

# Barro Colorado Island's phylogenetic assemblage structure across fine spatial scales and among clades of different ages

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**Abstract.** Phylogenetic analyses of assemblage membership provide insight into how ecological communities are structured. However, despite the scale-dependency of many ecological processes, little is known about how assemblage and source pool size definitions can be altered, either alone or together, to provide insight into how ecological diversity is maintained. Moreover, although studies have acknowledged that different clades within an assemblage may be structured by different forces, there has been no attempt to relate the age of a clade to its community phylogenetic structure. Using assemblage phylogenies and spatially explicit data for trees from Barro Colorado Island (BCI), we show that larger assemblages, and assemblages with larger source pools, are more phylogenetically clustered. We argue that this reflects competition, the influence of pathogens, and chance assembly at smaller spatial scales, all operating within the context of wider-scale habitat filtering. A community phylogenetic measure that is based on a null model derived explicitly from trait evolution theory,  $D$ , is better able to detect these differences than commonly used measures such as  $SES_{MPD}$  and  $SES_{MNTD}$ . We also detect a moderate tendency for stronger phylogenetic clustering in younger clades, which suggests that coarse analyses of diverse assemblages may be missing important variation among clades. Our results emphasize the importance of spatial and phylogenetic scale in community phylogenetics and show how varying these scales can help to untangle complex assembly processes.

**Key words:** *Barro Colorado Island, Panama; community assembly; community ecology; community phylogenetics; competition; ecophylogenetics; facilitation; habitat filtering; Janzen-Connell effects; phylogenetic scale; spatial scale; tropical forest.*

## INTRODUCTION

A major challenge for ecology is to understand how abiotic, biotic, and stochastic factors interact to filter a source pool of potential colonists down to an ecological assemblage (Vellend 2010), and to understand the spatial and temporal scales at which these processes operate (Levin 1992). This is driven, in part, by a need to explain how it is possible for so many species to coexist in highly diverse regions such as tropical forests. Among the theories that explain the maintenance of high diversity in tropical forests are Janzen-Connell effects (density-dependent recruitment; Janzen 1970, Connell 1971), the intermediate disturbance hypothesis (disturbance sufficient to facilitate coexistence without seriously degrading habitat; Connell 1978), stochastic drift (neutral theory; Hubbell 2001), and niche partitioning

along environmental gradients (Schoener 1974). Most ecologists would acknowledge that it is unlikely any single process can explain highly diverse assemblages, and that separating their relative contributions is difficult.

Community phylogenetic studies typically assess these processes within an evolutionary context by asking how closely related are the species within an assemblage, given a list of species that could plausibly be in that assemblage, i.e., the “source pool” (Webb et al. 2002, Cavender-Bares et al. 2009, Vamossi et al. 2009). Thus, under the assumption of niche conservatism (reviewed in Wiens et al. 2010), niche partitioning and habitat filtering produce phylogenetic clustering. In contrast, differential survival due to interspecific competition and lineage-specific pathogens (e.g., Gilbert and Webb 2007, Goßner et al. 2009) is expected to lead to phylogenetic over-dispersion, and stochastic neutral processes to random phylogenetic structure. By changing the spatial scale (size) of our definition of assemblage (Swenson et al. 2007, Kraft and Ackerly 2010) or source pool (Kembel and Hubbell 2006, Swenson et al. 2006, Webb et al. 2006, Lessard 2012), community phylogenetic

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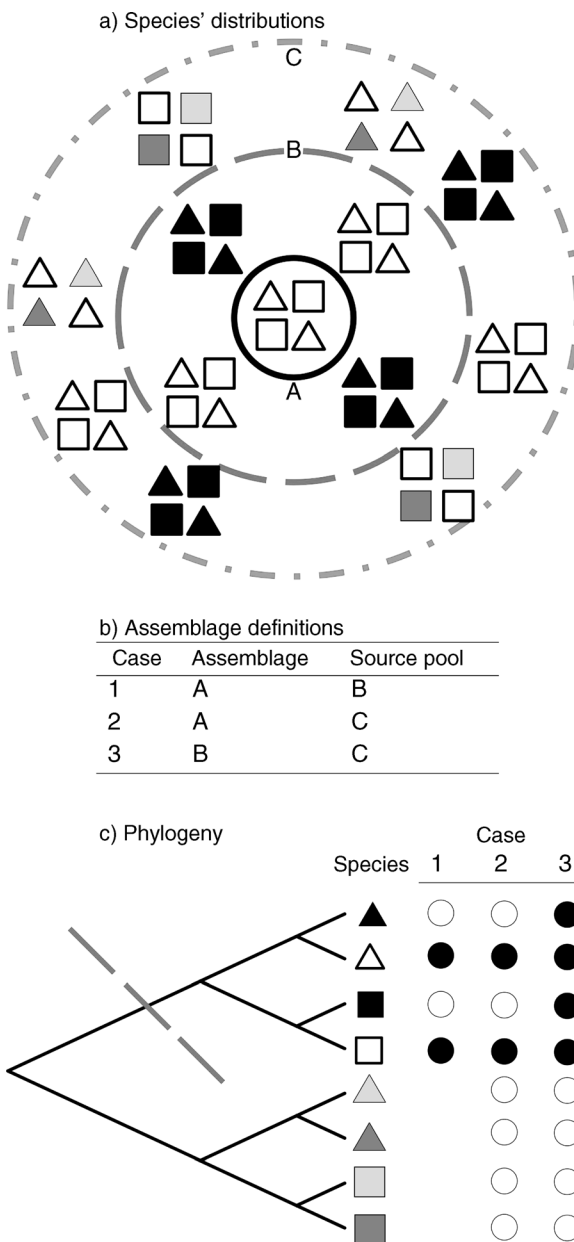


FIG. 1. The two components of spatial scale in tree communities on Barro Colorado Island (BCI), Panama. (a) Distributions of eight species in space, with three concentric circles used to delimit the assemblages. (b) Definition of the assemblages shown in panel (a) and their source pools. (c) Phylogeny of the eight species, with three columns (cases 1–3) for each of the assemblages in panel (b). In each column, species present in an assemblage’s source pool have open circles, while species also present in that assemblage have solid circles. These assemblages are referred to and described in the *Introduction*.

studies can detect the spatial scales over which these processes operate to create phylogenetic structure. However, to our knowledge, no study has examined the effect of varying both the size of an assemblage and its source pool simultaneously, which is likely to be

important if the relevant spatial scales of assembly processes are to be dissected and fully understood.

Assemblage and source pool size can influence the community phylogenetic patterns that are found and the resulting inferences (Fig. 1). Consider a small assemblage with a source pool defined by its immediate neighbors (case 1 in Fig. 1). This assemblage is phylogenetically overdispersed: its members are less closely related to each other than would be expected, given chance assembly from its source pool. However, the same assemblage in the context of a larger source pool (case 2) is more phylogenetically clustered. Its members are now more closely related to each other than would be expected, because the source pool contains more habitat types and the clades adapted to them. This pattern of phylogenetically conserved habitat preferences is found commonly (Cavender-Bares et al. 2006, Swenson et al. 2006, Willis et al. 2010, Lessard 2012). Source pools are often defined using species’ range data, but finer-scale data allow us to define source pools that highlight smaller-scale environmental variation and account for dispersal limitation.

There is an interplay between source pool and assemblage definitions: in case 3 (Fig. 1) a larger assemblage within the larger source pool is the most strongly phylogenetically clustered case of all. Simultaneously varying the spatial scale of assemblage and source pool can be more informative, and is so here because the source pool now contains those species that have a higher probability of dispersing propagules locally into an assemblage. In this example, we have isolated the local neighborhood of plants’ interactions by increasing the size of our assemblage beyond the scale at which competition, lineage-specific pathogens, and stochasticity are detectable. Assemblage size often receives little attention (but see Swenson et al. 2006, Lessard et al. 2009), perhaps because the necessarily lower number of species in smaller assemblages reduces statistical power (Heard and Cox 2007).

In recognizing that an increase in source pool size can increase the number of clades and lead to phylogenetic clustering, we implicitly acknowledge that the phylogenetic scale (the age of the clade) across which we are calculating dispersion values has changed. For example, if case 2’s dispersion value were calculated across the clade delimited on Fig. 1c with a dashed, heavy gray line, that value would be equal to that of case 1. This assemblage has not been formed by one process; local competition has taken place within the context of wider habitat-filtering, and the results at different phylogenetic scales reflect this. Using a phylogeny containing all species in a given source pool assumes that processes act identically throughout that phylogeny; yet researchers look for influential clades (e.g., Parra et al. 2010), and acknowledge different patterns of trait evolution across different phylogenetic scales (e.g., Ackerly et al. 2006, Uyeda et al. 2011). Greater phylogenetic clustering in higher taxonomic groups has been found in a meta-

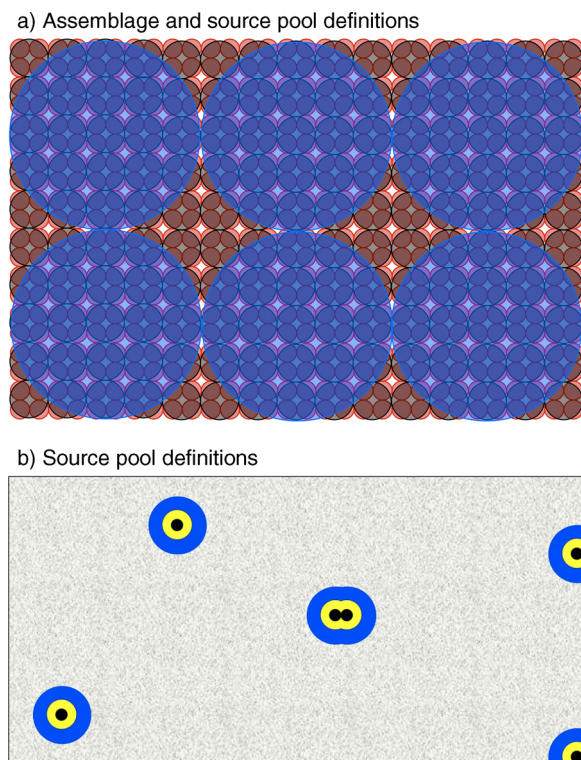


FIG. 2. Assemblage and source pool definitions. Panel (a) is to scale, but not of the whole site. It shows how the assemblages (overlapping 5, 10, and 50 m radius circles outlined in red, black, and blue, respectively) are nested within each other. Panel (b) is to scale and of the entire study site. It shows a 10 m radius assemblage (the small black circle) and three possible source pools around it: 100 m and 200 m radius circles (in yellow and blue, respectively), and all of the study site (the gray speckled box surrounding them all). Note that in some cases the circular source pools are cut by the limits of the BCI plot, which was accounted for in the analyses (see *Methods: Ecological data*).

analysis (Vamosi et al. 2009), but it is unknown whether this holds within a single community.

The 50-ha forest dynamics plot on Barro Colorado Island (BCI; Panama) offers a unique opportunity to study spatial processes, because we know the locations and species identities of all individual trees greater than 1 cm in diameter at breast height (Condit 1998, Hubbell 1999, Hubbell et al. 2005). BCI has well-documented spatial variation in the strength of density dependence (Comita et al. 2010), spatial aggregation (Condit et al. 2000), and dispersal ability (Muller-Landau et al. 2008). In addition, small-scale variation in habitat and soil types (Harms et al. 2001, John et al. 2007) and variation in phylogenetic dispersion across these habitat types (Kembel and Hubbell 2006, Kress et al. 2009, Schrege et al. 2010) has been described. Yet previous community phylogenetic studies in BCI have found no relationship between assemblage size and phylogenetic dispersion (Kembel and Hubbell 2006, Swenson et al. 2007), and have found relationships between source pool size and dispersion only at regional scales (Swenson et al. 2006).

Here, we evaluate the effect of spatial scale on phylogenetic structure by simultaneously varying the focal assemblage size and the size of the source pool from which the assemblage is drawn. We use a recently proposed measure of trait dispersion ( $D$ ; Fritz and Purvis 2010) that scales the observed measure of phylogenetic structure with simulated expectations under a null model based on an explicit evolutionary process (Brownian evolution of an underlying continuous trait) and random assembly. We find  $D$  to be more sensitive to shifts in phylogenetic structure within BCI tree communities than previously used measures (standard effect size of mean phylogenetic distance,  $SES_{MPD}$ , and of mean nearest taxon distance,  $SES_{MNTD}$ ; Kembel 2009). We find evidence of greater phylogenetic clustering in larger assemblages and assemblages with larger source pools across ecologically meaningful scales (i.e., measured in meters), and that younger clades are more phylogenetically clustered than one would expect from models of random assembly.

## METHODS

### *Ecological data*

The BCI forest dynamics plot data are freely available online (Hubbell et al. 2005), and are described in detail by Hubbell (1999). In brief, they consist of the location (to within 10 cm) and species identity of every woody free-standing tree or palm with a stem diameter  $\geq 1$  cm at breast height within the entire 50-ha plot. Data on trees recorded as alive during the 2005 census were downloaded and used for analysis. We split the data set into contiguous (but not overlapping) circular assemblages, with concentric source pool circles around them (see Fig. 2, Table 1), but used the entire species list for the “all BCI” results. Thus each assemblage had a list of species that made up its source pool, and for each of those species a binary variable indicated its presence or absence in that assemblage; note that assemblages on the edge of BCI often have their source pools cut by the edge of the plot. Because measures of phylogenetic community structure are uninformative for assemblages containing all, or all but one, species in the source pool, we excluded the three such assemblages from this analysis.

TABLE 1. Assemblage and source pool radii combinations used in these analyses of tree phylogenies on Barro Colorado Island, Panama.

Assemblage radius (m)	Source pool radii (m)
5	50, 100, all of study site
10	50, 100, all of study site
50	100, all of study site

*Notes:* We define an assemblage as the list of species found within a particular circle, and its source pool as the list of species found within another concentric circle around that. References to the size of assemblages or source pools in this paper refer to the radii of these circles.



TABLE 2. Comparison of community phylogenetic measures, with a brief description and comparison of some community phylogenetic measures.

Measure(s)	Source	Description	Notes
SES <sub>MPD</sub> /SES <sub>MNTD</sub>	Webb (2000); Webb et al. (2002); Kembel (2009)	compares observed phylogenetic distances with those under some null hypothesis	flexible null model definition; values are difficult to compare among systems
<i>D</i>	Fritz and Purvis (2010)	compares observed independent contrasts with those under a Brownian or random shuffling null model	comparable among systems; linked to trait evolution theory
Taxonomic distinctiveness	Clarke and Warwick (1998)	extension of Simpson's index to include taxonomic structure	
PSR/PSV/PSE	Helmus et al. (2007)	measures the richness, variability, and evenness of species' phylogenetic structure	comprehensive framework to assess many aspects of phylogenetic structure; no natural comparison with a given source pool
"Phylogenetic shape methods"	e.g., Heard and Cox (2007); Davies et al. (2012)	examines observed measures of phylogenetic shape, such as imbalance	
"Regression methods"	e.g., Slingsby and Verboom (2006); Willis et al. (2010)	correlates species' phylogenetic and coexistence matrices	unlike the above, operates at the level of species, such that each point in the correlation is a species-species pair
"Meta-community methods"	Peres-Neto and Legendre (2010); Pillar and Duarte (2010)	compares matrices of phylogenetic, ecological, and environmental data to assess overall structuring processes	like "regression methods," they do not produce a single value that can be compared among sites or species (and are no worse for that)

*Notes:* Measures of phylogenetic imbalance are common in the phylogenetic literature, but are relatively rarely used in the community phylogenetic literature. Regression methods, which compare species-species pairs, might allow the identification of particularly unusual species interactions within a data set. This is not intended to be an exhaustive list, and probably reflects the particular interests of the authors; in particular, terminology in quotation marks is the authors' own and not in widespread use. SES is the standard effect size of mean phylogenetic distance (MPD) and mean nearest taxon distance (MNTD); PSR, PSV, and PSE are, respectively, phylogenetic species richness, variability, and evenness.

### Phylogeny construction

Previous community phylogenetic studies have shown that results are sensitive to the phylogenetic structure of their source pool phylogeny (Kress et al. 2009, Swenson 2009), but a recent molecular phylogeny (from Kress et al. 2009) was missing some taxa, possibly introducing an ecological bias. Thus we used three different phylogenies: one modified from Kress et al. (the "Kress phylogeny"; 2009), another taken from Phylomatic (Webb et al. 2008) containing all of the species in BCI, but with less phylogenetic resolution (the "Phylomatic phylogeny"), and finally one with only the species in the Kress phylogeny but with the resolution of the Phylomatic tree (the "control phylogeny").

The Kress phylogeny was not ultrametric: its branch lengths were proportional to the rate of evolution at the three loci used to construct it. To make the tree's branch lengths proportional to divergence times, we rate-smoothed it using the Penalized-Likelihood method of Sanderson (2002) as implemented in "r8s" (Sanderson 2003) with its "Powell" algorithm, under the constraint that the root age was 1. The smoothing parameter of 0.1 was derived from cross-validation across six possible parameter values (0.1, 1, 10, 100, 1000, and 10 000). The final solution was found after 20 sets of perturbations with nudging parameters of 0.05 and 0.1, and had a flat solution gradient.

The Phylomatic phylogeny was made with "Phylomatic" (Webb et al. 2008) using the Davies et al. (2004) phylogeny as a reference. The control phylogeny was created in the same way, but using only those species also present in the Kress phylogeny. All three phylogenies are in the Supplement.

### Choice of dispersion metric

There are currently many measures of community phylogenetic dispersion, but no general consensus as to which is the best (for reviews, see Kembel 2009, Vellend et al. 2011). A dispersion metric should be sensitive to both under- and over-dispersion, and scaled such that it is comparable between study systems. Ideally, its observed values should be comparable with null distributions that are relevant to the questions of a study. We used three metrics: SES<sub>MPD</sub> (Kembel 2009), SES<sub>MNTD</sub> (Kembel 2009), and *D* (Fritz and Purvis 2010). These measures require definitions of source pool and assemblage, and so are useful for the present study of spatially delimited source pools and assemblages, but there are a variety of other measures (described in Table 2) that may be appropriate in other contexts. In the Appendix, we present spatial scale results using PSV (Helmus et al. 2007), which are qualitatively identical to the SES<sub>MPD</sub> results and so are not further discussed.

SES<sub>MPD</sub> and SES<sub>MNTD</sub> (Kembel 2009) are perhaps the most commonly used measures of phylogenetic

dispersion, and are directly related to the popular NRI (net relatedness index) and NTI (nearest taxon index) measures (Webb et al. 2002). They are known to have some biases (Kembel 2009), and we describe how they can perform poorly when comparing assemblages. As Eq. 1 shows,  $SES_{MPD}$  compares the observed mean phylogenetic distance (MPD) with the mean value observed under some null hypothesis ( $MPD_r$ , where subscript  $r$  stands for random), correcting for the standard deviation of that mean ( $SD_{MPD_r}$ ).  $SES_{MNTD}$  is analogous to  $SES_{MPD}$  (Eq. 2), but is based around the mean nearest taxon distance (MNTD), and so is sensitive only to the phylogenetic distance between each species and its closest relative in an assemblage. Both incorporate null distributions to control for phylogenies' differences in phylogenetic structure, but in essence calculate a test statistic; each can tell us when there has been a significant departure from a null distribution, but not the magnitude of that departure. By analogy, to assess the significance of differences in the means of two distributions one would divide that difference by its standard error to calculate a  $t$  statistic, but there is no unique mapping of a  $t$  statistic onto the differences in those means. Groups cannot be compared on the basis of test statistics, so  $SES_{MPD}$  and  $SES_{MNTD}$  values cannot be compared between assemblages:

$$SES_{MPD} = -1 \times \frac{MPD - MPD_r}{SD_{MPD_r}} \quad (1)$$

$$SES_{MNTD} = -1 \times \frac{MNTD - MNTD_r}{SD_{MNTD_r}} \quad (2)$$

Note that  $D$  (Fritz and Purvis 2010) offers an alternative that can compare dispersion values among assemblages. Originally proposed in another context,  $D$  is the only measure of phylogenetic dispersion based upon two null distributions: one in which community presence is phylogenetically random, and one in which it is determined by the value of an underlying continuous variable that evolves along the branches of a phylogeny by Brownian motion. We consider this to be a better way to control for phylogenetic structure; while  $SES_{MPD}$  averages out phylogenetic structure once its null distributions have been constructed,  $D$  incorporates phylogenetic structure when generating its Brownian null model.

A full account of  $D$  is available in Fritz and Purvis (2010), and it is defined in Eq. 3. Briefly, the method is based on the calculation of phylogenetically independent contrasts (Felsenstein 1985), whereby each node in a phylogeny is valued according to the mean of its descendent nodes, these having been weighted according to the lengths of the branches leading to them. These calculations are performed once for the observed values, giving species in the assemblage a value of 1 and those absent from the assemblage, but present in the source pool, a value of 0; the sum of these observed contrasts is

denoted  $d_{obs}$ . A maximally clumped trait will be in the same character state in all related species, whereas a maximally overdispersed trait cannot, causing  $d_{obs}$  to be lowest for clumped communities and highest for overdispersed communities. Two random distributions (denoted by subscript  $r$ ) are then generated, the first by permuting the observed values across the phylogeny and summing its contrasts (to obtain  $d_r$ ). For the other, the evolution of many continuous traits is simulated along the phylogeny under Brownian motion, a threshold applied to each trait to produce a series of binary traits with the same prevalence as the observed community presences (a Brownian threshold model; Felsenstein 2005), and the contrasts are again summed to obtain  $d_b$ .  $D$  is therefore independent of the shape and size of the phylogeny.  $D$  values greater than 1, less than 1, or less than 0 indicate greater than random, less than random, or less than expected under a Brownian model of trait evolution or levels of phylogenetic dispersion, respectively:

$$D = \frac{\sum d_{obs} - \text{mean}(\sum d_b)}{\text{mean}(\sum d_r) - \text{mean}(\sum d_b)} \quad (3)$$

#### Analysis

All analyses were conducted using R (R Development Core Team 2010). For the spatial analyses,  $D$  values were calculated using the “phylo.d” function in the package “CAIC” (Orme et al. 2009); for the phylogenetic scale analyses, the function “phylo.d.subsets” was written for the package “caper” (Orme et al. 2011).  $SES_{MPD}$  values were calculated using the “ses.mpd” function in the package “picante” (Kembel et al. 2010) under the “richness” null model. This null model is most similar to those of  $D$  and is appropriate for comparisons between assemblages with different source pools. The analyses were split into two parts: whether assemblage and source pool size affect phylogenetic dispersion (spatial scale), and the relationship between the age of a clade and its phylogenetic dispersion within an assemblage phylogeny (phylogenetic scale).

*Spatial scales.*—Mixed-effects models were used to account for spatial pseudo-replication and nestedness in  $D$  and  $SES_{MPD}$ , with assemblage and source pool size treated as fixed effects, and the nesting of the 50-, 10-, and 5-m circles fitted as random effects (using “lmer”; Bates and Maechler 2010). Although model estimates were computed under restricted maximum likelihood (REML), we compared models including assemblage and source pool size with null models containing only the random-effect terms under maximum likelihood (ML) using likelihood ratio tests (LRT) and comparing models' AIC values. Model estimates are contingent upon fixed-effect structure under REML, so comparison of different fixed-effects structures should be performed under ML, but estimation of model parameters is more

accurate under REML (Crawley 2013); thus REML parameter estimates are reported.

We used quantile regressions (in “quantreg”; Koenker 2011) to show whether assemblage and source pool size affect the distribution of  $D$  and  $SES_{MPD}$ , using the Frisch-Newton interior point method due to the large size of the data set. We estimated the 10th, 25th, 50th, 75th, and 90th quantiles, and used the “rank” method to calculate their standard errors.

A separate analysis was performed, excluding those assemblages with source pools that were constrained by the edge of the plot, and using fewer quantiles in the quantile regression (the 25th, 50th, and 75th) because there were fewer data. The results were qualitatively identical to those of the complete analysis, and are presented in the Appendix. In addition, we performed simulations looking at the distribution of  $D$  values in assemblages with very few species; these show that  $D$  performs well in small assemblages (fewer than five species) and source pools (fewer than 25 species); these simulations are presented in the Appendix.

*Phylogenetic scale.*—The large number of clades in the three phylogenies meant that calculating dispersion values for every clade in each assemblage phylogeny was not feasible.  $D$  values were thus calculated for a random subset of each assemblage size, picking 30 assemblages from each assemblage size class or the total number of assemblages of that size, whichever was smaller. In total, we chose 105 assemblages and used a phylogeny containing all species in the data set.

In extremely small phylogenies,  $D$  has lower statistical power (Fritz and Purvis 2010), so  $D$  estimates for clades containing fewer than 10 nodes were excluded from the analysis. Because  $D$ 's variance is greater in smaller clades, it is difficult to make solid inferences about changes in dispersion across clade age, because we might expect younger clades to have fewer species. Thus the observed relationship between clade age and dispersion in each assemblage was compared with five random assemblages with the same number of, but randomly assigned, present species (525 randomizations in total).

We fitted a generalized least squares (GLS) model (using “lmer”; Bates and Maechler 2010) with an exponential error structure based on clade age, and fixed effects of the interaction between clade age, whether the data were observed or simulated, and the assemblage from which the data were taken. Although model estimates were calculated under REML, we compared this model under ML with a null model in which dispersion was a function of clade age and its interaction with the assemblage from which the data were taken. Rejection of the null model indicates not just that phylogenetic dispersion is related to the phylogenetic scale across which it was calculated, but also that the relationship is different than the random expectation for that particular phylogeny.

## RESULTS

### *Spatial scales*

The results using each of the three phylogenies were qualitatively identical, so the results from the Phylo-matic and control phylogenies are presented only in the Appendix.  $D$  values were lower in larger assemblages and assemblages with larger source pools, reflecting an increase in phylogenetic clustering (Fig. 3a).  $SES_{MPD}$  and  $SES_{MNTD}$  values did appear to significantly depart from zero (Tables 3 and 4b, c), but their departures showed no systematic pattern with regard to assemblage or source pool size (Fig. 3b, c).

Mixed-effects models support an increase in phylogenetic clustering in larger assemblages and source pools, albeit with small effect sizes (Table 3). The upper bounds of the  $D$  distributions increase in smaller assemblages and source pools, with a reasonable proportion of their values being greater than 1, while the lower bounds remain relatively constant. Quantile regressions statistically support these distributional changes, and generally show larger effect sizes than do the mixed-effects models (Table 4a). However, they do not show a systematic effect of spatial scale on  $SES_{MPD}$  (Table 4b) or  $SES_{MNTD}$  (Table 4c).

### *Phylogenetic depth*

There is a negative relationship between variance and clade age in both the simulated and observed assemblages, as expected (Fig. 4). Each assemblage's linear slope of  $D$  against clade age is greater in the observed data than in the simulated data, supporting a (modest) tendency for more phylogenetic clustering in younger clades (Fig. 5). A GLS fitting separate slopes and intercepts for observed and simulated assemblages fits the data significantly better than a model where they had the same slopes (AIC = 4072.41 vs. 4360.03; likelihood ratio test  $P < 0.0001$ ). These trends are absent from the Phylo-matic and control phylogenies (Appendix), probably due to their lack of within-genus and within-family resolution.

## DISCUSSION

We have presented evidence that larger assemblages and assemblages with larger source pools are more phylogenetically clustered. This suggests a model of ecological assembly where competition and chance colonization take place in the context of wider-scale habitat filtering. Although these patterns are common in community ecology, this is the first demonstration of the simultaneous and opposing influences of assemblage and source pool definition on phylogenetic community structure. This explanation is contingent on niche conservatism, but tree functional traits are known to be phylogenetically conserved in BCI (Swenson et al. 2007). Thus phylogenetic distance is plausibly related to ecological distance, suggesting that phylogenetic clustering reflects habitat filtering, that over-dispersion

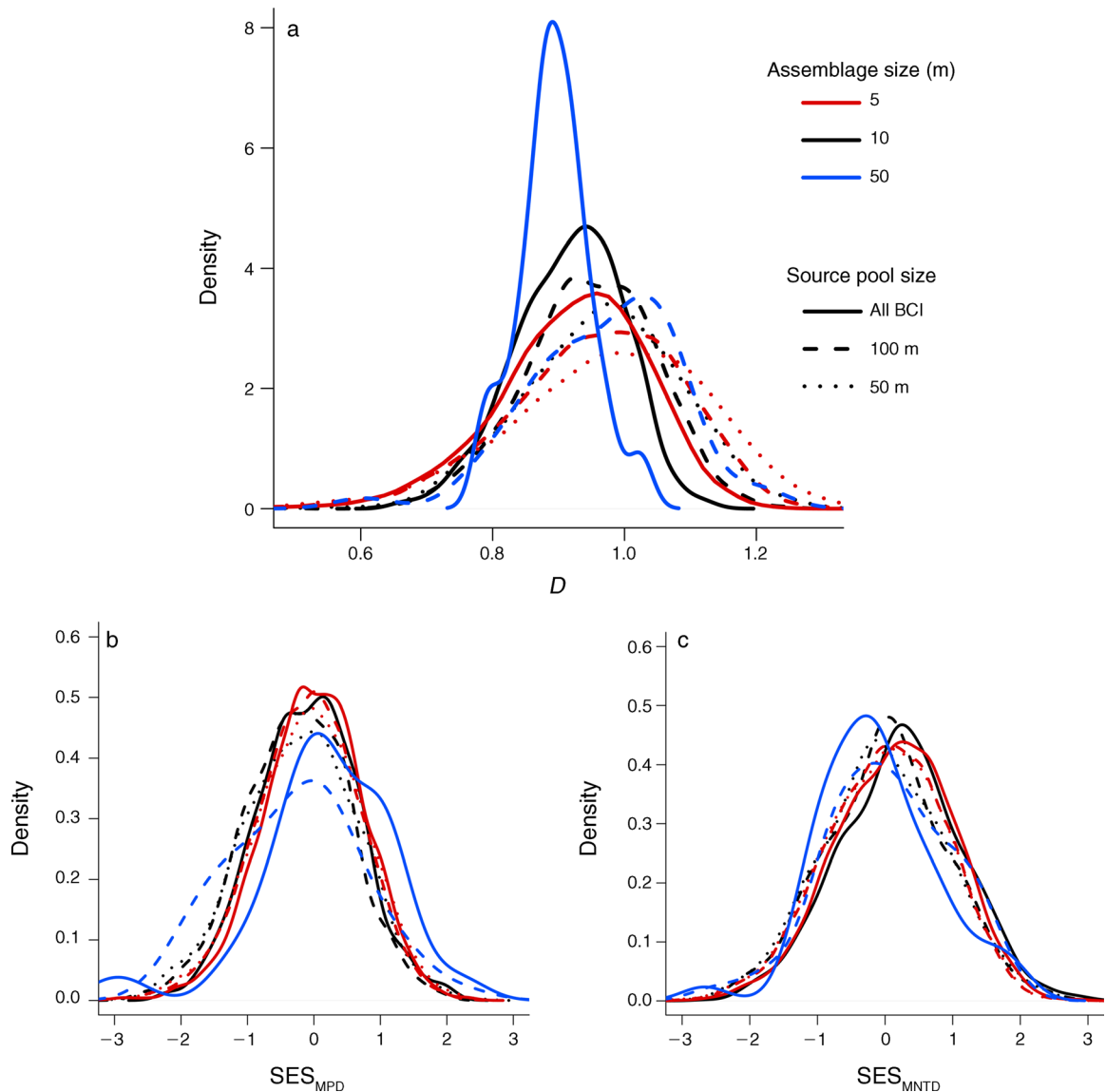


FIG. 3. Smoothed density plots of  $D$  (a community phylogeny measure),  $SES_{MPD}$ , and  $SES_{MNTD}$  (standard effect size of mean phylogenetic distance and mean nearest taxon distance). In (a), smaller assemblages and source pools (i.e., with a shorter radius) have higher  $D$  values, consistent with a shift from assemblages dominated by phylogenetic clustering to assemblages dominated by phylogenetic over-dispersion and random assembly. However, in (b) and (c), there is no shift in dispersion value according to assemblage size or source pool size. For details, see *Results: Spatial scales*. The key is common to all panels.

reflects competition or lineage-specific pathogens, and that random structure reflects stochastic drift or a mixture of clustering and over-dispersion. In addition, we show that younger clades are weakly, but significantly, more phylogenetically clustered within an assemblage. We caution that there are plausible alternative mechanisms for the patterns described, and that naïvely mapping phylogenetic pattern onto process is dangerous (reviewed in Mayfield and Levine 2010). However, alternative explanations for pattern do not detract from the main results of this study: that spatial scale can be partitioned into two components using a

phylogenetic approach, and that phylogenetic dispersion varies with clade age.

#### *Spatial scale*

Within the context of larger source pool areas, assemblages are more phylogenetically clustered. Although the effect sizes in our mixed-effects models may seem small, fitting a level of the random effect term for each 5-, 10-, and 50-m assemblage is a conservative way of dealing with spatial autocorrelation, and is likely to reduce the variation attributable to assemblage and source pool size. BCI's plant composition is known to vary with soil nutrients (John et al. 2007), and there is

TABLE 3. Mixed-effects models of the dispersion measures  $D$ ,  $SES_{MPD}$ , and  $SES_{MNTD}$  across BCI: estimated values (mean  $\pm$  SE) for each assemblage/source pool combination.

Assemblage radius (m)	Source pool radii (m)	$D$	$SES_{MPD}$	$SES_{MNTD}$
5	50	0.98 $\pm$ 0.0059	-0.05 $\pm$ 0.0247	-0.049 $\pm$ 0.0247
5	100	0.95 $\pm$ 0.0059	-0.08 $\pm$ 0.0247	-0.08 $\pm$ 0.0247
5	all BCI	0.92 $\pm$ 0.0059	0.02 $\pm$ 0.0247	0.02 $\pm$ 0.0247
10	50	0.97 $\pm$ 0.0083	-0.17 $\pm$ 0.0369	-0.17 $\pm$ 0.0369
10	100	0.95 $\pm$ 0.0083	-0.21 $\pm$ 0.0369	-0.21 $\pm$ 0.0369
10	all BCI	0.92 $\pm$ 0.0083	-0.04 $\pm$ 0.0369	-0.04 $\pm$ 0.0369
50	100	0.97 $\pm$ 0.0160	-0.17 $\pm$ 0.0977	-0.27 $\pm$ 0.0969
50	all BCI	0.89 $\pm$ 0.0160	0.29 $\pm$ 0.0968	0.28 $\pm$ 0.0969

Notes: Smaller assemblages and source pools have greater  $D$  values.  $D$  (AIC = -27 732 vs. 26 643;  $P$  value of likelihood ratio test < 0.0001),  $SES_{MPD}$  (AIC = 39 861 vs. 39 997;  $P$  value of likelihood ratio test < 0.0001), and  $SES_{MNTD}$  (AIC = 44 760 vs. 44 527;  $P$  value of likelihood ratio test < 0.0001) models showed statistically significant effects of source pool and assemblage size when compared with a null model containing neither variable.

documented variation in community type (Harms et al. 2001), so our result supports the idea that niche partitioning and habitat filtering may play a role in maintaining BCI's high diversity. Dispersal limitation might be expected to affect our results at scales beyond 100 m, especially as this is beyond the mean dispersal distance of most species modeled by Muller-Landau et al. (2008) in BCI. However, dispersal limitation should be random with respect to phylogeny: even sister species are likely to disperse independently of one another

(unless seeds are dispersed by common vectors; e.g., Poulin et al. 1999).

The higher dispersion within assemblages of smaller radius suggests that density-dependent processes, including increased mortality among phylogenetically closely related individuals due to interspecific competition and lineage-specific pathogens, may help to maintain diversity within BCI. To our knowledge, this is the first report of shifts in dispersion at such fine scales in BCI (c.f. Swenson et al. 2007) or elsewhere (c.f. Kraft

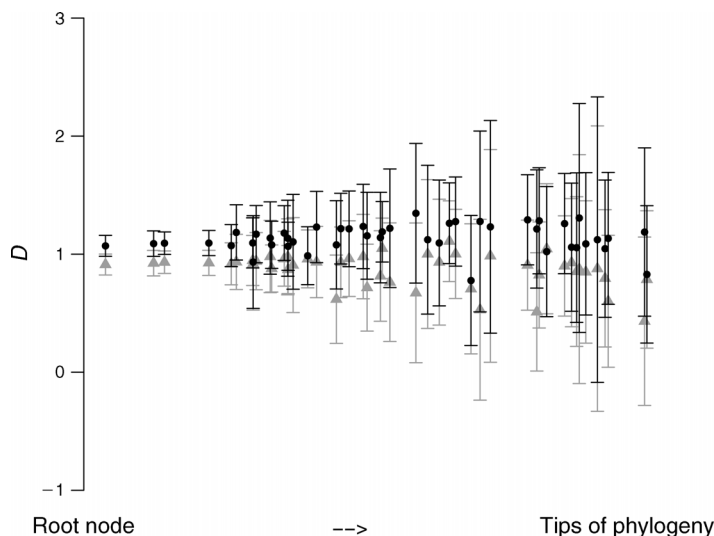
TABLE 4. Quantile regression of  $D$  values across BCI: estimates for each of the five measured quantiles ( $\tau$ ) of the distributions of  $D$  values in each of the three phylogenies.

Assemblage	Source pool	$\tau = 0.10$	$\tau = 0.25$	$\tau = 0.50$	$\tau = 0.75$	$\tau = 0.90$
a) $D$ values						
5	50	0.78	0.88	0.99	1.09	1.16
5	100	0.78	0.87	0.97	1.05	1.12
5	all BCI	0.77	0.85	0.93	1.00	1.06
10	50	0.81	0.89	0.97	1.05	1.12
10	100	0.82	0.88	0.95	1.02	1.07
10	all BCI	0.81	0.86	0.92	0.98	1.02
50	100	0.81	0.86	0.89	0.92	0.96
50	all BCI	0.82	0.89	0.98	1.04	1.09
Range		0.05	0.04	0.10	0.17	0.20
b) $SES_{MPD}$ values						
5	50	-1.14	-0.62	-0.05	0.50	0.98
5	100	-1.10	-0.61	-0.07	0.43	0.89
5	all BCI	-0.98	-0.50	0.00	0.51	0.96
10	50	-1.29	-0.80	-0.18	0.39	0.87
10	100	-1.24	-0.80	-0.23	0.31	0.70
10	all BCI	-1.05	-0.59	-0.07	0.43	0.83
50	100	-1.58	-0.93	-0.16	0.35	1.08
50	all BCI	-0.91	-0.27	0.20	0.91	1.25
Range		0.67	0.66	0.43	0.60	0.55
c) $SES_{MNTD}$ values						
5	50	-1.18	-0.62	0.03	0.64	1.12
5	100	-1.14	-0.58	0.04	0.64	1.11
5	all BCI	-0.99	-0.45	0.19	0.76	1.26
10	50	-1.21	-0.63	-0.04	0.64	1.17
10	100	-1.18	-0.60	0.02	0.59	1.18
10	all BCI	-0.92	-0.39	0.24	0.82	1.39
50	100	-0.98	-0.64	-0.01	0.64	1.26
50	all BCI	-1.07	-0.70	-0.19	0.41	1.21
Range		0.29	0.31	0.43	0.41	0.28

Notes: The range of estimates is greater for higher quantiles of  $D$ , but not  $SES_{MPD}$ . Standard errors are shown in the Appendix.



FIG. 4. Phylogenetic depth plots of  $D$  for the observed and simulated assemblages in the Kress phylogeny. The randomized assemblages are plotted in black, and the real data are in gray. Each black circle or gray triangle represents a clade's median value, and error bars represent the standard deviations of the data. The differences between the two distributions are slight, but a tendency for lesser  $D$  values in the observed assemblages is noticeable, as is the predicted decrease in variance with clade age.



and Ackerly 2010). Density-dependent recruitment is well-demonstrated within BCI (e.g., Harms et al. 2000, Comita et al. 2010), although distinguishing between competition and enemy-mediated Janzen-Connell effects is difficult. Lineage-specific pathogens, which are within the spirit of the Janzen-Connell hypothesis, have been found in BCI (Gilbert and Webb 2007). Using our method it is difficult to distinguish between the effects of competition and lineage-specific pathogens, and the widening of smaller assemblages' dispersal distributions in Fig. 3a makes it unlikely that the same processes are taking place in every assemblage. Indeed, the larger number of  $D$  values close to 1 in smaller assemblages would be consistent with neutral dynamics at smaller scales (Hubbell 2001).

It is unlikely that tendency for the greater dispersion at finer spatial scales is driven by facilitation between ecologically distinct, distantly related species (sensu Verdú and Valiente-Banuet 2008, Verdú et al. 2009). Facilitation is classically associated with severe environments, such as deserts and alpine regions (Brooker et al. 2008), or where there is particularly high consumer pressure or physical stress (Bertness and Callaway 1994); BCI is not such a system. Common mycorrhizal networks also facilitate growth when shared among species, but usually operate across larger spatial scales than those in which greater dispersion was observed (Selosse et al. 2006), and thus should not be driving patterns in the smaller assemblages.

Our results are unlikely to be an artifact of lower replication at high spatial scales; 50 assemblages of 50 m diameter is a reasonable level of replication for an ecological study. In addition, our tests of dispersion values in smaller assemblages show that the fewer species in each smaller assemblage are unlikely to have biased the results (Appendix). Were the smaller assemblages' results entirely random, source pool size would not affect them. It is, however, worth noting that this

study ignores belowground diversity, which can be high in BCI (Jones et al. 2011), and that plants can interact below ground over large spatial scales.

#### Choice of dispersion measure

In keeping with previous work on BCI (Swenson et al. 2006),  $SES_{MPD}$  and  $SES_{MNTD}$  plots showed no consistent pattern across these fine spatial scales; by contrast,  $D$  varied systematically with source pool and assemblage size. Additionally,  $D$ 's spatial scale results were consistent across all three phylogenies (Supplement), whereas there was little apparent pattern to  $SES_{MPD}$  and

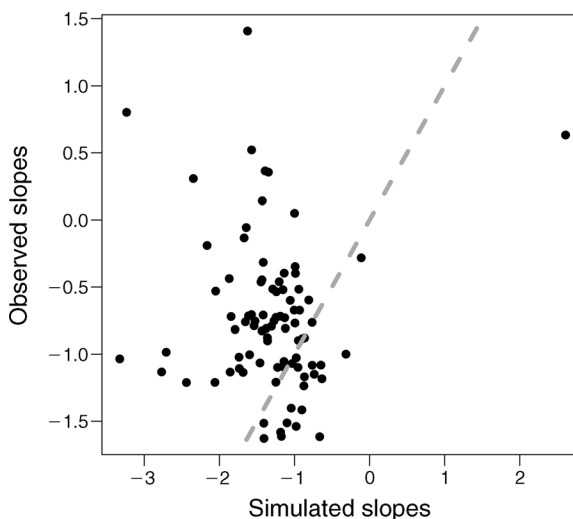


FIG. 5. Plot of observed and simulated slopes for regressions of  $D$  on clade age. The dashed line passes through the origin with a slope of 1 (the null expectation). That so many of the Kress phylogeny's observed slopes are greater than the simulated slopes suggests more phylogenetic clustering in younger clades in BCI, even accounting for the increase in variance in younger clades. These slope estimates are taken from the GLS models (see *Results: Phylogenetic depth*).

SES<sub>MNTD</sub>, suggesting that *D* was better at extracting signal from the BCI data set. This may be because the detected differences were in the degree of phylogenetic clustering; *D* is based around an explicit model of phylogenetic similarity (the Brownian model) and thus is likely to be more sensitive to such shifts. SES<sub>MNTD</sub> differs in 50 m radius assemblages with source pools that consist of the whole of BCI or the local area (Fig. 3c), which is interesting given the trend for younger clades to be more phylogenetically clustered (which we will discuss further). We note that, although we find that *D* is most sensitive to phylogenetic structure in this data set, alternative approaches such as the “meta-community” and “regression” methods described in Table 2 may provide a more natural way to incorporate species trait and environmental data into a single analysis.

#### *Phylogenetic scale*

The tendency for younger clades to be more phylogenetically clustered within assemblages shows that the effect of phylogenetic scale is not restricted to meta-analyses (e.g., Vamossi et al. 2009). The trend is weak, but is unlikely to be a statistical artifact of the ecological data because it is absent from the Phylomatic and control phylogenies' results (Supplement), which are based on the same ecological data. Moreover, because the data were compared with null simulations conducted across the observed phylogeny, they are unlikely to be an artifact of this particular phylogenetic topology. We argue the Kress phylogeny permits a more sensitive test of phylogenetic scale than the other phylogenies: it is bifurcating and thus has more power to detect the age at which changes in pattern occur. Non-monophyletic taxa may bias the topology of a phylogeny derived from Phylomatic because the method relies on taxonomy.

Increased phylogenetic clustering within younger clades could result from a number of (not mutually exclusive) hypotheses. Younger clades may contain species that are more finely partitioned within niche space and, as such, are not brought into excluding competition. Alternatively, if species in younger clades do have overlapping niches, they may have speciated through allopatry and are now in secondary contact, or diversification in these younger clades may have been driven by evolution along other niche dimensions, perhaps to avoid pathogens and parasites. This latter possibility is particularly interesting given our previous discussion of over-dispersion at finer spatial scales and the potential for Janzen-Connell effects in BCI. Simultaneously confronting ecological and phylogenetic data with more explicit mechanistic models that include speciation and extinction parameters would provide a more powerful test of how these dynamics change through the phylogeny.

Our work is complementary to that of Parra et al. (2010), who showed that particular clades can drive a dispersion value, and to that of Schreeg et al. (2010), who found variation in clades' responses to soil and

habitat types within BCI. For a particular clade to be different from the rest of the phylogeny necessarily implies variation among clades, and we extend their results by showing that filtering processes can extend throughout an entire community phylogeny, even increasing in strength in younger clades. We emphasize not just that there is variation in phylogenetic dispersion with clade age in this case, but also that there is variation among clades in general. This variation may be the imprint of evolutionary processes on present-day ecology, and warrants continued study.

#### *Conclusion*

Ecologists delimit the communities they study both spatially and phylogenetically. It is unsurprising that a single dispersion value of one definition of assemblage, or of one taxonomic delimitation of study species (e.g., “the plants”), does not perfectly describe a system. We have shown that community phylogenetic tools can help to distinguish among processes operating across spatial scales, but whether this is the case for other systems and with other taxa is an open question. Coupling our understanding of how phylogenetic structure varies across spatial and phylogenetic scales provides hope that ecologists can link observed ecological patterns (e.g., phylogenetic clustering) with the evolutionary processes (e.g., adaptive radiation) that generated species. To explore such questions, and not merely to contrast the phylogenetic dispersion of ecological communities, is one of the central aims of community phylogenetics.

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## SUPPLEMENTAL MATERIAL

### Appendix

Supplementary analyses described in the body of the manuscript: analyses of Barro Colorado Island's structure using PSV, and analyses of *D*, *SES<sub>MPD</sub>*, *SES<sub>MNTD</sub>*, and PSV excluding assemblages at the edge of the forest plot ([Ecological Archives E094-264-A1](#)).

### Supplement

Kress, phylomatic, and control phylogenies, in Newick format, used in the analyses ([Ecological Archives E094-264-S1](#)).