b}(r)$ the number of plots b that are located at distance r of a given plot a . Note that the second part of equation C.1 does not appear in equation C.2 because the sum already includes both, pairs $a-b$ and $b-a$.

To derive analytical expectations for our hypotheses we translate $D_{PW}(r)$ into the framework of spatial point pattern analysis (Illian et al. 2008; Wiegand and Moloney 2014).

First, we exchange the summations over species i and plot b in equation C.2:

$$D_{PW}(r) = \frac{1}{N_a} \sum_a \frac{1}{N_{a,b}(r)} \sum_{i=1}^S f_{i,a} \left[\mathbf{1}(\|a-b\| - r) \sum_b \frac{1}{n_b} \sum_{j=1}^{n_b} \delta_{ij} \right] \quad (\text{C.3})$$

Rearranging equation C.3

$$D_{PW}(r) = \frac{1}{N_a} \sum_a \sum_{i=1}^S f_{i,a} \left[\frac{1}{N_{a,b}(r)} \sum_b \frac{\mathbf{1}(\|a-b\| - r)}{n_b} \sum_{j=1}^{n_b} \delta_{ij} \right] \quad (\text{C.4})$$

shows that we now look from the perspective of an individual of species i (located in plot a) to all plots b located at distance r (i.e., the quantity in the angled brackets). This quantity can be expressed as

$$\frac{1}{N_{a,b}(r)} \sum_b \frac{\mathbf{1}(\|a-b\| - r)}{n_b} \sum_{j=1}^{n_b} \delta_{ij} = \sum_{j=1}^S f_{ij}(r) \delta_{ij} \quad (\text{C.5})$$

where the $f_{ij}(r)$ is the conditional probability that species j is present in a small subplot b which is located distance r away from an individual of species i , and S the total number of species in plot W . Because equation C.5 sums over all individuals of species i located in small subplots a we can replace the relative abundance $f_{i,a}$ of species i in subplot a by the probability f_i that a randomly selected individual in W is of species i and obtain

$$D_{pw}(r) = \sum_{i=1}^S f_i \left[\sum_{j=1}^S f_{ij}(r) \delta_{ij} \right] \quad (\text{C.6})$$

Reducing equation C.6 to two subplots a, b yields $D_{pw} = \sum_{i,j} f_i f_j \delta_{ij}$, thus D_{pw} is identical to Rao's quadratic entropy (i.e., Swenson 2011). The quantity $f_i f_j f_{ij}(r)$ yields the so-called mark-connection function $p_{ij}(r)$ which is the conditional probability that from two randomly taken individuals separated by distance r the first is one of species i and the second one is of species j (Illian et al. 2008; Getzin et al. 2008; Jacquemyn et al. 2012; Wiegand et al. 2013; Wiegand and Moloney 2014). The mark connection function is closely related with the better known pair correlation functions (Stoyan and Stoyan 1994; Wiegand and Moloney 2004; Illian et al. 2008) by

$$p_{ij}(r) = f_i f_j \frac{g_{ij}(r)}{g(r)} \quad (\text{C.7})$$

where the f_i is the relative abundance of species i in W , the $g_{ij}(r)$ is the partial pair correlation function of the species pair $i-j$, and the $g(r)$ is the pair correlation function of all individuals in W ,

regardless of their species. The partial pair correlation function can be defined using the quantity $\lambda_j g_{ij}(r)$ which yields the mean density of individuals of species j at distance r from individuals of species i where λ_j is the overall density of species i in W (Wiegand and Moloney 2004). Thus, we obtain

$$D_{PW}(r) = \sum_{i=1}^S \sum_{j=1}^S p_{ij}(r) \delta_{ij} = \sum_{i=1}^S \sum_{j=1}^S f_i f_j \frac{g_{ij}(r)}{g(r)} \delta_{ij} \quad (\text{C.8})$$

Note that the sum overall mark connection functions $p_{ij}(r)$ yields one, thus, the metric $D_{PW}(r)$ yields the mean phylogenetic (or functional) distance of all pairs of individuals that are distance r apart. Note that $D_{PW}(r)$ has been termed $\beta_{\text{phy}}(r)$ in Shen et al. (2013). It is also interesting to note that equation C.8 separates the overall effect of the clustering of all individuals in W [described by $1/g(r)$] from the joined effect of species interactions and phylogenetic relatedness [described by the $g_{ij}(r)\delta_{ij}$].

Some predictions on impact of different processes on beta diversity

The functional form of $D_{PW}(r)$ in equation C.8 allows us to make predictions on the impact of the different processes on the $D_{PW}(r)$. First, if all trees are randomly and independently of each other distributed we have no spatial structure as a consequence find $p_{ij}(r) = f_i f_j$ and $g_{ij}(r) = 1$ and $g(r) = 1$ (Wiegand and Moloney 2014). Thus, $D_{PW}(r)$ collapses to Rao's quadratic entropy of all individuals in the observation window W

$$D_{PW}(r) = \sum_{i=1}^S \sum_{j=1}^S p_{ij}(r) \delta_{ij} = \sum_{i=1}^S \sum_{j=1}^S f_i f_j \delta_{ij} = D^P \quad (\text{C.9})$$

Thus, the random placement hypothesis yields constant beta diversity and no distance decay of similarity.

For the spatially explicit Simpson index $\beta_S(r)$ that describes species beta diversity we can rewrite equation C.8 considering $\delta_{ii} = 0$ and $\sum_{ij} p_{ij}(r) = 1$ as

$$\begin{aligned}
 \beta_S(r) &= \sum_{i,j=1,\neq}^S p_{ij}(r) \\
 &= 1 - \sum_i^S p_{ii}(r) \\
 &= 1 - \frac{1}{g(r)} \sum_i^S f_i f_i g_{ii}(r)
 \end{aligned} \tag{C.10}$$

Thus, for species beta diversity we can estimate the (i) probability that two trees which are distance r apart are of different species or (ii) estimate first the probability that two trees distance r apart are conspecifics and then subtract this from one. The latter formulation has the advantage that we can relate it directly to the univariate species patterns which we can control in the dispersal limitation hypothesis, the combined dispersal limitation hypothesis and the independent placement hypothesis. If we use pattern reconstruction we faithfully reproduce the univariate pair correlation functions $g_{ii}(r)$ of all species. Thus, the term $f_i f_i g_{ii}(r)$ in equation C.10 is identical in the observed community and the corresponding null communities. Thus, differences between the observed beta diversity measure $\beta_S(r)$ and that of the null communities arise only due to different overlapping of individual species that may induce changes in the pair correlation function of all trees in the community. With equation C.10 we find:

$$\frac{1 - D_{PW}^{null}(r)}{1 - D_{PW}^{obs}(r)} = \frac{g^{obs}(r)}{g^{null}(r)} \quad (C.11)$$

Indeed, as Figure C1 shows, this explains the somewhat counterintuitive result for the joined habitat and dispersal limitation hypothesis for small trees at the Wabikon forest. Thus, even if the aggregation pattern of all individual species is faithfully reproduced, this does not mean that the dispersal limitation hypothesis (or the joined habitat and dispersal limitation hypothesis) must well reproduce the observed distance decay at small distances. For small trees at the Wabikon plot, the joined habitat and dispersal limitation hypothesis produced too high small scale clustering of the entire null community (Fig. C1a). This was because this null model tended to place smaller clusters of the three very abundant species (which accounted for 27.8, 25.5 and 21% of all small trees in the plot) in the same area, thereby increasing the overall small-scale clustering of all small trees. In contrast, the clusters of the three most abundant species in the observed data showed clusters at different locations, producing a flatter overall pair correlation function. Thus, the reason for the unexpected shape of the species beta diversity of small trees at the Wabikon plot is failure of the habitat model which produces too much overlap of the three most abundant species in areas of high tree density.

Phylogentic and functional beta diversity is more sensitive to environmental heterogeneity than species diversity

Habitat filtering has only limited influence on species beta diversity if the plot does not show strong heterogeneities (i.e., large values of $g_{ij}(r)$ for many species pairs) and it will be more strongly driven by overall clustering of species (represented by the factor $1/g(r)$ in equation C.8). However, positive or negative correlations between habitat mediated species association

[represented by $g_{ij}(r)$] and species dissimilarity (represented by δ_{ij}) have strong potential to influence the pattern of the $D_{PW}(r)$ because they occur as a product in equation C.8. A tendency of similar species to occur together at larger distances r , as in our study plots, produces an interaction effect with habitat filtering in the product $p_{ij} \delta_{ij}$ and reduces the $D_{PW}(r)$ predicted by the combined habitat filtering and dispersal limitation hypothesis at larger distances compared to that of the dispersal limitation hypothesis (Figs D2–D5).

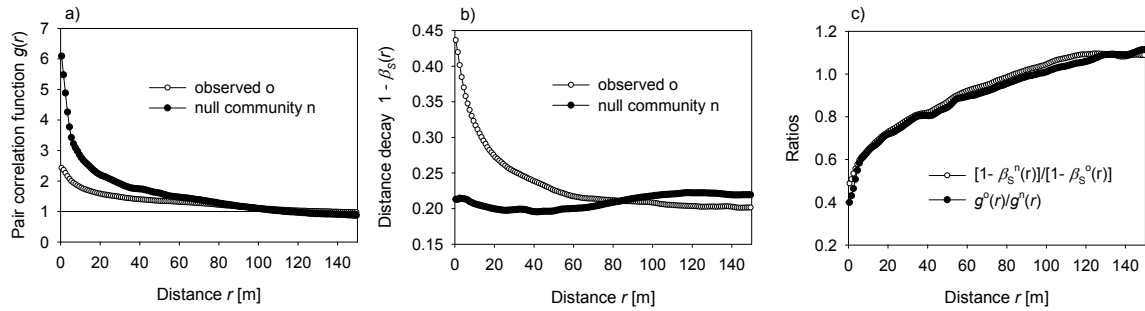


FIG. C1. Explaining the unexpected result for the joined habitat and dispersal limitation hypothesis for small trees at the Wabikon forest. (a) The observed pair correlation function $g^o(r)$ of all small trees (open disks) and that of one null community ($g^n(r)$; closed disks). (b) The observed species beta diversity $\beta_s^o(r)$ (open disks) and that of one null community ($\beta_s^n(r)$; closed disks). (c) the ratios $[1 - \beta_s^n(r)]/[1 - \beta_s^o(r)]$ and $[g^o(r)]/[g^n(r)]$ which are predicted to coincide for the joined habitat and dispersal limitation hypothesis.

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