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Phylogenetic diversity–area curves

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Abstract. Phylogenetic diversity–area curves are analogous to species–area curves and quantify the relationship between the phylogenetic diversity of species assemblages and the area over which assemblages are sampled. Here, we developed theoretical expectations of these curves under different ecological and macroevolutionary processes. We first used simulations to generate curves expected under three ecological community assembly processes: species sorting, where species have distinct environmental preferences; random placement, where species have no environmental preference but vary in their prevalence across communities; and limited dispersal, where species have no environmental preference but vary in their ability to disperse. Second, we simulated curves expected across regions (e.g., across oceanic islands) that are derived from colonization among regions, within-region speciation, and extinction. We also computed curves for two data sets, one on forest plots along an elevation gradient and the other on Caribbean island *Anolis* lizards. Of the three ecological processes, only species sorting produced strong relationships between phylogenetic diversity and area. The forest plot curves matched the species-sorting expectation, but only when phylogenetic repulsion (that caused closely related species to be found in similar habitats but not in the same plots) was also included in the simulation. Strong relationships between regional phylogenetic diversity and area were simulated if species were derived only from within-region speciation; colonizations among regions obscured the pattern. Similarly, larger Caribbean islands had more within-island speciation and contained more *Anolis* phylogenetic diversity than smaller islands, but colonizations among islands obscured this relationship. This work furthers our understanding of the processes that govern the phylogenetic diversity of ecological communities and biogeographic regions.

Key words: Anolis; *elevation; environmental gradient; island biogeography; Mt. Hood, Oregon, USA; phylogenetic community structure; phylogeny; random placement; spatial scale; species area relationship; species richness; species sorting*.

Introduction

A general pattern in ecology is that the number of species found in a geographical area increases with the size of the area. This pattern, termed the species–area curve (or the species–area relationship, SAR) has been recognized since the 19th century and is important for many issues in ecology, biogeography, evolution, and conservation (Rosenzweig 1995, Lomolino 2000, Tjørve 2003, Scheiner et al. 2011). The mechanisms underlying any specific SAR can vary (Palmer and White 1994, Drakare et al. 2006). Curves derived from data of small grain and extent (e.g., plots in a forest) tend to reflect ecological processes such as local-scale dispersal, habitat suitability, and species interactions. Curves built from data of coarse grain and broad extent (e.g., islands within a sea) tend to reflect macroevolutionary processes such as colonizations and extinctions, and allopatric and in situ speciation (Rosenzweig 1995).

The two main ecological processes that generate SARs are species sorting and random placement; these have been labeled the habitat–diversity and passive-sampling hypotheses, respectively (Williams 1943, 1964, Connor and McCoy 1979, Coleman et al. 1982). Random placement occurs when individuals of every species are randomly distributed among areas; populations are well mixed (Fisher et al. 1943). As greater area is sampled, there is an increasing chance that one or more individuals from a species are found, and thus, sampled species richness increases with area. Plausible SARs can be simulated by a simple model in which individual dispersal/establishment across sites on a landscape depends solely on the relative prevalence of species in the landscape (Coleman et al. 1982). In contrast, species sorting occurs when species have different environmental requirements, and as more area is sampled more distinct habitats and more species adapted to those habitats are found (Williams 1964). Under species sorting, individuals tend to be spatially

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clustered with their conspecifics in suitable environments. Species sorting is a niche-based process; however, spatially clustered conspecifics, as found under species sorting, can also be caused by neutral processes such as stochastic birth/death, limited dispersal, mass effects, and self-similar spatial aggregation (Harte et al. 1999, Plotkin et al. 2000, Hubbell 2001, He and Legendre 2002, Leibold et al. 2004, O'Dwyer and Green 2009). Thus, determining if a SAR is caused by niche, random, and/or neutral processes requires more information than is contained in a species–area curve.

Information on the phylogenetic relationships of species may help determine the ecological processes that underlie SARs. Niche-based processes such as species sorting may result in phylogenetic patterns in species distributions across communities because species phenotypes, niches, and ecology reflect evolutionary history (Harvey and Pagel 1991, Ackerly and Reich 1999, Prinzing et al. 2001, Webb et al. 2002, Blomberg et al. 2003, Donoghue 2008, Wiens et al. 2010). For example, closely related species may have similar environmental tolerances and similar resource requirements. Closely related species might thus be found in areas of similar environment, but not in the same communities within an area due to competition over similar resources (Elton 1946, Helmus et al. 2007*b*, Mayfield and Levine 2010, and many others). Thus, closely related species may show differing levels of spatial aggregation at different spatial scales (Swenson et al. 2006). Understanding how phylogenetic diversity changes with increased sampling area (what we term the phylogenetic diversity–area relationship, PDAR) may indicate if biodiversity was generated by niche-based processes (See Davies et al. 2012 and Peres-Neto et al. 2012 for other approaches). Here, we use the term PDAR to indicate any described relationship between phylogenetic diversity and area, and the term phylogenetic diversity–area curve to mean a quantitative, graphical, and/or mathematical representation of a PDAR, as suggested by Scheiner et al. (2011) when defining SARs and species–area curves.

Phylogenetic diversity–area curves may also elucidate the determinants of coarse-grained/broad-extent SARs such as among oceanic islands where colonization, extinction, and speciation play dominate roles. Extinction rates are hypothesized to be inversely proportional to population sizes, and population size is assumed to positively correlate with area. The overall extinction rate of species should thus be lower for large areas (Preston 1960, 1962*a*, *b*, MacArthur and Wilson 1963, 1967). Large areas might also have higher immigration rates (Gilpin and Diamond 1976, Simberloff 1976). Together, these predictions, termed the area-per-se hypothesis, create the expectation that larger areas contain more species than smaller areas (Connor and McCoy 1979). In addition, biogeographic regions of larger area tend to produce more species in situ than smaller regions. In situ speciation can occur through a combination of allopatric, sympatric, and peri-/parapatric events (Heaney 1999, Lomolino 2000). For example, Losos and Schluter (2000) found greater richness of *Anolis* lizard species on larger Caribbean islands compared to smaller islands due to diversification rates (i.e., in situ speciation minus extinction) being higher on the larger islands. However, other variables such as isolation may override any relationship between in situ speciation, phylogenetic diversity, and area. Small, isolated regions may have few colonists, and thus the biota may be derived mostly by in situ speciation as has been found for large, less isolated regions (Gillespie et al. 2008, Kisel and Barraclough 2010). Regardless, regions with species derived mostly from in situ speciation should contain phylogenetically closely related species in contrast to regions whose species are mainly derived from colonizations from outside regions. The PDARs of island biota may thus be affected by a balance of colonizations to in situ speciation (Gillespie 2004), and while area may affect this balance, other factors can as well.

Phylogenetic diversity–area relationships and curves have been little studied. It is unknown how PDARs differ under various ecological and macroevolutionary processes, if constructing phylogenetic diversity–area curves can elucidate mechanisms that determine biodiversity, and what methods are best for constructing curves for empirical data sets. Rodrigues and Gaston (2002) explored how the phylogenetic diversity of bird assemblages increases as more land area is selected to preserve. Their goal was to choose the fewest number of sites that maximize phylogenetic diversity; therefore, they chose a metric of phylogenetic diversity that always increases with species richness, the sum of the total phylogenetic branch lengths (Faith 1992). Morlon et al. (2011) derived an expectation under a random community assembly model for how this same metric changes with area. Both studies found that phylogenetic diversity always increases with area. However, because both studies used a metric of phylogenetic diversity that always increases with species richness, it was impossible to separate SARs from PDARs. Other studies have used null models to factor out possible changes in phylogenetic community structure that are caused by changes in species richness (e.g., Swenson et al. 2006); these studies have led to the tentative conclusion that as spatial area and species richness increases, communities should contain more closely related species than expected from null models (Cavender-Bares et al. 2009). Thus, based on previous work, phylogenetic diversity–area curves might be expected either to increase with area if a metric that correlates positively to species richness is used or to decrease with area if the metric is used with a null model to factor out patterns generated by changes in species richness (e.g., net relatedness index, NRI; Webb et al. 2002).

Here, we developed theoretical expectations for phylogenetic diversity–area curves built on data from ecological community assembly models of species sorting, random placement, and limited dispersal; and

macroevolutionary models that simulated regional species pools arising from a combination of extinctions, colonizations, and in situ speciation. We then built curves for two empirical data sets. The first data set is for plant assemblages in plots sampled across a large elevation gradient. We chose this data set because it is of a grain and extent at which ecological processes typically determine the shapes of SARs. Species sorting across the elevation gradient likely occurs, as it does for most plant communities (e.g., Whittaker 1960), but the data set is of such an extent that metacommunity and neutral processes affected by limited dispersal might also occur (Leibold et al. 2004, Stevens 2006). The second data set is for *Anolis* lizard assemblages that have evolved across Caribbean islands, the system where the effect of in situ speciation on SARs was first documented (Losos and Schluter 2000). This data set is of the grain and extent at which macroevolutionary processes largely determine SARs.

Methods

Constructing phylogenetic diversity–area curves

We built phylogenetic diversity–area curves with the phylogenetic species variability metric (PSV) that measures the phylogenetic diversity of a species assemblage as the expected variance of a hypothetical trait that evolves in a Brownian motion process along the branches of the assemblage phylogeny:

$$\mathrm{PSV} = \frac{n\mathrm{tr}C - \Sigma C}{n(n-1)} \quad (1)$$

where n is community species richness, $\mathbf{C}$ is the community phylogenetic covariance matrix, which is a submatrix of the covariance matrix of the species pool phylogeny (i.e., all the species in a data set), and tr$C$ and ΣC are the sum of the diagonal elements and sum of all the elements of $\mathbf{C}$, respectively. All phylogenetic diversity metrics are bounded since they are calculated from a defined species pool with a defined phylogenetic tree; PSV is standardized to vary between zero when species are closely related and one when species are distantly related. Given a pool, the PSV metric has an analytically derived statistical expectation that is independent of species richness (Helmus et al. 2007*a*), and therefore, the observed area curves calculated using PSV are not spurious artifacts of a statistical relationship between species richness and area.

Appropriate methods to construct species–area curves depend on the sampling design and structure of the underlying data sets (Scheiner et al. 2011). For simplicity, in constructing phylogenetic diversity–area curves, we do not address data sets that have nested sampling units. For data with sampling units that have varying area, such as islands, the process of constructing a species–area curve is simple: Order islands from smallest to largest area and plot on the number of species vs. area. We used this approach to construct curves for the Caribbean island *Anolis* data set. For data with sampling units of identical area, such as plots, curves can be constructed by retaining the spatial (or environmental) arrangement of the units, or by removing spatial structure (Chiarucci et al. 2009, Scheiner et al. 2011). For spatial curves, sampling units are aggregated to larger areas by taking adjacent units. This method retains the spatial clustering of individuals and species among spatially close units. For nonspatial curves, units are aggregated by randomly selecting units from the entire data set irrespective of physical location eliminating any observed spatial clustering of organisms among units. The methods by which spatial and nonspatial curves are built are analogous to sample-based accumulation curves and sample-based rarefaction curves, respectively (Gotelli and Colwell 2001). We constructed both spatial and nonspatial curves for the forest plot data set.

Ecological processes: species sorting, random placement, limited dispersal

We built simulation models to obtain expected PDARs and SARs under three ecological assembly processes: species sorting, random placement, and limited dispersal (Table 1). In the species-sorting model, we followed Ives and Helmus (2010, 2011) and Peres-Neto et al. (2012) in specifying an underlying relationship between assemblage composition and a single environmental driver. We assumed that 100 plots occurred along a continuous gradient of environmental driver x and that each of n species i had a unimodal optimal value of x, x_i^*. The probability that species i occurred in a plot given its environmental value x, $p_{x,i}$, decreased according to a Gaussian curve centered on x_i^* with a standard deviation σ that was set to be the same for all species. The random-placement model was the same as the species-sorting model, except the probability that a species occurred in any plot depended on a species-specific overall probability of establishment across all plots, p_i, and not an optimal value. In the limited-dispersal model, species probability distributions of occurrence were centered at particular plots, d_i^*. The probability that species i occurred in plot d, $p_{d,i}$, decreased according to a Gaussian curve centered on plot d_i^* with a standard deviation σ_i that varied among species. This variance among species in σ_i caused some species to have wide dispersal kernels and others to have narrow dispersal kernels away from d_i^*, which were randomly assigned to species and unrelated to the environmental gradient. The three models also included random variation in species richness across simulated assemblages independent of $p_{x,i}$, p_i, and $p_{d,i}$.

We simulated x_i^*, p_i, and σ_i as Brownian motion evolutionary processes along a fixed phylogenetic tree of n species. This resulted in phylogenetic signal where closely related species have either similar tolerances to environmental variation (x_i^*, species sorting), similar total relative abundances (p_i, random placement), or

TABLE 1. Simulation model overview showing (A) ecological and (B) macroevolutionary simulations.

A) Ecological simulations

Model name	Mechanism	Central value of occurrence probability distribution (x_i^*, d_i^*)	SD around central value (σ_i)	Overall occurrence probability (p_i)	Resulting phylogenetic pattern
Species sorting	niche	**matches environmental gradient**	same for all spp.	none	Closely related spp. are found in similar environments and generally at the same sites.
Species sorting with repulsion	niche	**matches environmental gradient**	same for all spp.	none	Closely related spp. are found in similar environments, but generally at different sites.
Random placement	neutral	none	none	**varies among spp.**	Closely related spp. have similar probability of establishing at any site.
Limited dispersal	neutral	random along gradient	**varies among spp.**	none	Closely related spp. have similar dispersal kernels.

B) Macroevolutionary simulations

Simulations	Mechanism	Extinction probability of new sp. on island $j(q_j)$	Overall colonization probability $(1 - k)$	Overall in situ speciation probability (k)	Determinants of island assemblages
$k = 0$	neutral	correlates with area	high	none	colonization among islands (allopatric speciation) and extinction of newly evolved spp.
$k = 0.6$	neutral	correlates with area	intermediate	intermediate	colonization among and in situ speciation within islands, and extinction of newly evolved spp.
$k = 0.9$	neutral	correlates with area	low	high	in situ speciation with few colonization events and extinction of newly evolved spp.
$k = 1$	neutral	correlate with area	none	high	in situ speciation only and extinction of the newly evolved spp.

Notes: Items in boldface in panel (A) indicate the characteristic of each model that has phylogenetic signal. Parameters in parentheses are fully described in the *Methods*.

similar dispersal kernels (σ_i, limited dispersal). Other evolutionary models besides Brownian motion can be envisioned and explored, but in general any model that reduces phylogenetic signal will reduce the strength of the simulated PDARs (Blomberg et al. 2003). We built phylogenetic diversity and species–area curves for assemblages with phylogenetic signal and those without phylogenetic signal where x_i^*, p_i, and σ_i were randomly selected with respect to phylogeny according to the standard uniform distribution.

The model of species sorting works via the general process of phylogenetic attraction (sensu Helmus et al. 2007*b*) in which phylogenetically related species are more likely to occur in the same site because they share similar environmental preferences (i.e., the specific mechanism in this model is habitat filtering; Webb et al. 2002). This can result in a phylogenetically clustered or underdispersed community structure. It is also possible that closely related species are less likely to co-occur in sites via the general process of phylogenetic repulsion (sensu Helmus et al. 2007*b*). There are several mechanisms, such as competitive exclusion among closely related species, that could generate this pattern (Cavender-Bares et al. 2009). Phylogenetic repulsion, in contrast to attraction, can result in a phylogenetically even or overdispersed community structure. Since both attraction and repulsion can simultaneously affect community structure (Helmus et al. 2007*b*), we added phylogenetic repulsion to the species-sorting model by assuming that following species-sorting, species were eliminated from sites such that more closely related species were less likely to co-occur. For this, we followed the mathematical approach detailed in Ives and Helmus (2011: Appendix A), which does not rely on specifying an underlying mechanism. Our formulation of the model assumes that phylogenetic repulsion occurs only at the

scale of individual sites, whereas phylogenetic attraction exists among environmentally similar sites and thus can occur at any spatial scale.

We explored these models with various numbers of species and communities, and different phylogenetic topologies; however, the results were similar. Thus, we only present results in which all models were run with a balanced phylogenetic tree with 32 species ($n = 32$) to create 100 simulated communities. We ran each of the models 100 times. All simulations were performed in MATLAB, and code is available as a supplement.

We computed the phylogenetic diversity and species–area curves of a set of reconnaissance plots (releves) sampled in the Mt. Hood National Forest of the Cascade Mountains, Oregon, USA (USDA Forest Service, Pacific Northwest Region, Area Ecology Program). A description of the plot design and sampling procedures can be found in Hemstrom et al. (1982) and McKenzie and Halpern (1999). The data set consists of 794 plots, each 500 m^2, and a total of 243 taxa (most identified to species, but some identified only to genus) that spanned angiosperms, conifers, and non-seed plants (Appendix A). The plots were in intact, undisturbed forests and were sampled to maximize variation in elevation (60–1700 m above sea level). McKenzie and Halpern (1999) found unimodal relationships between elevation and the distributions of eight of the nine species they studied from the data set. We used Phylomatic to construct a phylogeny of all the species based on the R20080417 megatree (Webb and Donoghue 2005) and branches dated according to Wikstrom et al. (2001). This is the most commonly used method to obtain plant phylogenetic trees for ecophylogenetic studies like ours, but other methods are increasingly becoming available (see Sanderson et al. 2008, Kress et al. 2009, Beaulieu et al. 2012). Phylomatic trees are typically not fully resolved at the younger nodes; for our tree many species within genera were not resolved and neither were many genera within families. Regardless, we used this tree because the deep nodes were resolved and dated (Appendix A), resolution at the tips has little effect on estimates of phylogenetic diversity when using a broad-scale tree (i.e., non-seed to seed plants, although lack of resolution above the family level may bias toward false negative results; Swenson 2009), and Phylomatic is so widely used that we wanted to know if we could find a strong PDAR with a phylogeny produced by this method.

We computed spatial and nonspatial phylogenetic diversity and species–area curves for the simulated and Mt. Hood data sets. We first calculated the mean species richness and PSV for the plots. We then randomly selected a plot and aggregated the species of either an adjacent plot (if building a spatial curve) or a second randomly chosen plot (if building a nonspatial curve), and calculated species richness and PSV, repeating this procedure 10 000 times to calculate the mean. We replicated this procedure, aggregating 3, 4, 5, and so on, plots, to generate the area curves. A generalized R function used to calculate these curves for other data sets is provided in the Supplement. To test how different the spatial curve was from the nonspatial curve, we compared the observed spatial curve to 100 curves built on the Mt. Hood data set after we permuted the location of plots. At each level of plot aggregation, we scored if the diversity value from the permuted spatial curve fell below the diversity value of the observed spatial curve. This gave us a percentage for each plot aggregation that the permuted spatial curve fell below the observed spatial curve and allowed us to assess where along the curves the spatial and nonspatial curves most strongly differed.

Macroevolutionary processes: extinction, colonization, in situ speciation

We built a simulation model to generate PDARs and SARs that arise from colonizations among islands and in situ speciation within islands. The model is neutral in that it treats all species as being ecologically equivalent (MacArthur and Wilson 1967, Hubbell 2001). Each time a species disperses to a new island, it is considered a new species derived via allopatric speciation, and thus, the simulated islands have distinct although evolutionarily related species pools. The evolution and establishment of a species on a particular island depend on two probabilities: the global probability of an in situ speciation vs. a colonization event, k, and the probability that a new species survives on an island j, q_j, which depends on island area. Specifically, q_j is a formulation of how area affects extinction rates as predicted by the equilibrium theory of island biogeography (MacArthur and Wilson 1967). When the probability $k = 0$, all speciation occurs as colonizations among islands, and when $k = 1$, all speciation is in situ resulting in only one island containing all species. The model begins with a single species that is randomly assigned to an island. A speciation event then occurs, which with probability k is in situ on the island and with probability $(1 - k)$ is an allopatric colonization to a different island. In the case of colonization, the new species is assigned randomly to another island. After speciation, the new species establishes on the island j with probability q_j. For the simulations, we assume that the values of q_j among m islands are exponentially distributed according to 0.9^j ($j = 1, 2, \ldots, m$); thus, on the largest island a new species has a probability of 0.9 of persisting, on the second largest island this probability is 0.81, and so on (i.e., a concave extinction curve). For successive speciation events, one species is randomly chosen to undergo speciation, and the per capita speciation rate is assumed to be constant through time. This stepwise process occurs until a designated total number of species across all islands has been reached. By keeping track of the speciation process and the identities of species on the islands, a simulated set of islands containing evolutionarily related species can be constructed. We ran 10 000

simulations for k equal to 0 (no in situ speciation), 0.6 (60% in situ speciation), and 0.9 (90% in situ speciation). We produced simulations with varying species and island numbers, but all resulted in similar area relationships; therefore, we only present the data for simulations of 15 islands with a total of 135 species. We also ran the model for the case in which each island assemblage was derived completely from in situ speciation. We built island assemblages from 2 to 52 species with $k = 1$, and then estimated how phylogenetic diversity relates to the number of simulated in situ speciation events. All simulations were performed in MATLAB, and code is available as a supplement.

We describe the PDAR and SAR of the *Anolis* lizard radiation across the islands of the Caribbean Sea (Losos 2009). We used the Caribherp database to compile a list of *Anolis* that were native to each of 27 Caribbean island banks, including banks of the Greater and Lesser Antilles and the Bahamas (Hedges 2011; J. Losos also proofed the data set). Fourteen of these banks had at least two species, enough species to calculate PSV. We used island banks (shallow areas that are connected by land at times of low sea level) instead of islands because they are distinct biogeographic regions, and there is low species dispersal among banks (see Fig. 1 in Losos 1996). Bank area was calculated as the total dry land area on a particular bank from published sources (Rand 1969, Losos 1996) and estimated with Google Earth v. 6.1.0.5001 (*available online*).[6] The measure is likely a slight underestimate of total land area, since the areas of very small satellite islands could not be included in all bank land area estimates. The phylogeny we used was based on a Bayesian maximum clade credibility tree calculated from 901 trees of a posterior distribution of the BEAST analysis of mitochondrial and nuclear sequences published in Mahler et al. (2010; the tree file was provided by R. Glor; Appendix B; also see Rabosky and Glor 2010). This phylogeny encompassed 126 out of the 147 native *Anolis* on the island banks of the Caribbean that have at least two native species according to the Caribherp database. The effect of the 21 missing species on our analyses was minimal because all but one were from the Greater Antilles (15 from Cuba, four from Hispanola, and one from Puerto Rico), and expected values of PSV are less variable for assemblages with high species richness, like the Greater Antilles *Anolis* assemblages (Helmus et al. 2007*a*). We used maximum likelihood ancestral trait reconstruction for discrete characters (Pagel 1994) to estimate the number of distinct lineages that had colonized each island bank and also the number of in situ speciation events that occurred. This method was used in Mahler et al. (2010) to reconstruct the colonization history of *Anolis* on the Greater Antilles (Appendix B).

[6] http://www.google.com/earth/index.html

Results

Ecological processes

We simulated local assemblages under a species-sorting process in which assembly depended on the differences between site environments and species optimum environmental preferences (x_i^*), a random-placement process in which assembly depended only on species-specific probabilities of establishment across all sites ($p_{i\cdot}$), and a limited-dispersal process in which species dispersal kernels varied, but species distributions were unrelated to site environments (Table 1). Species richness increased with area in all simulations, but the random-placement simulations plateaued at a lower species richness than the species-sorting and limited-dispersal simulations (Fig. 1A, B, E, F, I, J); this difference in plateaus was an artifact of maintaining the same parameter values over the three models. The important difference between the SARs expected under random placement and species sorting/limited dispersal was that for the species-sorting and limited-dispersal simulations, the increase in species richness with area was slower in curves that were constructed by aggregating adjacent sites (spatial curves) vs. randomly aggregating sites (nonspatial curves). This was because adjacent sites in the species-sorting/limited-dispersal simulations were more likely to contain the same species; conspecifics were spatially aggregated.

There were positive relationships between phylogenetic diversity and area in all simulations that contained phylogenetic signal (Fig. 1C, G, K). However, the species-sorting simulations with phylogenetic signal produced strong PDARs, and also produced spatial curves that were lower and accumulated phylogenetic diversity at a much slower rate than nonspatial curves. This is because closely related species tended to have similar x_i^* values and thus tended to be found in communities with similar environments. Random-placement and limited-dispersal simulations with phylogenetic signal, in contrast, produced identical spatial and nonspatial curves with weak PDARs. All simulations without phylogenetic signal produced identical, flat spatial and nonspatial curves that indicated no relationship between phylogenetic diversity and area (Fig. 1D, H, L).

The contrast between spatial and nonspatial species–area curves for Mt. Hood plants suggests spatial aggregation of conspecifics as expected under the species-sorting and limited-dispersal processes; aggregating plots spatially led to a slower rise in the spatial curve (Fig. 2A). The two curves started to converge only at the very largest areas as estimated by the permutation procedure (Fig. 2A, inset). The spatial phylogenetic diversity–area curve was generally lower than the nonspatial curve suggesting a species-sorting process, not a limited-dispersal process, where closely related species are spatially clustered (Fig. 2B). In contrast to the species-sorting simulation model with phylogenetic

signal (Fig. 1C), both the Mt. Hood spatial and nonspatial phylogenetic diversity–area curves were decreasing; in small areas plant assemblages contained more distantly related species than aggregated plots of large area (Fig. 2B). This pattern was also found for the simulation model that contained both species sorting and phylogenetic repulsion that excluded closely related species from being in the same plots (Fig. 2D). These results indicate that closely related Mt. Hood plant species tended to be found in plots sampled at similar elevations (species sorting and phylogenetic attraction), but just not in the same plots (phylogenetic repulsion).

Macroevolutionary processes

The area curves of Caribbean *Anolis* lizards resembled expectations derived from a macroevolutionary, island biogeography model with extinctions, colonizations, and within-island in situ speciation (Fig. 3). The relationship between species richness and bank land area was positive in both *Anolis* and simulated data sets (Fig. 3A, C), and the simulated SARs were stronger when both colonizations and in situ speciation generated diversity (compare the $k = 0$ result to those of $k = 0.6$ and $k = 0.9$ in Fig. 3C). In contrast, phylogenetic diversity did not vary with area (Fig. 3B, D). Instead, phylogenetic diversity in the simulations varied greatly with the level of colonizations to in situ speciation (k). Phylogenetic diversity was lowest when in situ speciation was high ($k = 0.9$), and was highest when all speciation events were allopatric colonizations among islands ($k = 0$; Fig. 3D). Like the simulations, *Anolis* island bank assemblages derived from multiple colonization events tended to have high phylogenetic diversity (Fig. 3B).

A more complex PDAR emerges if we focus only on those island banks where in situ speciation has occurred (Fig. 4). Phylogenetic diversity for these seven banks strongly correlates to island bank area (Fig. 4A), and phylogenetic diversity increases with the number of estimated in situ speciation events that occurred on each bank (Fig. 4B). This relationship was also found in simulated data without colonizations ($k = 1$). Banks that had more in situ speciation events, and therefore larger assemblages, had higher phylogenetic diversity than banks with fewer in situ speciation events and therefore fewer species (Fig. 4C).

Discussion

Phylogenetic diversity–area relationships are the changes in the phylogenetic composition of species assemblages that occur as sampling area is increased. At small spatial extents, such as among forest plots, phylogenetic diversity depends largely on ecological processes such as habitat suitability and local dispersal of individuals. At large extents, such as among oceanic islands, phylogenetic diversity depends largely on macroevolutionary processes such as ancestral colonization and speciation events. Here, we developed theoretical expectations for PDARs under different

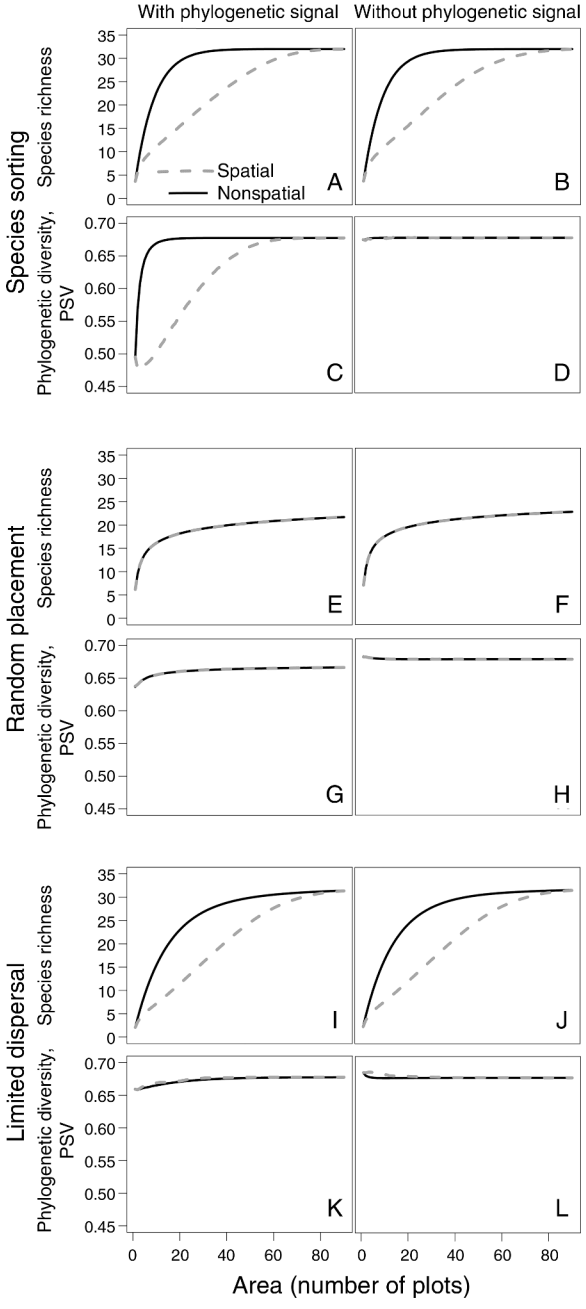

Fig. 1. Phylogenetic diversity and species–area curves for data simulated under (A–D) species-sorting, (E–H) random-placement, and (I–L) limited-dispersal hypotheses of community assembly. Simulations were run with and without phylogenetic signal in species optimum preferred values along an environment gradient (species sorting), in species relative prevalence across all plots (random placement), or in dispersal kernel size (limited dispersal). Spatial curves were constructed by retaining the spatial arrangement of plots along an environmental gradient, and nonspatial curves were constructed by randomly selecting plots irrespective of location. The plotted lines are the means over 100 simulations. PSV is the phylogenetic species variability metric from Helmus et al. (2007*a*).

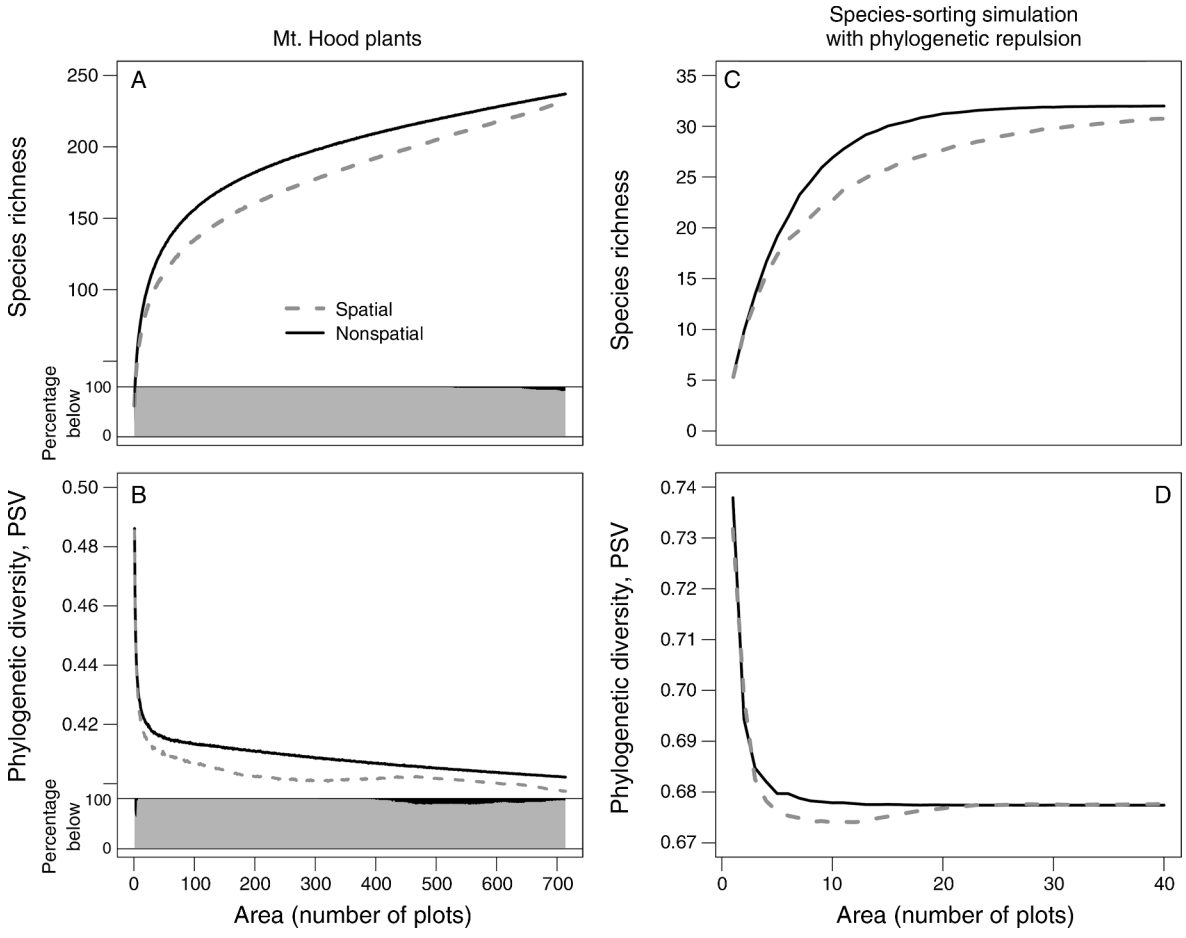

FIG. 2. Species sorting is evident in Mt. Hood (Oregon, USA) plant (A) species–area relationships and (B) phylogenetic diversity–area relationships, since the spatial phylogenetic diversity–area curves are lower than the nonspatial curves even though there is phylogenetic repulsion at small areas. The Mt. Hood plots were sampled along an elevation gradient, and area on the *x*-axes correlates to grouping plots from increasingly different elevations. The insets [gray blocks in panels (A) and (B)] give an estimate of the difference at each area between the spatial and nonspatial curves; the black shows the percentage of times the observed spatial curve fell below the spatial curves of 100 permuted data sets with randomized spatial locations. Note that the insets share the same *x*-axis, but not the same *y*-axis. (C, D) A species-sorting simulation model with both phylogenetic signal in species optimum environmental preferences and phylogenetic repulsion at the plot level produced curves that were qualitatively similar to those from the Mt. Hood data (compare panels B and D).

processes and developed methods to construct phylogenetic diversity–area curves (i.e., quantitative representations of PDARs) from empirical data sets.

Ecological processes

When there was phylogenetic signal in species environmental preferences (species sorting), strong PDARs could be generated and spatial phylogenetic diversity–area curves generally fell below nonspatial curves (Fig. 1C). In contrast, neither phylogenetic signal in species relative prevalence across sites (random placement; Fig. 1G) nor phylogenetic signal in species dispersal kernels (limited dispersal; Fig. 1K) generated strong PDARs. Phylogenetic diversity–area curves may distinguish neutral community assembly processes (limited dispersal, random placement) from niche-based processes (species sorting). Closely related species must be spatially clustered in order to get strong PDARs, and phylogenetic patterns in species overall prevalence and dispersal ability are not sufficient to create this clustering. Phylogenetic diversity–area curves may provide tests for phylogenetic community structure that are relatively insensitive to phylogeographic patterns in species ranges, distributions, abundances, dispersal ability, and prevalences, unlike many null model tests for phylogenetic community structure (Hardy 2008, Kembel 2009).

Mt. Hood plant assemblages contained relatively unrelated species at small areas and increasingly more related species at larger areas (Fig. 2B). This indicates that local-scale patterns are dominated by mechanisms that repulse closely related species. For example,

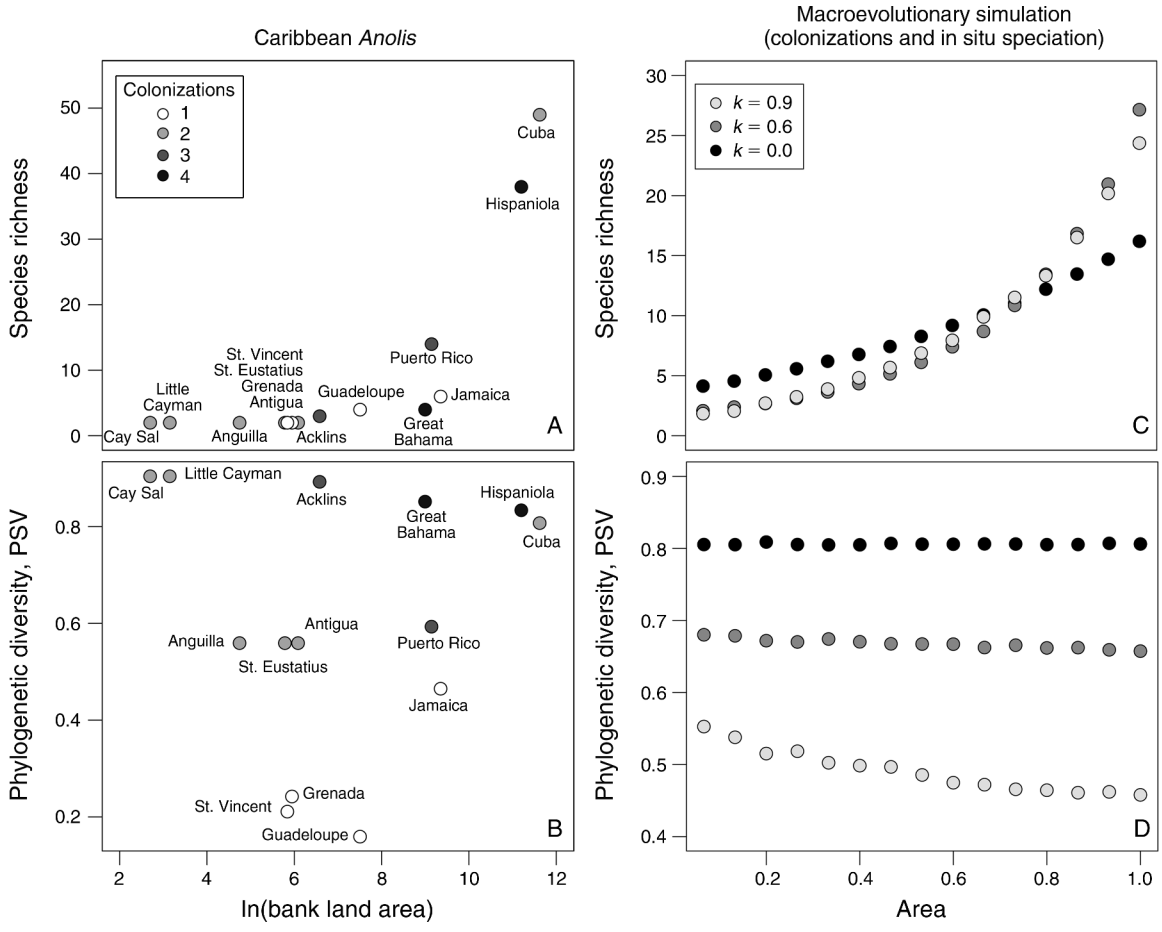

FIG. 3. There is no overall relationship between *Anolis* phylogenetic diversity and area. (A) *Anolis* species richness, but not (B) phylogenetic diversity, varies with island bank land area (originally measured in ha). (C, D) Similar relationships were found in a macroevolutionary simulation model where we varied the relative level of in situ speciation within islands to colonizations among islands (i.e., among-island allopatric speciation). In both the *Anolis* and simulated data sets, phylogenetic diversity varies with the number of estimated colonization events that gave rise to the species on each bank. (D) When k, the probability of an in situ vs. a colonization event, was high, more in situ speciation occurred and simulated islands contained low phylogenetic diversity. When k was low, more colonization among islands occurred and simulated islands contained high phylogenetic diversity. The highest phylogenetic diversity was observed when all island assemblages were derived from colonization events (i.e., $k = 0$). For the simulation, points are mean values of 10 000 simulation runs for each k value. The units for area in the simulation are arbitrary.

competitive exclusion through limiting similarity, local-scale habitat preferences that are evolutionarily convergent, pathogens that infect closely related hosts, and facilitation among distantly related plant species are all mechanisms that can underlie the general process of phylogenetic repulsion (Cavender-Bares et al. 2009). For larger areas, the Mt. Hood spatial phylogenetic diversity–area curve was lower than the nonspatial curve indicating that at these larger areas, mechanisms that attract closely related species, such as phylogenetically conserved competitive dominance or habitat filtering, dominate (Cavender-Bares et al. 2009, Mayfield and Levine 2010). Thus, both phylogenetic attraction and phylogenetic repulsion occur in this data set (Helmus et al. 2007*b*). Dominance by repulsion was lost at an area of ~12 km^2 (25 plots) above which the spatial curve was lower than the nonspatial curve (Fig. 2B, inset). This area on average contained 75 species that each contained, on average, about 169 million years (Ma) of evolutionary history (0.4220 PSV $\times$ 400 Ma, phylogeny root age), a 13% drop in phylogenetic diversity from the smallest area (500 m^2), whose average of 19 species contained 194 Ma. At the largest area (397 km^2), the phylogenetic diversity was only 159 Ma per each of the 243 species. Thus, even though there was a 10^6-fold increase in area and a 10-fold increase in species richness across the entire data set, phylogenetic diversity was relatively unchanged. Simulations with repulsion, no matter what parameter values we tried, always produced much weaker PDARs with less variance in PSV than those without (e.g., compare the y-axes on Figs. 1C and 2D). This result suggests that repulsion at small scales, regardless of the actual mechanisms, causes phylogenetic diversity to be preserved across spatial

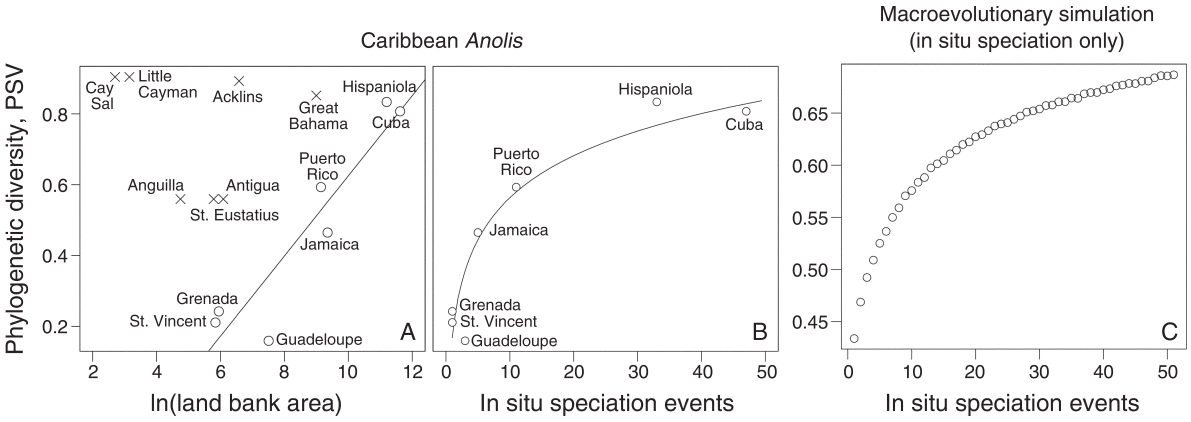

FIG. 4. Colonization among island banks obscures a strong *Anolis* phylogenetic diversity–area relationship determined by in situ speciation. (A) The best fit linear model (black line) for the seven banks that have had in situ speciation (open circles) is PSV = $-0.51 + 0.11 \times \ln(\text{area})$, $R^2 = 0.87$. The plotted data are the same as in Fig. 3A, and the banks without in situ speciation are plotted as X's. (B) The relationship between phylogenetic diversity and the number of in situ speciation events on the seven banks is shown by the black curve (PSV = $-0.17 + 0.17 \times \ln[\text{number of events}]$, $R^2 = 0.90$); (C) a similar relationship can be simulated using the same macroevolutionary model as in Fig. 3, but without colonizations ($k = 1$). Points are mean values of 10 000 simulation runs.

scales. Thus, alterations to the mechanisms that create phylogenetic repulsion within local assemblages, such as pollution, invasive species, and other anthropogenic disturbances that can reduce phylogenetic diversity (Helmus et al. 2010), could cascade to affect the phylogenetic diversity encompassed by broader areas.

Macroevolutionary processes

While there was a strong relationship between *Anolis* species richness and Caribbean island bank area (Fig. 3A; Losos 1996, Losos and Schluter 2000), we found no overall relationship between *Anolis* phylogenetic diversity and island bank area (Fig. 3B). Results from the macroevolutionary simulation model with both in situ and among-island allopatric speciation resembled the *Anolis* data with no expected relationship between phylogenetic diversity and area (Fig. 3D). The greatest variation in phylogenetic diversity was associated with the overall level of in situ speciation. Regardless of area, simulated islands with low levels of in situ speciation and high numbers of ancestral colonizations had high phylogenetic diversity (Fig. 3D). However, there is a strong PDAR for the seven Caribbean island banks with at least one in situ speciation event (Fig. 4A). The estimated phylogenetic diversity values of these seven banks are dominated by in situ speciation as opposed to among-island allopatric events (Cuba had 2, 47, 49 colonizations, in situ events, species richness, respectively; Hispaniola had 4, 33, 37; Puerto Rico had 3, 11, 14; Jamaica had 1, 5, 6; Guadeloupe had 1, 3, 4; Grenada had 1, 1, 2; and St. Vincent had 1, 1, 2). The strong *Anolis* SAR causes a strong positive PDAR for these banks because species richness and the number of in situ speciation events positively correlate (Figs. 3A and 4B). If island assemblages were only derived from in situ speciation, then, according to the neutral macroevolutionary model we used, phylogenetic diversity is expected to positively increase, and then plateau with the number of in situ speciation events (Fig. 4C), which is the same relationship we found for the seven island banks (Fig. 4B). On at least the four Greater Antilles islands, island area sets a limit to the number of *Anolis* species that can arise via in situ speciation (Rabosky and Glor 2010). Thus, when there are no external colonizations that add large amounts of external evolutionary history to island assemblages, positive PDARs are expected.

It is the balance of ancestral colonizations to in situ speciation, therefore, that affects regional phylogenetic diversity. This balance is thought to be determined by a race between colonists, where initial colonist species will diversify if another colonist species does not arrive and establish too soon after the initial colonization event (Gillespie 2004). For *Anolis*, this balance is related to island area, the timing of island emergence and species diversification, and island isolation (Losos 2009). For example, the largest island bank, Cuba, is the center of Caribbean *Anolis* diversity and was likely colonized twice, by the ancestor of most Caribbean *Anolis*, and possibly to all *Anolis* (Nicholson et al. 2005), and more recently by a colonist species from Hispaniola, whose ancestor was originally Cuban (Mahler et al. 2010). Cuba thus contains a large amount of phylogenetic diversity, not because it has received outside colonists, but because it is large in area and contains old diverse lineages that have arisen via in situ speciation. Small and spatially isolated banks such as those in the lower Lesser Antilles (e.g., Grenada) have had few ancestral colonizations and few in situ speciation events that together result in low phylogenetic diversity. In contrast, species assemblages on small and non-isolated banks (e.g., the Acklins bank of the Bahamas) are completely derived from among-island colonization's, and thus, have high phylogenetic diversity similar to the Cuban bank (Fig.

3B). Macroevolutionary simulations should thus be extended to include these isolation effects. However, the model and the *Anolis* data suggest that, in general, PDARs should be flat for oceanic islands whose species assemblages are an outcome of both in situ speciation and multiple colonizations.

Current caveats and future directions

We focused on only a small subset of the potential uses and research avenues for PDARs. Phylogenetic diversity–area relationships might be used to estimate phylogenetic α-, β-, and γ-diversity, and to explore how phylogenetic community structure changes with spatial scale and relates to β-diversity (Swenson et al. 2012). For example, Morlon et al. (2011) derived a neutral expectation for how phylogenetic α- and β-diversity changes with sampling area and the spatial distance separating assemblages. This avenue could inform how to best use phylogenetic diversity–area curves to identify and predict biodiversity hotspots for conservation (Rodrigues and Gaston 2002). Theoretical expectations for PDARs under other ecological and macroevolutionary processes, and the interaction between, should be explored. For example, simulation models where local-scale diversity is determined by ecological process and broad-scale diversity is determined by macroevolutionary processes may have overall PDARs that are triphasic, with distinct PDARs for local, intermediate, and broad-regional areas as is typical of SARs (Rosenzweig 1995). Finally, a fruitful avenue of investigation would be to examine how phylogenetic diversity varies with both time and area, as has been done for species richness (Adler et al. 2005, Rabosky and Glor 2010, Kozak and Wiens 2012).

Phylogenetic diversity–area curves can be constructed with other metrics besides PSV (Vellend et al. 2011); however, care must be taken when using metrics that are not statistically independent of species richness. For example, the relative invariance that we found in PSV for the Mt. Hood data set (Fig. 2B) would have been obscured if we had used the sum of the total phylogenetic branch lengths, a metric that always increases with species richness (Faith 1992, Morlon et al. 2011); the estimated phylogenetic diversity of the largest scale in the Mt. Hood data set based on this metric (11 596 Ma), is five times that estimated for the smallest scale (2271 Ma). When a dated phylogeny is available, the age of the root node can be multiplied by assemblage PSV values to give measures of the average evolutionary history encompassed by each species of each assemblage (see *Ecological processes* above). This would make it possible to compare the PDARs of assemblages from different species pools with varying diversification rates. Also, the phylogenetic diversity–area curves constructed from different species pools can then be used to weight the corresponding species–area curves to make the SARs of species pools that vary in diversification rates more comparable. This could be easily done with curves built from PSV, since PSV × SR (species richness) gives a phylogenetically weighted measure of species richness, phylogenetic species richness (Helmus et al. 2007*a*). This type of analysis might, for example, be informative for the globally distributed long-term forest plots of the Center for Tropical Forest Science (Plotkin et al. 2000; P. Fine, *personal communication*).

While we found that PDARs vary under different ecological community assembly processes, we believe that PDARs and phylogenetic diversity–area curves, like SARs and species–area curves, have limited utility when trying to understand assembly processes (Scheiner et al. 2011). For example, phylogenetic β-diversity can give a better picture of the distributions of species across a landscape, and β-diversity metrics can be used to look for changes in phylogenetic species composition at different spatial scales, across environmental gradients, and among geographic regions (Graham and Fine 2008, Ives and Helmus 2010, Swenson et al. 2012). Furthermore, model-fitting approaches that use species traits, environmental variables, space, and phylogeny to predict the distributions of species will be more powerful for inferring processes underlying assemblage composition than PDARs (e.g., Ives and Helmus 2011, Peres-Neto et al. 2012).

Even though phylogenetic diversity–area curves might not be the best tool for making inferences about the processes structuring ecological assemblages at local-scales and PDARs might be weak at broad-scales, they are nonetheless inherently interesting in their own right, as are SARs and species–area curves, and could prove a useful conservation tool. We recommend future research on PDARs focus on understanding the processes that determine curve shape, the statistical qualities of curve construction methods, and the potential uses of phylogenetic diversity–area curves in comparative studies, ecological and biogeographic theory, and conservation planning.

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Supplemental Material

Appendix A

Phylogenetic tree for the Mt. Hood, Oregon, USA, data set (*Ecological Archives* E093-176-A1).

Appendix B

Anolis phylogeny and estimates of ancestral colonizations in the Caribbean (*Ecological Archives* E093-176-A2).

Supplement

MATLAB code for the ecological and macroevolutionary simulation models and general R code to calculate spatial and nonspatial phylogenetic diversity–area curves (*Ecological Archives* E093-176-S1).