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Mechanisms underlying local functional and phylogenetic beta diversity in two temperate forests

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Abstract. Although trait information has been widely used to explore underlying mechanisms of forest community structure, most studies have focused on local patterns of phylogenetic or functional alpha diversity. Investigations of functional beta diversity, on the other hand, have not been conducted at local scales in a spatially explicit way. In this study, we provide a powerful methodology based on recent advances in spatial point pattern analysis using fully mapped data of large and small trees in two large temperate forest plots. This approach allowed us to assess the relative importance of different ecological processes and mechanisms for explaining patterns of local phylogenetic and functional beta diversity. For both forests and size classes, we found a clear hierarchy of scales: habitat filtering accounted for patterns of phylogenetic and functional beta diversity at larger distances (150–250 m), dispersal limitation accounted for the observed decline in beta diversity at distances below 150 m, and species interactions explained small departures from functional and phylogenetic beta diversity at the immediate plant-neighborhood scale (below 20 m). Thus, both habitat filtering and dispersal limitation influenced the observed patterns in phylogenetic and functional beta diversity at local scales. This result contrasts with a previous study from the same forests, where dispersal limitation alone approximated the observed species beta diversity for distances up to 250 m. In addition, species interactions were relatively unimportant for predicting phylogenetic and functional beta diversity. Our analysis suggests that phylogenetic and functional beta diversity can provide insights into the mechanisms of local community assembly that are missed by studies focusing exclusively on species beta diversity.

Key words: Changbaishan, China (CBS); dispersal limitation; habitat filtering; pattern reconstruction; phylogenetic and functional beta diversity; point pattern analysis; species interaction; temperate forest; Wabikon Lake State Natural Area, Wisconsin, USA.

INTRODUCTION

One of the most important and widely used relationships in spatial biodiversity research is the distance decay of similarity, which describes how species similarity between two communities varies with the spatial distances that separate them. This distance decay is induced by directional turnover along a spatial gradient and represents one approach to defining beta diversity (Anderson et al. 2011). The distance-decay relationship has received some attention since the 1960s, but became increasing popular after Nekola and White (1999) formalized its ability to describe and compare biodiversity patterns. The importance of the distance-decay relationship is now recognized in many fields, including biogeography, community ecology, and conservation biology (Soininen et al. 2007, De Caceres et al. 2012), and it is used to infer community assembly processes (Condit et al. 2002, Morlon et al. 2008, Wang et al. 2011), and to predict the complementarities of sites within reserve networks (Ferrier et al. 2007).

When the distance-decay relationship is estimated at local scales, it links the immediate neighborhood of plants (in forests, distances up to about 30 m; Hubbell et al. 2001) with local scales of several hectares, and tends to reflect ecological processes such as habitat filtering, dispersal limitation, and species interactions (Wang et al. 2011). However, the relative importance of these processes in explaining the distance-decay relationship remains largely controversial. For instance, at intermediate spatial scales (0.05–82 km), Myers et al. (2013) found that habitat filtering had a stronger effect than dispersal limitation in temperate forests, whereas dispersal limitation was the dominant driver of species

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turnover in tropical forests. In contrast, Wang et al. (2011) found that both habitat filtering and dispersal limitation determined the distance-decay relationship in temperate forests at local (<500 m) scales, but dispersal limitation generally contributed more than habitat filtering.

While quantification of biodiversity has focused primarily on patterns of alpha and beta species diversity (Swenson et al. 2012*a*), more recent studies argue that mechanisms influencing patterns of community assembly and dynamics act not on the number of species, but rather on ecological differences among species (e.g., Weiher and Keddy 1995, Swenson 2011). The two main approaches to quantifying ecological differences among species are to consider (1) functional differences based on traits and (2) phylogenetic differences based on genetic relationships (Webb 2000). Both approaches are now increasingly used to complement the distance-decay relationship and other species-based biodiversity patterns in inferring the degree to which ecological processes such as habitat filtering, dispersal limitation, and species interactions contribute to the spatial distribution and assembly of species in plant communities (Webb 2000, Swenson et al. 2007, Kraft et al. 2008, Swenson and Enquist 2009, Helmus and Ives 2012). It is therefore somewhat surprising that the distance-decay concept has only rarely been extended to include phylogenetic relatedness or functional dissimilarity (but see Swenson et al. 2011, Siefert et al. 2013).

Phylogenetic and functional attributes of tree species may help us to assess the ecological processes influencing biodiversity patterns in forest communities. For example, communities with species that are more dissimilar than expected by chance at local spatial scales (e.g., <30 m) may be structured by competition for biotic resources, which tends to select species with low niche overlap (Weiher and Keddy 1995, Webb et al. 2002, Cavender-Bares et al. 2006, 2009). However, Mayfield and Levine (2010) showed that competitive exclusion may also promote coexistence of similar species, depending on how functional trait differences relate to stabilizing niche differences and relative fitness differences between species (Mayfield and Levine 2010). Conversely, communities that are comprised at within-habitat scales (e.g., 30–200 m) of more similar species than expected by chance may be structured by abiotic conditions that select for suitable trait values (Helmus et al. 2010; but see Mayfield and Levine 2010). Thus, the influence of phylogenetic relatedness and functional traits on spatial turnover of species in plant communities may differ at different spatial scales, including the plant-neighborhood scale, the within-habitat scale, and the between-habitat scale (Webb 2000, Swenson et al. 2007, Kraft et al. 2008, Swenson and Enquist 2009). The complexity of these relationships calls for a quantification of the change in phylogenetic or functional dissimilarity of local communities with distance (i.e., phylogenetic or functional beta diversity; Graham and Fine 2008, Swenson et al. 2011, Shen et al. 2013).

Previous studies have shown that individuals of different stem size classes within a forest community may show different phylogenetic structure (Swenson et al. 2007, Letcher 2010). For example, phylogenetic overdispersion increased in tropical rain forests with stem size, which was interpreted as an outcome of increasing importance of species interactions with cohort age, given that a phylogenetic signal is associated with differences in ecological function (Swenson et al. 2007). If a forest undergoes succession, the communities of different stem sizes can provide insights into successional dynamics. For example, Letcher (2010) observed increased phylogenetic evenness over succession due to the recruitment of more distantly related late-successional species, and Norden et al. (2012) found that relatedness among tree individuals decreased as succession unfolded. While these studies provide insights into local phylogenetic and functional diversity patterns (i.e., phylogenetic alpha diversity) with respect to stem size and successional stage, little is known about the corresponding changes in phylogenetic or functional beta diversity.

One recent approach for investigating the relative importance of different processes and mechanisms underlying diversity patterns is to compare observed species distributions to spatially explicit null communities (Shen et al. 2009, Wang et al. 2011, 2013, Wiegand and Moloney 2014: section 4.3.4). This approach is based on the classical strategy of randomizing certain elements of the model system while holding others fixed (Gotelli and Graves 1996). For example, a null model may conserve the observed habitat association of a species by assigning individuals to tentative random locations within the plot, but designating each assigned record with a probability proportional to habitat suitability (as determined in a previous step by a species distribution model based on environmental variables; Shen et al. 2009, Wiegand and Moloney 2014). Repeating this for all species and superimposing the null distribution patterns of individual species produces null community patterns that are expected only by operation of habitat filtering in the absence of species interactions and dispersal limitation. The phylogenetic and functional beta diversity of the observed community are then compared with these same metrics for replicates of the null community.

In this study, we quantified species, phylogenetic, and functional beta diversity in two fully mapped 25-ha temperate forests located in the United States and China, and tested five competing hypotheses on the relative importance of different ecological processes (i.e., habitat filtering, dispersal limitation, and species interactions) in explaining the pattern of phylogenetic and functional beta diversity. We selected the two forests because they are the only large, fully mapped plots of temperate forest for which sufficient functional trait data exist to conduct our analysis. In earlier studies, we used the same forest plots to analyze the distance decay of similarity and the species area relationship (Wang et al. 2011), and phylogenetic and functional diversity area relationships (Wang et al. 2013). This facilitates direct comparison of our results with other biodiversity patterns. Additionally, the two forests represent an early- and a late-successional forest, which allows us to compare our findings with those of earlier studies regarding phylogenetic structure in forests at different successional stages.

More specifically, we divided all individuals into two size classes, based on diameter at breast height (dbh; measured at 1.3 m aboveground); small (dbh < 10 cm) and large (dbh ≥ 10 cm), and estimated the observed phylogenetic, functional, and species beta diversity for each size class in the two forests. We then examined the patterns of phylogenetic and functional beta diversity for different size classes and forests and related these patterns to findings of earlier studies on phylogenetic alpha diversity during succession (e.g., Swenson et al. 2007, Letcher 2010, Norden et al. 2012). To examine the relative importance of different processes in explaining the observed phylogenetic and functional beta diversity patterns, and to determine if these relationships changed with size classes and successional stages, we generated 99 null communities and evaluated their match with the observed phylogenetic and functional beta diversity.

METHODS

Study areas

The Changbaishan forest dynamics plot comprises a 25-ha (500 × 500 m) area located in the Changbaishan (CBS) Nature Reserve, one of the largest biosphere reserves in northeastern China (42°23′ N, 128°05′ E). The CBS forest represents a late-successional stage without logging and other human disturbances for at least 300 years. The terrain of the CBS is relatively gentle, with elevation ranging from 791.8 to 809.5 m. The mean annual temperature is ~3.6°C, and the mean annual precipitation is ~700 mm. Each individual with a dbh ≥ 1 cm was mapped, measured, and identified in the plot. According to the first census in 2004, there were 38 902 individuals, comprising 52 species, 32 genera, and 18 families (Wang et al. 2010*a*).

The Wabikon forest dynamics plot comprises a 25.2-ha (300 × 840 m) area located in the Wabikon Lake State Natural Area in the Chequamegon-Nicolet National Forest in northeastern Wisconsin, USA (45°33′ N, 88°48′ W). The Wabikon forest is a mid-successional forest, which was partly logged during the early 1900s. The elevation of the Wabikon plot ranges from 488.3 to 514.2 m. The mean annual temperature is ~4.1°C, and the mean annual precipitation is ~819 mm. The first census in 2008 documented 48 849 individuals (dbh $\geq$ 1cm) belonging to 38 species, 26 genera, and 16 families (Wang et al. 2011).

Environmental variables

To estimate habitat suitability models for each species, we used several environmental covariates hypothesized to describe the local habitat suitability (Wang et al. 2011, 2013). They included three topographic variables (elevation, slope, and aspect) at a resolution of 5 × 5 m in the two plots. Tree density was included as a bio-environmental variable to capture the overall biotic conditions in the 5 × 5 m quadrats (Wang et al. 2011). This was especially important for the Wabikon plot, which shows two localized hotspots of species richness in areas of high tree density (see Fig. S2 in Wang et al. [2011]). Additionally, soil samples were taken using a regular grid of points every 30 m in the CBS plot. Two additional samples at 2, 5, or 15 m were taken in a random compass direction from each grid point to capture variation in soil factors at finer scales. In total, 967 points were sampled and 8 soil factors (pH, organic matter, total N, total P, total K, available N, available P, and available K) were measured for each soil sample. The mean values for soil factors at the 5 × 5 m grid were then calculated using kriging interpolation.

Phylogenetic construction

We used the Phylomatic informatics tool (Webb and Donoghue 2005) to construct a phylogenetic tree for each plot (Appendix A). The Angiosperm Phylogeny Group III (APG III 2010) phylogeny was utilized by Phylomatic as a backbone. Branch lengths for each tree species were estimated using the BLADJ algorithm (Webb et al. 2008), and node dates were estimated from Wikstrom et al. (2001). Given the low number of species per genus in the two temperate forests, the soft polytomies of the phylogenetic tree were few, which would have little to no effect on phylogenetic dissimilarity.

Functional trait collection

Six functional traits were collected for each species in the two plots: maximum height, wood density, leaf area, specific leaf area, leaf N, and leaf P. Although these traits cannot represent all aspects of plant function, they robustly indicate several major axes of plant functional strategy in trees (Swenson et al. 2012*a*, *b*). The trait data were measured from >10 individuals when possible, but sample sizes were lower for the rare species. Trait collection protocols followed Cornelissen et al. (2003).

To utilize identical methods on the traits and phylogenetic data, we generated a functional trait dendrogram representing functional dissimilarity of species, which is analogous to the phylogenetic tree depicting phylogenetic dissimilarity. The dendrogram for each plot was constructed based on species' position along the first five principal coordinate analysis (PCA) axes. The PCA analyses were performed because some traits were correlated with each other. Prior to the PCA, the trait data were standardized by subtracting the mean value of the traits of all species and dividing by one standard deviation. A functional distance matrix for each plot was constructed by computing the Euclidean distances of the first five components, explaining >96% of the total variance in traits. This approach avoids the over- or underrepresentation of some functional strategy axes in the distance matrix.

POINT PATTERN METHODS

Ecological processes and hypotheses

We simulated five different types of spatially explicit null communities that represented different hypotheses on the relative importance of habitat filtering, dispersal limitation, and species interaction on functional and phylogenetic beta diversity. This was accomplished by representing the distribution pattern of each species by a specific point process model that conserved certain properties of the observed species pattern while randomizing others. All null communities were then assembled by independent superposition of the patterns of individual species generated by a given point process model. Thus, all hypotheses assume locally independent species placement and therefore the absence of local species interactions (McGill 2010).

Random placement hypothesis.—This hypothesis represents the case of no spatial structure in the community and assumes that the individuals of all species are independently and randomly distributed in the study area W. We generated these null distribution patterns by randomly relocating the individuals of all species in the given study area W (Appendix B: Fig. B1).

Dispersal limitation hypothesis.—This hypothesis assumes that the community is assembled only by action of dispersal limitation and other internal mechanisms of population dynamics. These intrinsic demographic factors can create intraspecific species clustering, but habitat filtering or species interactions do not influence the placement of trees. To represent this hypothesis, we used nonparametric techniques of pattern reconstruction (Tscheschel and Stoyan 2006, Wiegand et al. 2013) for each species, creating null distribution patterns that very closely resemble the possibly complex spatial structure of the observed species distribution pattern (see Appendix B for a detailed explanation of this technique and Fig. B2 for example patterns).

Habitat filtering hypothesis.—This hypothesis assumes that the distribution pattern of a given species i is only driven by local habitat suitability, but that the species does not show additional clustering independent of habitat. We represent the habitat suitability of species i by the intensity function $\lambda_i(x)$, where $\lambda_i(x)dx$ yields the probability that an individual of species i is found in a small area dx centered on location x. To estimate $\lambda_i(x)$, we fit the log-linear species distribution model $\lambda_i(x) = \exp(c_{i0} + c_{i1}\, v_1(x) + \ldots + c_{in}v_n(x))$ to the species location x_i where the c_{ik} are regression coefficients and the $v_i(x)$ are our environmental covariates (Waagepetersen and Guan 2009). We generated null distribution patterns by randomly relocating the individuals of all species within study area W, but accepting a given location only with probability $\lambda_i(x)/\lambda_i{}^*$, where $\lambda_i{}^*$ is the maximal value of $\lambda_i(x)$ in W (Appendix B: Fig. B3).

Combined habitat and dispersal hypothesis.—This hypothesis assumes that the community is assembled by the joint action of internal cluster mechanisms and habitat filtering. We generated null distribution patterns similar to those generated by the dispersal limitation hypothesis, but constrained the placement of individuals by the intensity function $\lambda_i(x)$ used in the habitat filtering hypothesis (Wiegand et al. 2013; Appendix B). The null distribution patterns therefore faithfully reflected both the observed habitat associations and intrinsic demographic processes that can produce the observed clustering (Appendix B: Fig. B4). Departures from this hypothesis may be caused by unobserved environmental variables that are missed in the habitat model and by species interactions that are ignored by the dispersal hypothesis.

Independent placement hypothesis.—This null hypothesis generates null communities that are expected in the absence of smaller-scale species interactions. We therefore randomized only the smaller-scale placement of species, but held the observed intensity function and the observed intraspecific species clustering process constant. We generated the corresponding null distribution patterns (Appendix B: Fig. B5) similarly to those of the combined habitat filtering and dispersal limitation hypothesis, but used a nonparametric kernel estimate of the intensity function $\lambda_i(x)$ (with bandwidth $R = 50$ m) that resembled at larger distances exactly the observed intensity function (Appendix B; Wiegand et al. 2013) instead of a parametric estimate of $\lambda_i(x)$ based on environmental variables (as was used for the combined habitat filtering and dispersal limitation hypothesis). Departures from this hypothesis can only occur at distances smaller than 50 m and may be mainly caused by species interactions (or imperfect pattern reconstructions).

Measuring phylogenetic and functional beta diversity

To measure the change in functional or phylogenetic dissimilarity with spatial distance in a given study area W, we start heuristically with the abundance-weighted pairwise phylogenetic dissimilarity D_{pw} of two small subplots a and b distance r apart. This measure has been used to quantify phylogenetic and functional beta diversity (Swenson 2011, Swenson et al. 2011)

$$D_{\mathrm{pw}} = \frac{\left(\sum_{i=1}^{n_a} f_{i,a}\bar{\delta}_{ib} + \sum_{j=1}^{n_b} f_{j,b}\bar{\delta}_{ja}\right)}{2} \tag{1}$$

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

$$\bar{\delta}_{ib} = \frac{1}{n_b}\left(\sum_{j=1}^{n_b} \delta_{ij}\right)$$

is the mean pairwise phylogenetic or functional distance between species i (in a) and all species present in b; and δ_{ij} is the functional or phylogenetic dissimilarity between species i and j. We now estimate the average of D_{pw} for all subplots a and b that are distance r apart. In Appendix C, we translated this average into theoretically well-founded quantities of spatial statistics to obtain the simple expression

$$D_{\mathrm{pw}}(r) = \sum_{i=1}^{S} \sum_{j=1}^{S} \delta_{ij} p_{ij}(r) \qquad (2)$$

where S is the number of species and $p_{ij}(r)$ is a mark-connection function, which is defined as the conditional probability that from two randomly taken individuals separated by distance r, the first is of species i and the second is of species j (Getzin et al. 2008, Wiegand and Moloney 2014).

Eq. 2 can be rewritten by expressing the mark-connection function by means of a pair-correlation functions (Illian et al. 2008) as

$$D_{\mathrm{pw}}(r) = \sum_{i=1}^{S} \sum_{j=1}^{S} \delta_{ij} f_i f_j \frac{g_{ij}(r)}{g(r)} \qquad (3)$$

where the f_i is the relative abundance of species i in W; $g_{ij}(r)$ is the partial pair-correlation function of the species pair ij (i.e., the mean density of individuals of species j at distance r from individuals of species i divided by the intensity λ_j of species j); and $g(r)$ is the pair correlation function of all individuals in W, regardless of their species label. Note that the measure $D_{\mathrm{pw}}(r)$ has been termed the phylogenetic (spatially explicit) Simpson index $\beta_{\mathrm{phy}}(r)$ (Shen et al. 2013; section 3.1.7.6 in Wiegand and Moloney 2014).

Eq. 3 generalizes Rao's quadratic entropy (Rao 1982, Shimatani 2001*a*, Hardy and Senterre 2007), which is given as

$$D^{\mathrm{p}} = \sum_{i=1}^{S} \sum_{j=1}^{S} \delta_{ij} f_i f_j \qquad (4)$$

and yields the expected value of the phylogenetic (or functional) distance for randomly selected pairs of individuals in the study area W. Note that Rao's quadratic entropy corresponds to a community without spatial structure (i.e., the random placement hypothesis) where $D_{\mathrm{pw}}(r) = D^{\mathrm{p}}$ because in this case $g_{ij}(r)/g(r) = 1$. Eq. 3 captures spatial structure by introducing the condition that the two individuals must be located distance r apart (represented by the term $g_{ij}(r)/g(r)$). Thus, our measure $D_{\mathrm{pw}}(r)$ yields the expected phylogenetic (or functional) distance of randomly selected pairs of individuals that are distance r apart.

To understand the relationship between the measure $D_{\mathrm{pw}}(r)$ of functional (or phylogenetic) beta diversity and that of species diversity, we reduce the distance measure δ_{ij} to a value of one for heterospecifics and zero for conspecifics (i.e., a "star phylogeny"). In this case, the measure $D_{\mathrm{pw}}(r)$ collapses to the spatially explicit Simpson index $\beta_{\mathrm{S}}(r)$ (Shimatani 2001*b*, Chave and Leigh 2002, Shen et al. 2013), which yields the probability that two arbitrarily chosen individuals within W that are distance r apart are heterospecifics. This index of species turnover is related to the measure of beta diversity used in Chave and Leigh (2002) and Condit et al. (2002) by $F(r) = 1 - \beta_{\mathrm{S}}(r)$. Thus, the metric $D_{\mathrm{pw}}(r)$ is a natural extension of the spatially explicit Simpson index to measure spatial phylogenetic (or functional) turnover instead of spatial species turnover.

Evaluating the different hypotheses

The fitted point process model generated a stochastic realization for each species at the CBS and Wabikon plots, and the simulated patterns of all species were then independently superimposed to yield one null community. We averaged the $D_{\mathrm{pw}}(r)$ functions estimated from the 99 null communities to derive expectations for the five hypotheses, and then constructed simulation envelopes for each predicted $D_{\mathrm{pw}}(r)$ from the lowest and highest values of the $D_{\mathrm{pw}}(r)$ from the 99 null communities.

We compared the observed $D_{\mathrm{pw}}(r)$ from the original communities at the CBS and Wabikon plots with the predicted $D_{\mathrm{pw}}(r)$ from the null communities generated by the five process models. A model was rejected if the observed $D_{\mathrm{pw}}(r)$ fell clearly outside the simulation envelopes of the predicted $D_{\mathrm{pw}}(r)$; otherwise, the model was considered adequate. In addition, to identify the model that produced the best fit, we used a statistic $R^2 = 1 - \mathrm{SSE}/\mathrm{SST}$, which is analogous to the method in linear regression, where $\mathrm{SSE} = \Sigma_r[D_{\mathrm{obs}}(r) - D_{\mathrm{pre}}(r)]^2$ and $\mathrm{SST} = \Sigma_r[D_{\mathrm{obs}}(r) - \mathrm{mean}(D_{\mathrm{obs}})]^2$. $D_{\mathrm{pre}}(r)$ is the predicted $D_{\mathrm{pw}}(r)$, $D_{\mathrm{obs}}(r)$ is the observed $D_{\mathrm{pw}}(r)$, and $\mathrm{mean}(D_{\mathrm{obs}})$ is the mean value of the observed $D_{\mathrm{pw}}(r)$ over all distances r analyzed. In cases where SSE has negative values, the mean of the data (i.e., an intercept-only model) provides a better fit than the $D_{\mathrm{pw}}(r)$ of the null communities.

Phylogenetic and functional distances were estimated in R (R Core Team 2013) using the picante package (Kembel et al. 2010). The habitat distributions were estimated in R using the spatstat package (Baddeley and Turner 2005); pattern reconstruction was simulated with the software presented in Wiegand et al. (2013; T. Wiegand, *unpublished software*); and the $D_{\mathrm{pw}}(r)$ were estimated with the software Programita (*available online*).[6]

RESULTS

Observed patterns in species, phylogenetic, and functional beta diversity

We used the normalized measure $D_{\mathrm{pw}}(r)/D^{\mathrm{p}}$ (using Eqs. 3 and 4) to directly compare the different measures

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[6] www.programita.org

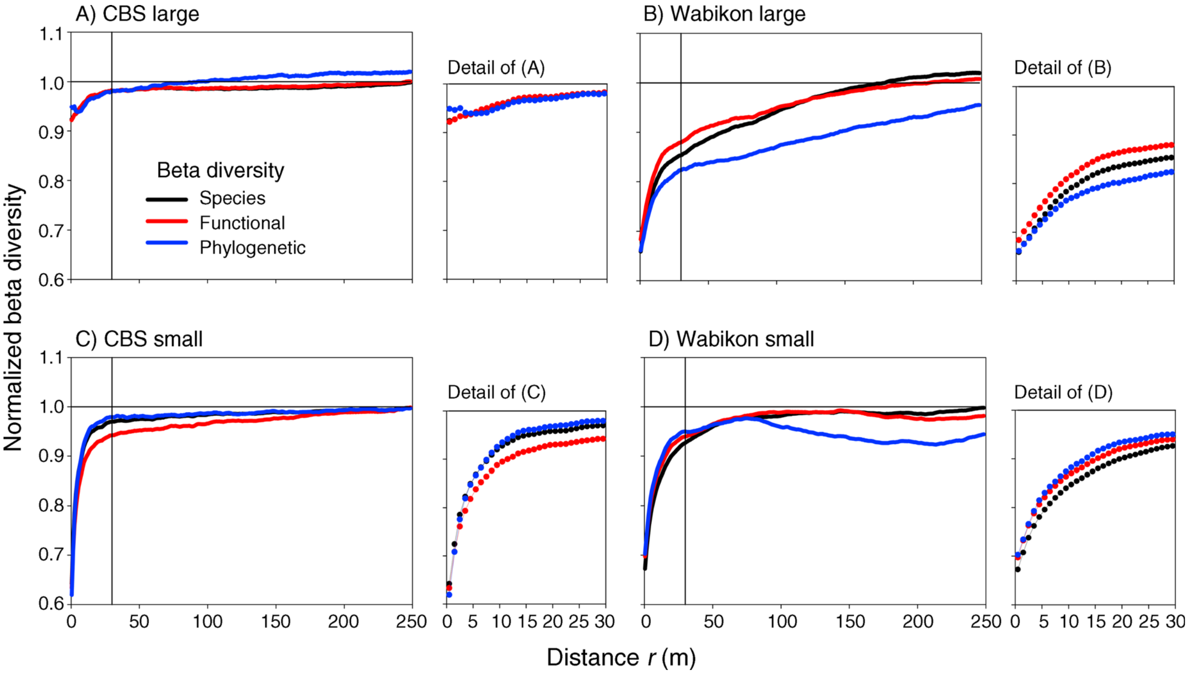

FIG. 1. Species, functional, and phylogenetic beta diversity for the two forest plots (Changbaishan [CBS], China, and Wabikon, Wisconsin, USA) and the two size classes (small and large). The figures show the normalized species beta diversity $\beta_S(r)/\beta^*_S$ (for distance r; black lines), the normalized functional beta diversity $\beta_{func}(r)/\beta^*_{func}$ (red lines), and the normalized phylogenetic beta diversity $\beta_{phy}(r)/\beta^*_{phy}$ (blue lines), respectively. Lines with circle data points correspond to the data at small scales (0–30 m). The normalization constant β^*_S is the Simpson index, and β^*_{func} and β^*_{phy} are the index D^p (Rao's quadratic entropy; Eq. 4; Rao 1982, Shimatani 2001*a*, Hardy and Senterre 2007) for functional and phylogenetic distances, respectively.

of beta diversity (Fig. 1). In almost all cases $D_{pw}(r)/D^p < 1$, which means that small, nearby subplots tend to be more similar with respect to functional and phylogenetic beta diversity and composition than expected in a completely mixed community (represented by Rao's quadratic entropy D^p of all individuals of a given size class within the study area W). The only exceptions were for large trees and phylogenetic beta diversity at the CBS plot at distances larger than 100 m, and large trees and species beta diversity at the Wabikon plot at distances larger than 150 m (Fig. 1A, B).

All three beta diversity measures for large trees at the CBS forest showed values close to one with slightly smaller values at smaller distances (Fig. 1A). This indicates only weak spatial structuring with respect to species, phylogenetic, and functional beta diversity, and a spatially well-mixed forest community. In contrast, for small trees, we observed a strong spatial structuring at distances below 15 m that disappeared for larger distances where beta diversity measures quickly approximate the expected value of D^p (except for functional beta diversity that showed a somewhat stronger spatial structuring; Fig. 1C). In contrast, large trees at the Wabikon plot showed substantial spatial structuring with respect to species, phylogenetic, and functional beta diversity, with a steep increase in $D_{pw}(r)$ at small distances (<15 m) and a shallower increase at distances larger than 50 m (Fig. 1B). Small trees at the Wabikon plot showed patterns similar to those of small trees at the CBS plot, but a somewhat stronger spatial structuring at intermediate spatial scales (Fig. 1D).

Comparing the normalized metrics $D_{pw}(r)/D^p$ for functional or phylogenetic beta diversity (red and blue lines in Fig. 1, respectively) with corresponding measures of species beta diversity (black lines in Fig. 1) allows us ask if functional or phylogenetic turnover is fully driven by species turnover (i.e., functional or phylogenetic relationships do not provide extra information) or if functional or phylogenetic turnover is smaller or larger than explained by species turnover (Shen et al. 2013). For the CBS plot, we found differences in phylogenetic beta diversity for large trees at larger scales (Fig. 1A) and in functional turnover for small trees at intermediate scales (Fig. 1C). For the Wabikon plot, we found strong differences in phylogenetic beta diversity for large trees at almost all scales and for functional beta diversity at intermediate scales (Fig. 1B) and for small trees differences in phylogenetic beta diversity at larger scales (Fig. 1D).

Phylogenetic beta diversity differed for large trees and small trees; large trees at the later-successional CBS forest had substantially higher values of the phylogenetic $D_{pw}(r)$ than small trees (Appendix D: Fig. D1a), while opposite results occurred at the earlier-successional Wabikon forest (Appendix D: Fig. D1c). Large trees at CBS had higher functional $D_{pw}(r)$ than small trees (Appendix D: Fig.

TABLE 1. The proportion of variation (R^2) explained for distances r = 1–250 m by the five ecological process hypotheses for forests in Changbaishan (CBS), China, and Wabikon, Wisconsin, USA.

	Hypothesis				
Forests	Random placement	Dispersal limitation	Habitat filtering	Habitat and dispersal	Independent placement
Large trees					
Phylogenetic D_{pw}					
CBS	0.8	65.2	59.2	91.4	98.3
Wabikon	−452.9	−393.8	−300.3	62.1	96.4
Functional D_{pw}					
CBS	−143.3	22.4	28.9	87.8	94.3
Wabikon	−70.2	53.4	−19.5	79.3	96.6
Species D_{pw}					
CBS	−202.7	28.7	5.5	82.1	94.0
Wabikon	−55.5	45.6	4.4	84.4	98.1
Small trees					
Phylogenetic D_{pw}					
CBS	−25.3	89.0	−0.8	33.5	93.1
Wabikon	−328.4	−253.8	−466.4	−271.5	87.9
Functional D_{pw}					
CBS	−82.4	19.4	32.1	46.8	97.5
Wabikon	−63.3	68.2	−89.3	−78.7	98.4
Species D_{pw}					
CBS	−36.1	73.4	16.5	51.0	96.0
Wabikon	−47.3	85.0	−22.0	−22.3	98.2

Notes: The proportion of variation explained by a model is calculated by $1 - \mathrm{SSE/SST}$, where $\mathrm{SSE} = \Sigma_r(D_{\mathrm{obs}}(r) - D_{\mathrm{pre}}(r)]^2$ and $\mathrm{SST} = \Sigma_r[D_{\mathrm{obs}}(r) - \mathrm{mean}(D_{\mathrm{obs}}))^2$, in which $D_{\mathrm{pre}}(r)$ is the predicted phylogenetic or functional pairwise phylogenetic dissimilarity $D_{\mathrm{pw}}(r)$, and $D_{\mathrm{obs}}(r)$ is the observed phylogenetic and functional $D_{\mathrm{pw}}(r)$. Note that R^2 yields negative values if the intercept-only model (i.e., the mean value of $D_{\mathrm{obs}}(r)$ averaged over all r fits better than the model.

D1b), while at Wabikon, small trees had higher functional $D_{\mathrm{pw}}(r)$ than large trees (Appendix D: Fig. D1d).

Hypothesis testing

As expected, the random placement hypothesis provided the poorest fit to the observed phylogenetic and functional beta diversity measures (Table 1, Fig. 2; Appendix D: Figs. D2–D5); in all cases, the intercept-only model provided a similar or better fit (i.e., negative or close to zero R^2 values in Table 1). The observed functional or phylogenetic beta diversity was in most cases clearly below the expectation under random placement (i.e., the index D^{p}), except phylogenetic beta diversity of large trees at CBS at larger distances (Fig. 2A).

The dispersal limitation hypothesis, which accounts for the observed species clustering, produced a good approximation of phylogenetic and functional beta diversity, except for the phylogenetic $D_{\mathrm{pw}}(r)$ of large and small trees at Wabikon and the functional $D_{\mathrm{pw}}(r)$ of large and small trees at the CBS plot (Table 1; Appendix D: Figs. D2–D5). In these cases, it overestimated functional and phylogenetic beta diversity. When assessing the fit only at the plant-neighborhood scale (i.e., 1–50 m; Appendix D: Table D1), the dispersal limitation hypothesis provides excellent fits in all cases except phylogenetic beta diversity of large trees at the Wabikon forest (Appendix D: Fig. D3). However, this hypothesis failed at larger between-habitat scales (i.e., 150–250 m), except for functional beta diversity of large trees at the Wabikon forest and phylogenetic beta diversity of small trees at the CBS plot (Appendix D: Table D3). Thus, an additional factor (other than pure species clumping) must be causing more similar individuals to be placed together at the larger between-habitat scales of more than 150 m.

Our results show that habitat filtering has a strong tendency to place individuals of similar species together at between-habitat scales. In almost all cases, it approximated the observed beta diversity at the 150–250-m scales well (Appendix D: Table D3). The exception was phylogenetic beta diversity of small trees at Wabikon (Appendix D: Fig. D5). However, the habitat filtering hypotheses performed poorly at intermediate and smaller scales (Appendix D: Tables D1 and D2), where it generally overestimated phylogenetic and functional beta diversity (Appendix D: Figs. D2–D5).

Additional consideration of the observed species clustering in the combined habitat and dispersal hypothesis produced beta diversity patterns that approximated the observed $D_{\mathrm{pw}}(r)$ quite well (Fig. 2, Table 1). The only exception was the community of small trees at the Wabikon plot (Appendix D: Fig. D5), where the $D_{\mathrm{pw}}(r)$ was severely overestimated at distances below 100 m. The reason for this somewhat unexpected result was that the

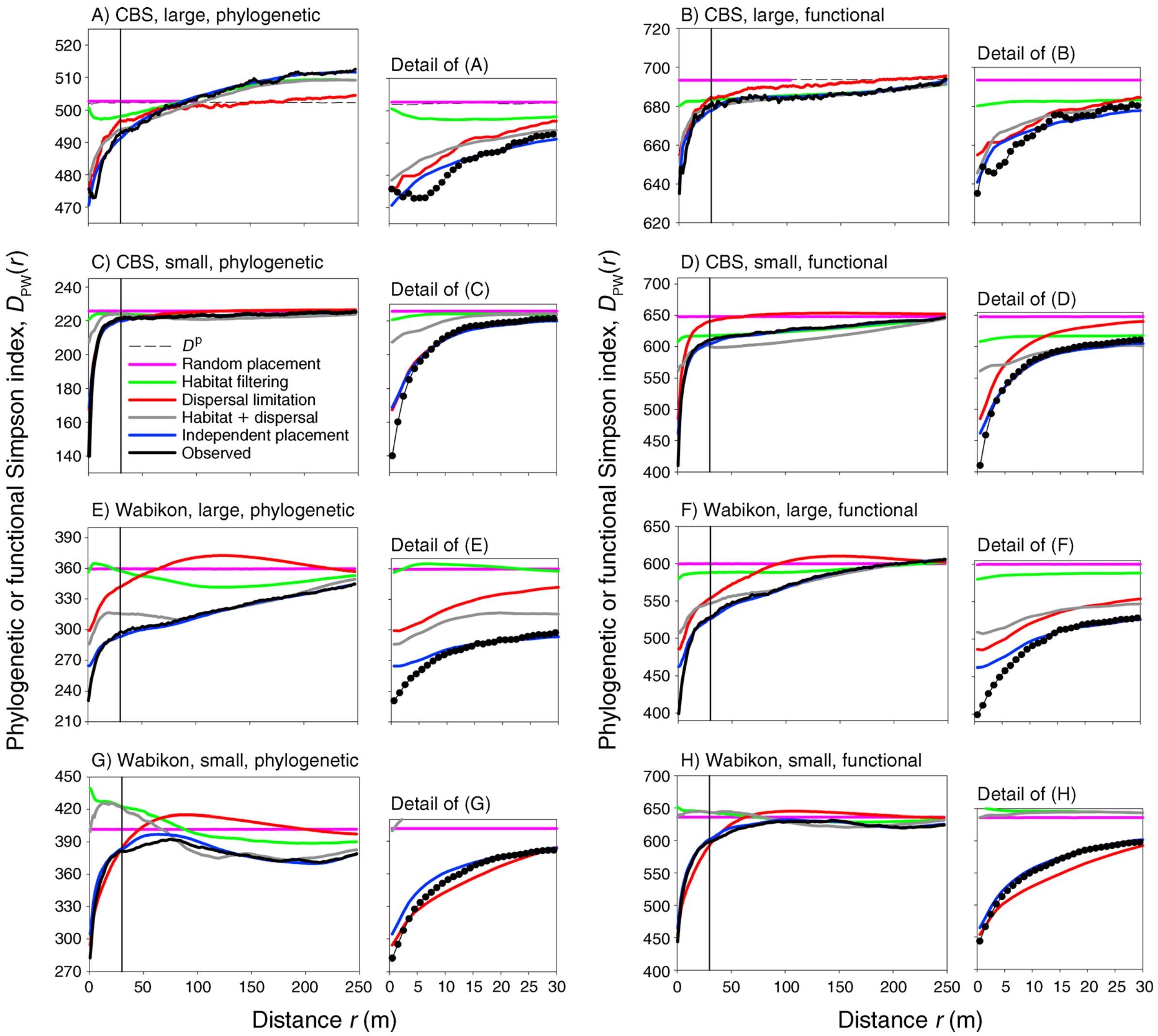

FIG. 2. The observed phylogenetic and functional beta diversity pairwise phylogenetic dissimilarity $D_{\mathrm{pw}}(r)$ (black lines) and that predicted by the five ecological process hypotheses (colored lines) for the communities of small and large trees at the (A–D) CBS and (E–H) Wabikon forests. Lines with circle data points correspond to the data at small scales (0–30 m).

habitat models poorly described the placement of the three most abundant species (that made up almost 80% of the small trees; see Appendix C for more detail). However, this hypothesis still produced smaller departures from the observed $D_{\mathrm{pw}}(r)$ (Fig. 2; Appendix D: Figs. D2–D5). This indicated that the available environmental variables did not fully describe habitat suitability for small trees at the CBS plot (Appendix D: Fig. D4, functional beta diversity) and for small trees at the Wabikon plot (Appendix D: Fig. D5).

Effect of species interactions

As expected, the null communities of the independent placement hypothesis yielded excellent agreement in $D_{\mathrm{pw}}(r)$ for distances larger than 50 m (Fig. 2, Table 1; Appendix D: Figs. D2–D5, Tables D2 and D3). This was expected because our algorithm that generated the null communities conserved the observed intensity function of individual species (at scales larger than 50 m) and conserved the small-scale characteristics of species clustering at distances below 50 m. For this reason, this null community is sensitive to effects of small-scale species interactions at distances below 50 m. Interestingly, the independent placement hypothesis also yielded a good agreement at small distances, explaining more than 90% of the variation in $D_{\mathrm{pw}}(r)$ (Appendix D: Table D1), which indicates that species interactions are relatively unimportant for prediction patterns of functional or phylogenetic beta diversity at the local-plot scale (Appendix D: Fig. D6).

DISCUSSION

We used fully mapped data of large and small trees in two temperate forest plots to discriminate among five competing hypotheses representing different ecological processes and mechanisms underlying local phylogenetic and functional beta diversity patterns. We found a clear scale hierarchy in the relative importance of processes explaining local functional and phylogenetic beta diversity: habitat filtering was required to account for patterns of phylogenetic or functional beta diversity at distances between 150 and 250 m, processes of internal population dynamics (such as dispersal limitation that can generate species clustering independent on habitat gradients) were required to account for the observed patterns of phylogenetic and functional beta diversity at distances below 150 m, and species interactions accounted for small displacements in the locations of trees at the immediate plant-neighborhood scale of below 20 m. Unexpectedly, this general scale hierarchy of processes was unaffected by size class and forest. Thus, both habitat filtering and dispersal limitation, but not small-scale species interactions, were needed to explain the observed patterns of phylogenetic and functional beta diversity at the local scales of 1–250 m examined here. This result contrasts with a previous study with data from the same forests that showed that the dispersal limitation hypothesis alone provided a good approximation of the observed species beta diversity patterns (Wang et al. 2011; see also Table 1). However, in the present study, the dispersal limitation hypothesis yielded poor fits of the data at larger distances (Appendix D: Table D3), overestimating phylogenetic and functional beta diversity. This means that additional factors (other than species clumping) must cause functionally or phylogenetically more similar individuals to be placed together at larger scales. Our results indicate that habitat filtering has a strong potential to achieve this. Thus, using additional information from functional traits and phylogenetic relatedness improved our ability to distinguish among competing hypotheses of community assembly.

The relative importance of habitat filtering and dispersal limitation

Habitat filtering and dispersal limitation are two key processes structuring the forest communities presently studied, but their relative importance across forests remains controversial and depends on spatial scale. Current studies on phylogenetic and functional beta diversity have been primarily conducted at broad spatial scales using tree plots often separated by many kilometers, with phylogenetic and functional beta diversity partitioned into environmental and spatial components (e.g., Myers et al. 2013). Generally, broader-scale environmental factors or the interactions between environmental and spatial factors (e.g., dispersal limitation) can explain a large proportion of the variance of phylogenetic beta diversity, indicating the greater contribution of habitat filtering than dispersal limitation (Hardy and Senterre 2007, Swenson et al. 2011, Siefert et al. 2013). However, this result does not necessarily hold on local scales of several hectares, where environmental differences are smaller.

Our study showed that habitat filtering was a major factor in explaining functional and phylogenetic beta diversity patterns in the two communities at scales larger than 150 m, but not at smaller distances. The underlying mechanism appears to be a positive larger-scale correlation in the spatial placement of functionally (or phylogenetically) similar species, which reduces functional and phylogenetic beta diversity at distances between 150 and 250 m. However, beta diversity was reduced at smaller scales, a pattern that can be explained by the additional effect of species aggregation (i.e., the combined habitat filtering and dispersal limitation hypothesis). We found previously (Wang et al. 2011, 2013) that the dispersal limitation hypothesis approximated species beta diversity at both forests and size classes reasonably well (Table 1). However, the dispersal limitation hypothesis failed in predicting phylogenetic beta diversity for small and large trees at Wabikon and functional beta diversity for small and large trees at CBS. In these cases, the additional information on habitat filtering was needed to yield good approximation of the observed phylogenetic and functional beta diversity (Table 1). For small trees at the Wabikon forest, we still obtained poor fits of the combined habitat filtering and dispersal limitation hypothesis because the available habitat variables did not describe the habitat filtering sufficiently (Table 1; Appendix C). These results indicated that local phylogenetic and functional beta diversity were more sensitive to environmental heterogeneity than were species diversity. This becomes clear when we look at our analytical formula for the phylogenetic or functional beta diversity (Eq. 3; Appendix C).

Missing factors in the combined habitat and dispersal hypothesis

The combined habitat and dispersal hypothesis did not fully explain the observed $D_{\mathrm{pw}}(r)$ at some distances for both large and small trees in the two forests. Because we used a nonparametric technique that was able to closely reconstruct the spatial structure of observed species distributions (Wiegand et al. 2013), we attribute the departure to omission of important abiotic, biotic, or historical factors in the estimation of the intensity.

Indeed, previous studies have found that such factors often affect the spatial distribution of tree species. For example, other soil factors such as aluminum have been shown to be highly associated with the spatial distributions of species (John et al. 2007, Schreeg et al. 2010). Also, a substantial phylogenetic signal has been found in plant pathogens or predators (Gilbert and Webb 2007), where closely related species tended to share similar pathogens or predators, opening space for more distantly related species. Additionally, historical factors such as the pattern of 20th century forest harvesting at Wabikon may have strongly affected the spatial pattern of species. Note that the poor fit of the combined habitat and dispersal hypothesis for small trees at the Wabikon forest points to such an effect. This forest contains a patch of successional forest that was logged ~40 years ago, and this disturbance may mask the effects of topographic factors and reduce the predictive ability of the species distribution model (Wang et al. 2013), and thus the combined habitat and dispersal hypothesis, especially for small trees.

Effects of species interactions

The independent placement hypothesis produced a good approximation of phylogenetic and functional $D_{\mathrm{pw}}(r)$ for distances larger than 50 m. Tables D2 and D3 (Appendix D) showed that this was indeed the case. We found only smaller departures at distances below 10 or 20 m (Appendix D: Fig. D6), where the observed phylogenetic or functional beta diversity was below the simulation envelopes of the null communities. However, the independent placement hypothesis still yielded an R^2 of 0.93 at distances of 1–20 m (Appendix D: Table D4).

Our results suggest that the effects of species interactions had a relatively minor influence on community assembly with respect to functional and phylogenetic beta diversity. Thus, we obtained excellent predictions of phylogenetic and functional beta diversity under the assumption that species were placed independently (McGill 2010, Wiegand et al. 2012), except within the direct neighborhood of trees. This result contradicts previous studies, which have identified the importance of species interactions, especially for plant species (Uriarte et al. 2004, Canham et al. 2006, Wang et al. 2010*b*). For example, Wang et al. (2010*b*) found that for the community of large trees at the CBS plot, one-third of all pairs of species showed evidence of interspecific interactions. However, the small-scale interaction of species pairs might cancel out and may not leave a strong signal on community-level summary statistics, such as the species area relationship, species turnover (Wang et al. 2011), and phylogenetic and functional diversity area relationships (Wang et al. 2013). Analysis of all these patterns indicated that smaller-scale species interactions may not be the key factor for explaining overall spatial patterns of diversity in the two temperate forests.

Effects of life stage and successional stage

We found the same ranking of our hypotheses for small and large trees in both forests (Table 1; Appendix D: Tables D1–D3); the combined habitat heterogeneity and dispersal limitation hypothesis best approximated the observed patterns in phylogenetic or functional beta diversity of tree assemblages. Thus, somewhat unexpectedly, the relative importance of habitat heterogeneity and dispersal limitation did not shift with life stage and successional stage.

Large trees at the CBS plot showed much higher values of functional and phylogenetic $D_{\mathrm{pw}}(r)$ than small trees, but large trees at the Wabikon forest showed smaller values than those of small trees (Appendix D: Fig. D1). This indicates that the large trees at the CBS plot showed a strong mixing of distantly related species compared with the Wabikon plot (and small trees at CBS). Phylogenetic and functional similarity declined quickly at the Wabikon forest with distance and produced locally more similar species assemblages than expected in a well-mixed forest. This is consistent with the presence of a young forest patch and a distinct lowland patch that contained gymnosperm species (*Picea mariana*, *Pinus strobus*, *Thuja occidentalis*, *Tsuga canadensis*) and several others (*Alnus incana*, *Ilex verticillata*, *Populus balsamifera*) that were rare or absent from other portions of the Wabikon plot.

A direct comparison of our results with studies on phylogenetic alpha diversity during forest succession is difficult because local beta diversity studies assess spatial changes in phylogenetic similarity among local assemblages, whereas studies of alpha diversity assess how the species composition of a plot changes during succession relative to the species pool. For example, large trees at the CBS plot showed higher values of the phylogenetic $D_{\mathrm{pw}}(r)$ and Rao's D^{p} than small trees, which is probably an effect of changes in relative abundances. Small trees at the old-growth CBS plot are subject to biotic filters that select for local assemblages of more distantly related species (Swenson et al. 2007). The generally higher values of the phylogenetic beta diversity (and Rao's D^{p}) of small trees vs. large trees at the Wabikon forest can be attributed to the recruitment of phylogenetically distant species in the patch of cleared forest, but probably not to recruitment of more distantly related late-successional species.

Limitations

Our study constructed phylogenetic dissimilarity among species using the Angiosperm Phylogeny Group III (APG III 2010) phylogeny, which has a lower resolution than the increasingly used molecular phylogenies. However, this will not affect the general results of our analyses because of the low numbers of species within genera in the temperate forest analyzed here. Also, construction of functional dissimilarity among species was only based on six functional traits, although these traits represented a wide spectrum of plant function and are widely used. Future studies may include more physiological and defensive traits.

CONCLUSIONS

Although phylogenetic and functional trait information have been widely used to make inferences about processes and mechanisms that structure forest communities, most studies have focused primarily on patterns of phylogenetic or functional alpha diversity across large spatial or temporal scales (Graham and Fine 2008, Swenson et al. 2012*a*, *b*), or on analysis of phylogenetic and functional turnover in small plots separated by variable distances along environmental gradients (e.g., Nekola and White 1999, Swenson et al. 2011). Surprisingly, however, the concept of phylogenetic or functional beta diversity has not been applied at local scales in a spatially explicit way when large, fully mapped plots are available (but see Shen et al. 2013). We showed here that this can provide important additional information that allows for an assessment of the relative importance of processes and mechanisms underlying community assembly at the local scale, and we provide a powerful methodology for doing this based on recent advances in spatial point pattern analysis (Wiegand and Moloney 2014). Our analysis demonstrated that using phylogenetic and functional beta diversity can provide additional information on mechanisms of local community assembly that would be missed by only focusing on species beta diversity. We presented here a methodology that can be widely used in fully mapped plots and conducted a detailed pilot study to illustrate its potential. Future analyses will show if the spatial hierarchy of processes discovered here will hold in general.

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SUPPLEMENTAL MATERIAL

Ecological Archives

Appendices A–D are available online: http://dx.doi.org/10.1890/14-0392.1.sm