

# Trait Evolution, Community Assembly, and the Phylogenetic Structure of Ecological Communities

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**ABSTRACT:** Taxa co-occurring in communities often represent a non-random sample, in phenotypic or phylogenetic terms, of the regional species pool. While heuristic arguments have identified processes that create community phylogenetic patterns, further progress hinges on a more comprehensive understanding of the interactions between underlying ecological and evolutionary processes. We created a simulation framework to model trait evolution, assemble communities (via competition, habitat filtering, or neutral assembly), and test the phylogenetic pattern of the resulting communities. We found that phylogenetic community structure is greatest when traits are highly conserved and when multiple traits influence species membership in communities. Habitat filtering produces stronger phylogenetic structure when taxa with derived (as opposed to ancestral) traits are favored in the community. Nearest-relative tests have greater power to detect patterns due to competition, while total community relatedness tests perform better with habitat filtering. The size of the local community relative to the regional pool strongly influences statistical power; in general, power increases with larger pool sizes for communities created by filtering but decreases for communities created by competition. Our results deepen our understanding of processes that contribute to phylogenetic community structure and provide guidance for the design and interpretation of empirical research.

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An important goal of ecology is to understand the processes that generate variation in the diversity, identity, and abundance of co-occurring species. The presence of taxa in communities may be mediated by their physical and behavioral characteristics (e.g., Diamond 1975; Westoby and Wright 2006; but see Hubbell 2001). Because recently diverged taxa tend to be ecologically similar (Darwin 1859; Lord et al. 1995; Wiens and Graham 2005), a direct link may exist between the evolutionary relatedness of organisms in a community, the characters they possess, and the ecological processes that determine their distribution and abundance. In fact, many communities exhibit nonrandom patterns of evolutionary relatedness among constituent species (reviewed in Webb et al. 2002), a phenomenon we refer to as phylogenetic community structure.

Early workers relied on taxonomic ranks (e.g., species-to-genus ratios; Elton 1946) to infer ecological processes that structure communities. However, the availability of molecular phylogenies has paved the way for new methods (e.g., Webb 2000) that more accurately treat evolutionary relatedness as a continuum, renewing empirical interest in this area. For example, co-occurring tree species in a Borneo rainforest (Webb 2000) and certain bacterial communities (Horner-Devine and Bohannan 2006) are phylogenetically more closely related than expected by chance, while co-occurring species of Florida *Quercus* (Cavender-Bares et al. 2004), California *Ceanothus* (Ackerly et al. 2006), and South African sedges (Slingsby and Verboom 2006) are more distantly related than expected. Relatedness among species in communities may also vary with their abundance or with spatial or phylogenetic scale (e.g., Cavender-Bares et al. 2006; Kembel and Hubbell 2006; Swenson et al. 2006). For example, rare yeasts growing on columnar cacti tend to be closely related but abundant species more distantly related (Anderson et al. 2004). Communities may also exhibit random patterns of relatedness (Silvertown et al. 2006).

Phylogenetic community structure is most meaningfully

interpreted, from an ecological standpoint, in the context of community assembly theory. A local community can be considered to be a subset of a larger pool of potential community members (Diamond 1975; Weiher and Keddy 1999). Numerous processes contribute to the assembly of communities (e.g., Ricklefs and Schluter 1993; Snyder and Chesson 2004), including niche differentiation (e.g., MacArthur and Levins 1967; Stubbs and Wilson 2004), environmental filters (e.g., Woodward and Diament 1991; Weiher and Keddy 1995a; Ackerly 2003), and limited dispersal coupled with demographic stochasticity (Hubbell 2001). The outcome of these processes may be reflected in the distribution of phenotypes among co-occurring taxa (e.g., Ricklefs and Travis 1980; Weiher and Keddy 1995b; Stubbs and Wilson 2004; Cornwell et al. 2006) and in patterns of relatedness within the community if phenotypes are nonrandomly distributed on the underlying phylogeny.

Patterns of phylogenetic community structure can be interpreted using a simple framework (table 1; Webb et al. 2002): when traits of interest are phylogenetically conserved, a habitat filter that limits the range of viable ecological strategies at a site is expected to generate patterns of phylogenetic clustering (co-occurring species more related than expected by chance). Conversely, competitive exclusion that limits the ecological similarity of co-occurring species should generate phylogenetic evenness (species less related than expected by chance; we use “evenness” in place of “phylogenetic overdispersion”; see table 1 for discussion). On the other hand, if the traits of interest are convergent, habitat filtering should produce evenly dispersed patterns of relatedness, while competition or limiting similarity should produce random, or possibly clustered, patterns. If communities are assembled independently with respect to traits (e.g., Hubbell 2001), then patterns of relatedness should be indistinguishable from random expectation.

Phylogenetic community methods hold great promise for the study of community assembly, particularly in communities that are not amenable to manipulative experi-

mentation. Here, we focus on four outstanding issues that have not been examined from a theoretical perspective. First, explicit tests have not been conducted to connect known assembly processes to the generation of phylogenetic community structure. Second, the statistical power of phylogenetic methods to detect patterns produced by community assembly processes in different evolutionary contexts is unexplored. This includes variation in phylogenetic tree topology as well as the rate and pattern of trait evolution. Third, membership in a local community may be determined by one or many ecologically important traits (e.g., Keddy 1992), and it is unclear how the number of relevant traits influences phylogenetic community structure. Fourth, empirical studies vary in the species richness of the community and in the size and phylogenetic “scope” of the regional pool. This variation has an unknown effect on the power of community phylogenetic methods to detect nonrandom patterns.

We constructed a simulation model of community assembly to examine the phylogenetic patterns produced by known assembly processes (limiting similarity, habitat filtering, and neutral assembly) operating in relation to different patterns of phylogenetic topology and trait evolution (fig. 1). The implicit model is one of colonization and establishment in a novel area by species from a regional pool with existing trait values (i.e., the taxa do not coevolve). We modified existing approaches to generate phylogenies and traits (Raup et al. 1973) and to assemble local communities (Colwell and Winkler 1984). We then applied recently developed phylogenetic community metrics to the simulated communities and explored parameter space to determine patterns of statistical power.

## Methods

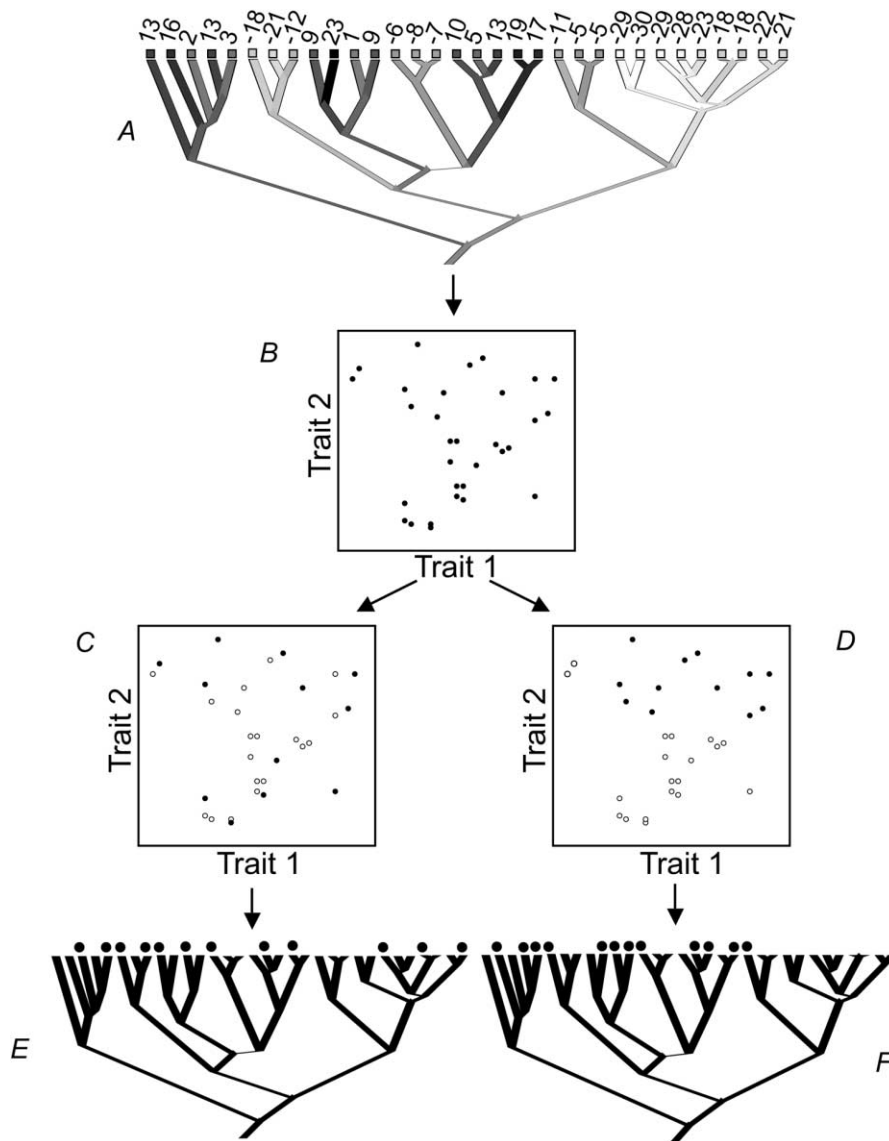
We ran four distinct sets of simulations (table 2) that follow the same template. In each simulation run, we generated a phylogenetic tree with one or more traits evolving with varying degrees of trait conservatism (fig. 1A). The

**Table 1:** Patterns of community phylogenetic dispersion predicted to be produced by various community assembly processes when phenotypic traits of interest are phylogenetically conserved or convergent

Assembly process	Traits conserved	Traits convergent
Limiting similarity	Even dispersion <sup>a</sup>	Random or clustered dispersion
Habitat filtering	Clustered dispersion	Even dispersion <sup>a</sup>
Neutral assembly	Random dispersion	Random dispersion

Note: Modified from Webb et al. (2002) and Cavender-Bares et al. (2004).

<sup>a</sup> Earlier works used the term “overdispersion” for cases in which taxa are less related than expected (e.g., Webb et al. 2002); however, this term has been used to refer to both aggregated (e.g., Connor et al. 1997) and evenly dispersed (e.g., Condit et al. 2000) patterns in the ecological literature. We follow the suggestion of others (Southwood 1966; Perry et al. 2002; R. K. Colwell, personal communication) that “evenness” is preferable to “overdispersion” because it is less ambiguous.



**Figure 1:** Schematic of the simulation process. Tree topologies and trait evolution patterns are generated either by hand (parts of simulation 1) or using a Yule branching process and Brownian motion model of trait evolution (A). The taxa at the tips of the resulting tree are placed into trait space, as shown here for a two-trait case (B), and represent the regional pool of taxa used to populate a local community. A community is created from the pool by a process of limiting similarity (C), habitat filtering (D), or neutral (random) assembly (not shown). Filled circles show the trait values of taxa in the community; open circles indicate taxa in the regional pool absent from the community (C, D). The resulting community is tested for phylogenetic community structure to see whether community members are evenly dispersed (E) or clustered (F) on the regional pool phylogeny. Filled circles (E, F) indicate the positions of local community members.

resulting species and corresponding trait values constituted the regional pool for the following tests (fig. 1B). Each regional pool of species was run through community assembly algorithms to produce a smaller local community (fig. 1C, 1D). The resulting community was then tested for phylogenetic community structure, taking into account the phylogeny of the regional pool (fig. 1E, 1F). We used

two metrics, a nearest-taxon-based measure sensitive to patterns at the “tips” of the phylogeny (nearest-taxon index [NTI]; Webb 2000) and a mean pairwise distance metric sensitive to phylogeny-wide patterns (net relatedness index [NRI]; Webb 2000). Finally, we calculated the statistical power of the phylogenetic methods to detect community structure, expressed as proportion of simulation

**Table 2:** Parameters of the simulations in this study

Simulation and trait evolution pattern	Balance ( $I_c$ )	No. traits	$K$	Pool size	Community size	No. replicates
1:						
Conserved	0	1	5.25	32	16	1,000 <sup>a</sup>
Brownian	0	1	$.99 \pm .36^b$	32	16	1,000
Random	0	1	$.66 \pm .07^b$	32	16	1,000
Convergent	0	1	.28	32	16	1,000 <sup>a</sup>
2:						
Brownian with variable rates	.03–.65	1	.01–10.5	16	8	3,000
3:						
Brownian	$.15 \pm .04^c$	1–5	$1.00 \pm .53^b$	32	16	2,000
4:						
Brownian	$.09 \pm .05^c$	1	$1.05 \pm .39^b$	30, 50, 100, 150, 200	10, 20, 30, 40, 90, 140, 190 <sup>d</sup>	2,000

Note: Trait evolution patterns used in simulation 1 were generated by hand or by simulation (see fig. A1) on balanced bifurcating trees, while in simulations 3 and 4, we used a Yule branching process to generate trees and a Brownian motion model of trait evolution. Simulation 2 used a modified Brownian model in which trait change accelerated or decelerated with time. The degree of trait conservatism was quantified using the  $K$  statistic. Cases where  $K < 0$  indicate convergent traits,  $K = 1$  perfectly meets a Brownian expectation, and  $K > 1$  indicates traits that are more conserved than a Brownian expectation. Tree balance ( $I_c$ ) ranges from 0 (perfectly balanced) to 1 (ladderlike).

<sup>a</sup> One pattern of trait evolution was used across all replicates (see fig. A1 in the online edition of the *American Naturalist*).

<sup>b</sup> Denotes geometric mean  $\pm$  untransformed standard deviation.

<sup>c</sup> Denotes mean  $\pm$  standard deviation.

<sup>d</sup> By definition, community size was always less than pool size; therefore, not all community sizes were used for every pool.

runs that produced significant results in the predicted direction (table 1) for a given set of parameters.

In simulation 1, we held tree topology, regional pool size, and local community size constant while varying the pattern of evolution of a single trait in order to explore the interaction of trait conservatism and community assembly processes in creating community phylogenetic structure. In simulation 2, we generated phylogenies with a wide range of topologies and a trait that exhibited a wide range of trait conservatism while keeping pool and community size constant. In simulation 3, we held pool size, community size, and trait evolution pattern constant while varying the number of traits. Finally, in simulation 4, we held trait evolution pattern for a single trait constant while varying pool and community size (table 2). Tree topology varied in simulations 3 and 4, though much less than in simulation 2 (see “Results”). To account for variation introduced by random tiebreaking in the community assembly models and by stochastic tree generation and trait evolution processes, we replicated each parameter combination 1,000 times (simulation 1) or 2,000 times (simulations 3 and 4). In simulation 2, we generated 3,000 trees in order to sample from a broad spectrum of trait conservatism and tree balance values.

### Regional Phylogeny Generation

For simulation 1, we used a balanced, 32-taxon, bifurcating phylogeny with branch lengths set to 1.0 (fig. A1 in the online edition of the *American Naturalist*) in every run. While a perfectly balanced tree is biologically unrealistic, it allows a clear demonstration of the effect of a range of trait evolution patterns. For simulations 2–4, we generated trees using a constant birth probability through time (Yule process; fig. 1A; Yule 1925; Martins 1996). While Yule trees represent a reasonable choice of model (Nee 2006), they are often more balanced than observed phylogenies (Mooers and Heard 1997). To explore tree shape as a potential source of bias, in simulation 2 we produced 16-taxon trees with a wide range of shapes through random cladogenesis. We quantified shape using the  $I_c$  metric (Colless 1982; Heard 1992), which ranges from 0 (perfectly balanced; fig. A1) to 1 (ladderlike). In simulation 2,  $I_c$  ranged from 0.03 to 0.65 (table 2). For simulation 3, we used 32-taxon trees (average  $I_c = 0.15 \pm 0.04$ ), while for simulation 4, we used 30-, 50-, 100-, 150-, and 200-taxon trees (average  $I_c$  across all pool sizes =  $0.09 \pm 0.05$ ).

### Trait Generation

We used the  $K$  statistic (Blomberg et al. 2003) generated by the program PHYSIG (kindly provided by T. Garland) to quantify trait conservatism. Cases where  $K = 1$  indicate that the distribution of trait values on the tree matches the expectation of a Brownian motion model, in which trait changes along each branch are random and related species exhibit a moderate degree of phenotypic similarity due to shared ancestry. Cases where  $K > 1$  indicate more conserved trait values than expected, whereas  $K < 1$  indicates trait values that are less conserved than expected.

In simulation 1, we generated extreme examples of trait evolution patterns. A strongly conserved trait pattern was created by ordering trait values along the tips of the tree (fig. A1A), corresponding to a consistency index (CI) of 1 in parsimony terms (Maddison and Maddison 2000) and a  $K$  value of 5.25. A random trait arrangement may be generated by shuffling values at tips of the tree; we examine results for 1,000 random shuffles of the tips of the convergent tree (fig. A1C), with average  $K$  values of 0.66. To generate strong convergence, we selected four trait values and assigned them in a repeated pattern to the eight four-taxon clades on our balanced tree (fig. A1D;  $K = 0.28$ ). This produced a pattern where identical values occur in independent clades, as might occur when independent lineages radiate across the same suite of habitats or niches (e.g., Price 1997; Cavender-Bares et al. 2004).

As a final trait evolution pattern in simulation 1 (fig. A1B) and for all trees used in simulations 3 and 4, we generated traits using a Brownian motion-like model (Felsenstein 1985) in the program ECOVOLV (Webb et al. 2006a). These trees exhibited trait conservatism intermediate to that of the convergent and conserved trees from simulation 1 (table 2). Invoking a Brownian model does not mean that we assume that traits are evolving by random drift. Rather, Brownian motion represents a pattern of evolution, with a normal distribution of changes centered around 0, that does not assume a particular cause for any one change. Brownian models cannot simulate sustained evolutionary trends, but this is not an issue here because phylogenetic community structure is influenced only by the distribution of trait values among extant taxa. This Brownian model was modified for simulation 2 to generate a wider range of trait conservatism ( $K$ ) values. We exponentially increased or decreased the magnitude of the trait change parameter as a function of elapsed time of phylogeny generation. Decreasing rates cause initial radiation followed by greater similarity of close relatives (conservatism), while increasing rates create parallel divergence in terminal clades across a similar range of trait values among terminal clades (convergence; cf. ACDC model in Blomberg et al. 2003). In simulation 3, we gen-

erated five Brownian traits for each tree. Traits were generated independently and exhibited a range of correlation values by chance. While we did examine the effect of this correlation, a more detailed investigation of evolutionarily nonindependent traits is needed.

### Community Assembly Models

We wrote the program EVELYN (in honor of G. E. Hutchinson) to simulate assembly of local communities from regional pools. The program takes the identities and continuous trait values of the species within the regional pool (fig. 1B) and removes species from the community in a stepwise manner following one of three community assembly models to produce a local community (fig. 1C, 1D).

*Limiting similarity.* Following Colwell and Winkler's (1984) GAUSE model of direct competition followed by diffuse competition, we first generated a matrix of pairwise Euclidean distances between all species in trait space. Multivariate distances were used in simulation 3. The species pair with the smallest distance separating them was selected, and from that pair, the species with the smallest mean distance to all other species in the community was removed (ties were broken randomly; fig. 1C). This produces communities with less phenotypic similarity than randomly assembled communities of the same size (Colwell and Winkler 1984). Such patterns have been observed in plant (Stubbs and Wilson 2004; W. K. Cornwell, unpublished data) and animal communities (Juliano and Lawton 1990; Wiens 1991). The process was run to one of two end points: a specified minimum trait spacing (i.e., a limit to similarity; MacArthur and Levins 1967) or a specified community richness. Because both end points produced identical communities of a given size from the same pool, only the results of the second end point are presented.

*Habitat filtering.* Here we followed a conceptual model in which only taxa whose trait values fall within a certain range survive in a given set of environmental conditions (e.g., van der Valk 1981; Keddy 1992). We set a "niche optimum" point in trait space and systematically removed species with trait values farthest from that optimum until a specified community size was achieved (again, ties were broken randomly, and multivariate distances were used in simulation 3). Empirical evidence for a limit to the range of viable strategies has been found in plant systems (van der Valk 1981; Weiher et al. 1998; Cornwell et al. 2006), marine invertebrate communities (McClain et al. 2004), and parasite systems (Mouillot et al. 2005). For each simulation run, we ran the filtering model twice, once with the niche optimum near the ancestral trait state of all of the taxa in the regional pool (corresponding to the center

of the trait volume in trials with Brownian traits), and once near a highly derived trait state (corresponding to one extreme corner of trait space; fig. 1D). We explored an additional model in which a window of trait values was selected and all species outside of that window were removed. Because both models produced identical communities of a given size from the same pool, only the results of the first model are presented.

*Neutral assembly.* Our final algorithm randomly selected a specified number of species without respect to trait values, consistent with dispersal-based or lottery models of assembly (e.g., Sale 1977; Hubbell 2001).

#### *Testing for Phylogenetic Community Structure*

Local communities were tested for nonrandom phylogenetic community structure using two metrics generated by the program PHYLOCOM (Webb et al. 2006a). Net relatedness index (NRI) is derived from the sum of the branch lengths that connect all co-occurring taxa (mean pairwise distance [MPD]). Nearest-taxon index (NTI) is derived from the average branch length to the nearest co-occurring taxon (mean nearest-taxon distance [MNTD]). Observed values of MPD and MNTD are compared to null distributions generated by creating communities of identical size by random draws from the source pool. NRI is calculated by subtracting the null model MPD mean from the observed MPD value, dividing by the standard deviation of null model trials, and then multiplying by  $-1.0$  (Webb 2000; Kembel and Hubbell 2006); NTI is calculated in the same way from MNTD. Positive values of NRI or NTI indicate phylogenetic clustering; negative values indicate phylogenetic evenness.

#### *Assessing Significance and Power*

The rank of the observed MPD or MNTD value, respectively, relative to the values obtained from the null model, can be used to detect an NRI or NTI value that significantly deviates from the null expectation (we used 999 null model runs for all tests). We used one-tailed tests to assess the significance of NRI and NTI for communities produced by competition and filtering models, where we had clear prior predictions about the expected phylogenetic community structure (table 1). Communities produced by random assembly were not predicted to exhibit phylogenetic structure, and therefore we used two-tailed tests to assess Type I error rates. We set  $\alpha = 0.05$  for all tests. Statistical power was calculated as the proportion of significant simulation runs for a given set of parameters.

## Results

### *Simulation 1: How Do Trait Evolutionary Patterns and Community Assembly Processes Interact to Produce Phylogenetic Community Structure?*

We used simplified, perfectly balanced, 32-taxon trees to define distinct trait evolution patterns (table 2): strong trait conservatism, moderately conserved Brownian traits, randomly shuffled traits, and repeated convergence. As predicted, strongly conserved traits produced evenly dispersed communities when coupled with limiting similarity (mean NRI =  $-2.038$ , NRI power = 1.0, mean NTI =  $-2.605$ , NTI power = 1.0; table 3) and produced phylogenetic clustering when coupled with habitat filtering (all mean NRI and NTI values  $> 4.0$ , all power values = 1.0; table 3). Clustering (as detected by NRI) was stronger when the filter was in a derived, as opposed to ancestral, area of trait space. Our phylogenetic metrics performed differently: NRI indicated a stronger nonrandom pattern in filtered communities, while NTI indicated a stronger pattern in competitively structured communities (table 3). Power was reduced with moderately conserved (Brownian) traits, particularly in communities created by limiting similarity (table 3).

As predicted, convergent trait evolution and habitat filtering produced evenly dispersed communities (mean NRI and NTI  $< -2.0$  in both filtering models; table 3), particularly when measured with NTI. However, no structure was detected as a result of trait convergence and limiting similarity (NRI power = 0.055, NTI power = 0.035). Neutral assembly, as well as communities assembled by any process when traits were randomly distributed on the phylogeny (tip shuffling) did not produce phylogenetic structure. Type I error rates were close to or below 0.05 in all cases (table 3).

### *Simulation 2: How Does Variation in Trait Conservatism and Tree Topology Influence Power to Detect Phylogenetic Community Structure?*

Our 3,000 trees exhibited broad, orthogonal variation in shape and trait conservatism ( $r^2 = 0.001$ ; table 2; fig. A2 in the online edition of the *American Naturalist*), suggesting unbiased trait and tree generation methods. As traits became more conserved (higher  $K$  values), power to detect expected phylogenetic community structure increased (fig. 2). The effect was strongest for filtered communities measured with NRI (fig. 2A). Effects of tree topology were quite subtle and only detectable in some cases (figs. A3–A5 in the online edition of the *American Naturalist*).

**Table 3:** Mean net relatedness index (NRI) and nearest-taxon index (NTI) from simulation 1 and the power of each metric to detect expected nonrandom patterns across 1,000 runs

Trait evolution	Neutral assembly		Limiting similarity		Habitat filtering (ancestral)		Habitat filtering (derived)	
	NRI	NTI	NRI	NTI	NRI	NTI	NRI	NTI
Conserved ( $K = 5.25$ ):								
Mean	.023	-.049	<b>-2.038</b>	<b>-2.605</b>	<b>6.982</b>	<b>4.729</b>	<b>17.288</b>	<b>4.727</b>
Power	.036 <sup>a</sup>	.026 <sup>a</sup>	<b>1.000</b>	<b>1.000</b>	<b>1.000</b>	<b>1.000</b>	<b>1.000</b>	<b>1.000</b>
Brownian ( $K = .99 \pm .36$ ):								
Mean	-.003	-.013	.140	.064	<b>1.509</b>	<b>1.342</b>	<b>3.798</b>	<b>2.143</b>
Power	.062 <sup>a</sup>	.085 <sup>a</sup>	.053	.058	<b>.306</b>	<b>.292</b>	<b>.667</b>	<b>.554</b>
Random ( $K = .66 \pm .07$ ):								
Mean	.011	.000	-.008	-.050	.057	-.067	.050	-.008
Power	.037 <sup>a</sup>	.015 <sup>a</sup>	.047 <sup>a</sup>	.026 <sup>a</sup>	.026 <sup>a</sup>	.010 <sup>a</sup>	.028 <sup>a</sup>	.016 <sup>a</sup>
Convergent ( $K = .28$ ):								
Mean	.028	.001	.086	.066	<b>-2.035</b>	<b>-2.604</b>	<b>-2.037</b>	<b>-2.605</b>
Power	.035 <sup>a</sup>	.033 <sup>a</sup>	.055	.035	<b>1.000</b>	<b>1.000</b>	<b>1.000</b>	<b>1.000</b>

Note: One-tailed tests used; see table 1. Positive NTI and NRI values indicate phylogenetic clustering; negative values indicate even dispersion. Data in boldface correspond to conditions where tests had a power greater than 0.2. Neutral (random) assembly, as well as assembly using tip-shuffled (random) traits, was not predicted to generate phylogenetic structure; results in these cases indicate two-tailed Type I error rates. Trait conservatism is quantified using the  $K$  statistic; see table 2 for interpretation. Example trees shown in figure A1 in the online edition of the *American Naturalist*.

<sup>a</sup> Value represents Type I error rate.

### Simulation 3: How Does the Number of Traits Alter Phylogenetic Community Structure?

We used 16-taxon communities drawn from 32-taxon Yule trees, with one to five traits evolving independently under Brownian motion (for each trait,  $K = 1.05 \pm 0.53$ ; table 2). Power increased as more traits were used to create communities by limiting similarity (fig. 3), particularly when measured with NTI (fig. 3E), while no trend was observed with habitat filtering (fig. 3B, 3C, 3F, 3G). Surprisingly, there was no effect of chance trait correlation on power (fig. A7 in the online edition of the *American Naturalist*). As in simulation 1, NTI had higher power to detect patterns due to limiting similarity, while NRI performed better with filtering (fig. 3). Likewise, communities were more significantly clustered when the habitat filter was set to a derived, as opposed to an ancestral, area of trait space (fig. 3B, 3C).

### Simulation 4: How Does the Relative Size of the Local Community and the Regional Pool Influence the Power of Community Phylogenetic Tests to Detect Structure?

We used five sizes of Yule trees and a single Brownian trait ( $K = 1.05 \pm 0.39$  across all sizes; table 2) to generate up to seven community sizes (table 2). Pool and community size strongly influenced power (fig. 4; see fig. A6 in the online edition of the *American Naturalist* for NRI and NTI means). At given pool size, power was generally greatest at intermediate community sizes. At given community size,

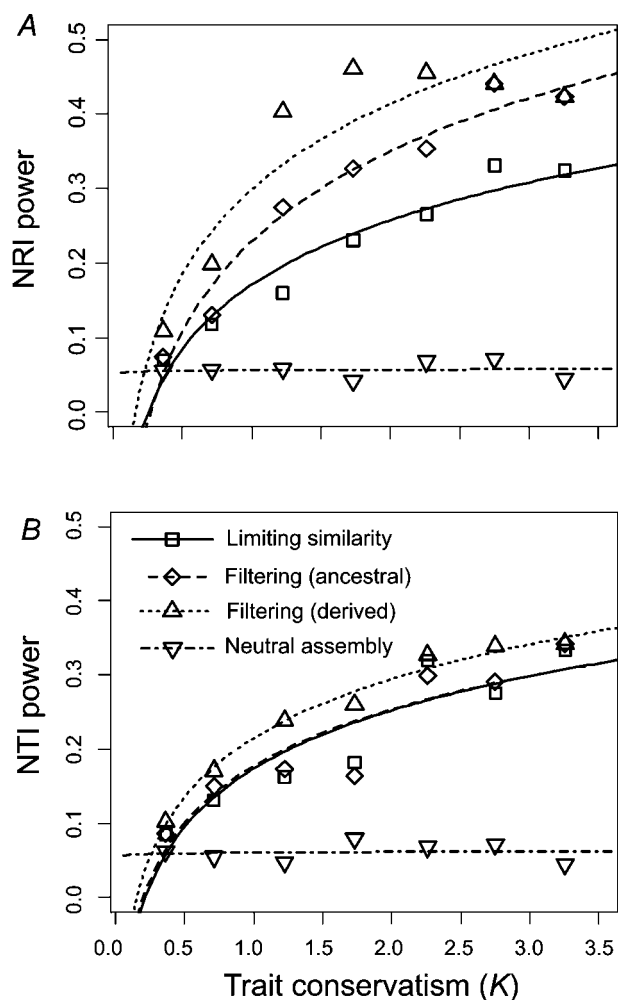
power increased with pool size for communities created by filtering but tended to decrease for communities created by limiting similarity (fig. 4). Across all pool and community sizes, power was low for communities created by limiting similarity (fig. 4; note different scale used for panels A and D). In contrast, power was greater in communities created by filtering, particularly when the habitat filter was placed in a derived area of trait space (e.g., fig. 4F).

In communities created by limiting similarity, NTI showed greater power across the range of pool and community sizes in our simulation. In filtered communities, NTI showed greater power when pool size was large and community size was 30%–60% of the pool size. However, NTI lost power rapidly as pool size decreased and as community size approached 0% or 100% of pool size. In these circumstances, NRI proved to be a more powerful metric. Communities created by neutral assembly produced Type I error rates of less than 5% for all pool and community size combinations (results not shown).

## Discussion

### Interaction of Trait Conservatism and Community Assembly Process

Heuristic predictions about the interaction of trait conservatism, community assembly, and phylogenetic community structure (table 1) were generally supported by our results: when ecological traits are conserved, limiting



**Figure 2:** Results of simulation 2, showing the relationship between the degree of trait conservatism ( $K$ ) and the power of net relatedness index (A) or nearest-taxon index (B) to detect phylogenetic community structure in the expected direction (table 1) for each of four community assembly models. Neutral (random) community assembly was not predicted to generate phylogenetic structure, so results in these cases indicate two-tailed Type I error rates. Cases where  $K = 1$  indicate that traits perfectly met a Brownian motion expectation, while  $K > 1$  indicates that traits are more conserved than that expectation. Cases where  $K < 1$  are less conserved (more convergent) than a Brownian expectation. Continuous  $K$  values generated in the simulation (fig. A3 in the online edition of the *American Naturalist*) were placed into equal-sized bins. Semilog fits have been added for heuristic purposes. Note the overlapping fits for the limiting similarity and filtering (ancestral) models in B. Further results from simulation 2 are shown in figures A2–A5 in the online edition of the *American Naturalist*.

similarity tends to produce phylogenetically even communities, while habitat filtering tends to produce phylogenetically clustered communities. Conserved traits led to congruence between trait- and phylogeny-based descriptions of community structure. Thus, community assembly

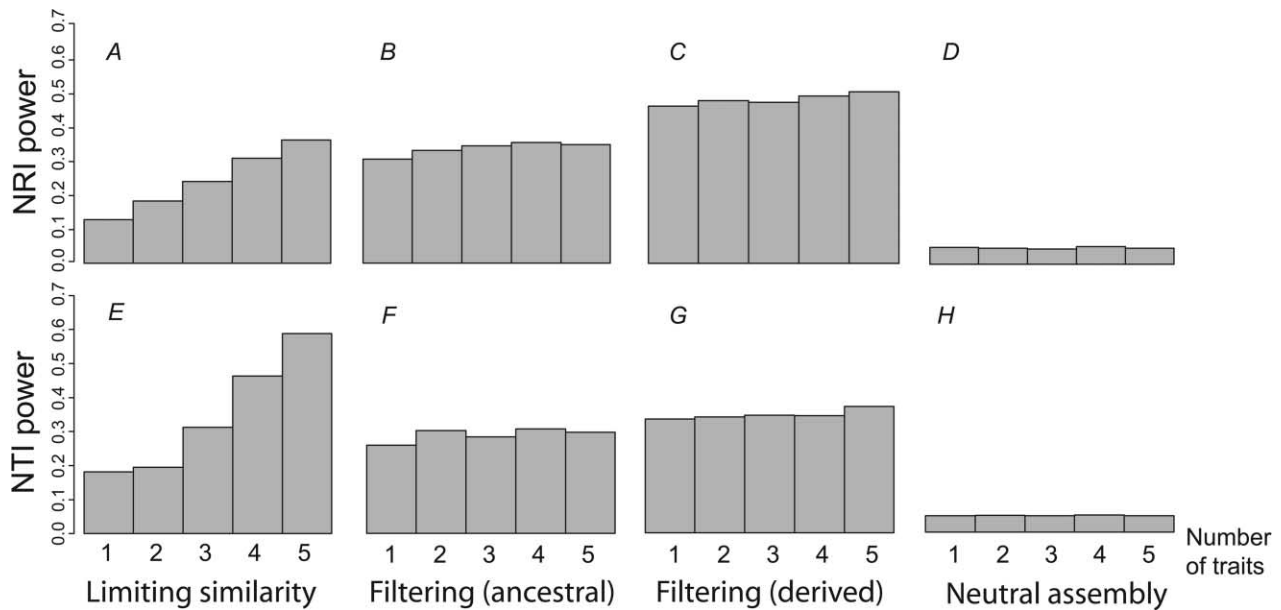
processes that led to clustered or evenly dispersed patterns of traits within communities (e.g., Colwell and Winkler 1984; Stubbs and Wilson 2004) led to clustered or evenly dispersed patterns of community relatedness. This was true whether we used artificial tree shapes and patterns of trait evolution (simulation 1), or a set of conditions (simulations 2–4) that better approximates observed phylogenies.

The story becomes more complicated when ecological traits are convergent. Systematic patterns of trait divergences repeated across clades (fig. A1D) produce even dispersion when coupled with habitat filtering (table 3). Cavender-Bares et al. (2004) suggested that competition (limiting similarity) coupled with convergent trait evolution could produce either random or clustered patterns of relatedness. In our study, we found only random patterns in these circumstances. There may be convergent patterns of trait evolution that we did not explore that produce stronger patterns, but at this point it appears that limiting similarity acting on convergent traits is not detectable.

It is critical to recognize that phylogenetically evenly dispersed communities can arise from two diametrically opposed processes: limiting similarity combined with conservative traits and filtering combined with convergent traits (table 1; Cavender-Bares et al. 2004). Therefore, the observation of phylogenetic evenness cannot be interpreted in ecological terms without careful consideration of the underlying traits that may influence community assembly. In contrast, within our framework, phylogenetic clustering arises only from filtering processes acting on conserved traits, so clustering provides provisional evidence of filtering processes, even in the absence of detailed knowledge of the traits involved. However, at large spatial scales, clustering may also arise from biogeographic processes of local radiation and limited dispersal, so that close relatives co-occur at a regional scale (Pennington et al. 2006).

The degree of trait conservatism influenced the strength of phylogenetic community patterns. Simulations with strongly conserved traits ( $K = 5.25$ ; simulation 1; table 2) produced strong signals of phylogenetic community structure (table 3), while simulations using moderately conserved (Brownian) traits (mean  $K \sim 1.0$ ; simulations 1, 3, 4) showed weaker results in the same direction (table 3; figs. 3, 4). Within the Brownian trials, stochastic variation produced a range of trait conservatism ( $K$ ) values (table 2). When we examined the effect of continuous variation in  $K$  (simulation 2), we saw a clear increase in power with increasing  $K$  (fig. 2). It is worth noting that in the Brownian simulations with low conservatism (fig. 2, where  $K < 1$ ), the power of phylogenetic methods was strongly reduced, approaching the results of random (tip shuffling) trait trials in simulation 1 (table 3).





**Figure 3:** Results of simulation 3, showing the effect of the number of traits on power to detect phylogenetic community signal as produced by one of four community assembly processes. A Brownian motion model ( $K \sim 1$ ) was used to produce traits in this simulation. *A–D*, Power to detect phylogenetic community structure as measured by net relatedness index (*NRI*); *E–H*, results using the nearest-taxon index (*NTI*). Power is calculated as the proportion of 2,000 runs in which a significant result was detected in the expected direction (table 1). Random assembly is not predicted to produce phylogenetic structure, so two-tailed Type I error is plotted instead.

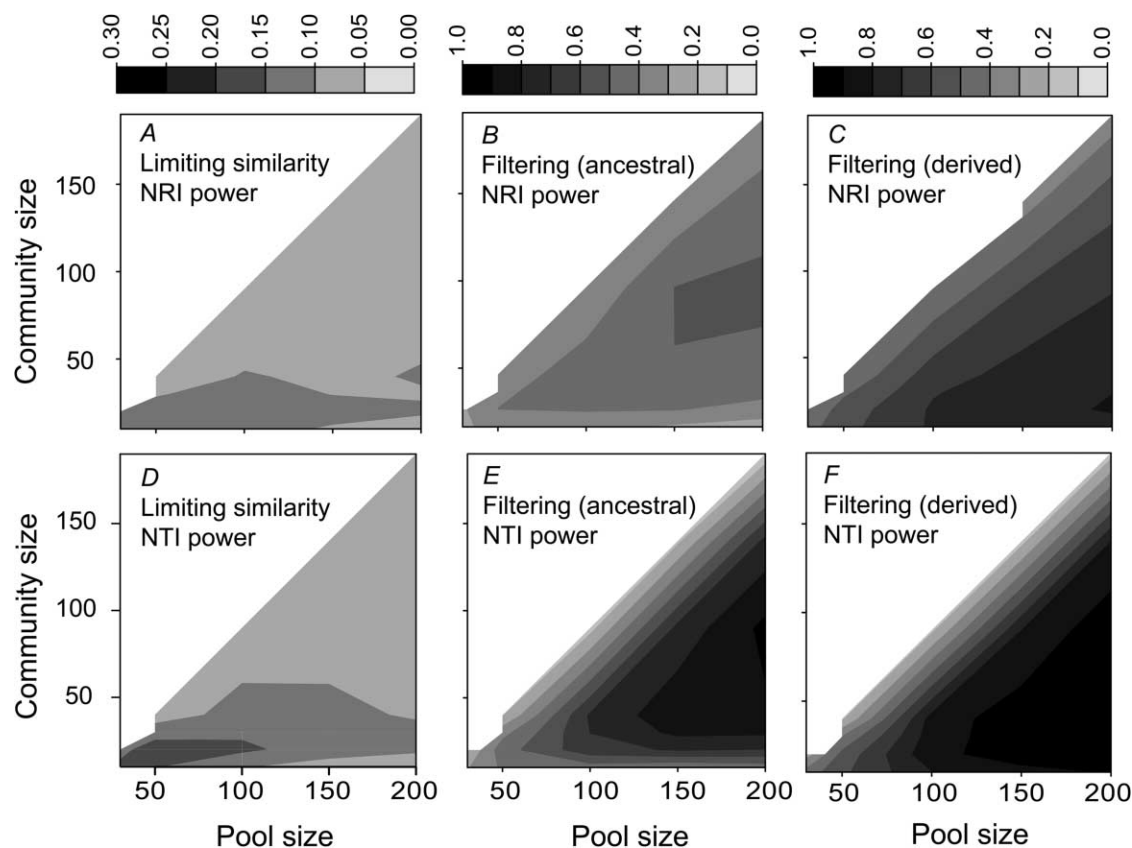
#### *Derived versus Ancestral Traits*

One of our most striking and consistent results is that the location of a habitat filter in trait space has a strong effect on the resulting phylogenetic structure of the community. We experimented with two extremes: selecting taxa with trait values close to the ancestral state for all taxa in the pool and selecting taxa from a highly derived area of trait space. The latter consistently yielded stronger patterns. This is presumably because many lineages may retain (or depart from and regain) trait values close to an ancestral trait optimum, whereas only one or a few lineages occupy the areas of trait space favored by a derived optimum. This has implications for the analysis of communities in which taxa are derived from disparate ancestral environmental conditions or for communities assembled in novel or extreme environments (Ackerly 2003). For example, among angiosperms, at a global scale, temperate and boreal communities may appear more clustered than tropical communities if frost tolerance is a recently derived trait in formerly tropical lineages (Wiens and Donoghue 2004; Feild and Arens 2005).

#### *Choice of Phylogenetic Community Statistics*

In this study, we used two phylogenetic community structure measures, *NRI* and *NTI*, although others exist (e.g.,

phylogenetic diversity; Faith 1992; see also Cavender-Bares et al. 2004). *NRI*, which is based on the total relatedness of the community, reflects patterns that occur across the entire phylogenetic tree, while *NTI*, which is based solely on nearest phylogenetic neighbors, is focused on the tips of the tree. *NTI* showed greater power to detect evenly dispersed patterns that are due to limiting similarity (e.g., fig. 3). The likely explanation lies in the limiting-similarity model in which the success of each species is determined by its proximity in trait space to other species. If traits are conserved and a species' closest neighbors in trait space are also its closest relatives, then a phylogenetic method that focuses on close relatives, such as *NTI*, will have more power to detect the patterns created by this assembly process. Practically, this result suggests that the selection of test statistics should be tailored to the empirical questions being tested. For example, if a community is expected to be structured by limiting similarity (competition) and major ecological traits of concern are known to be conserved, then a metric that focuses on the tips of the phylogenetic tree will have more power. Recent community studies have found phylogenetic clustering when including all flowering plants but have detected a shift toward evenness when phylogenetic scope is restricted to particular clades (Cavender-Bares et al. 2006; Swenson et al. 2006). Combining whole-tree and tip-level metrics with analyses at different



**Figure 4:** Results from simulation 4, showing the effect of variation in pool and community size on the detection of phylogenetic structure using one of three community assembly processes and a single trait evolving by Brownian motion. Power of net relatedness index (NRI; A–C) and nearest-taxon index (NTI; D–F) to detect phylogenetic community structure in the expected direction (table 1) over 2,000 runs is shown. Pool and community sizes used to generate the contours are indicated in table 2. Gray-scale bars at the top of each column indicate power; note the smaller scale used for results from the limiting similarity model (A, D). Neutral (random) assembly is not predicted to produce phylogenetic structure, so two-tailed Type I error was calculated instead and was consistently close to or below 0.05 in all areas of parameter space (not shown). See figure A6 in the online edition of the *American Naturalist* for mean NRI and NTI values. We experimented with randomly creating regional pools from a single large (1,000-taxon) pool and found similar trends but reduced power.

phylogenetic scales will be important in testing the generality of these patterns.

#### *Multiple Traits*

Results from simulation 3 suggest that in communities assembled by limiting similarity, the number of traits strongly influences the phylogenetic structure of the community (fig. 3). We addressed this problem using evolutionarily independent traits, but in a posteriori analyses based on stochastic variation in trait correlations, we did not find that the degree of trait covariance influences these patterns (fig. A7). Adding additional traits to a group of taxa increases the ways in which a given taxon may become ecologically differentiated from its neighbors and may strengthen the congruence between phylogenetic and eco-

logical distance. This points to the power of phylogenetic methods in cases where membership in a community may be determined by multiple ecological traits (e.g., Keddy 1992; Westoby et al. 2002; Cornwell et al. 2006) or by complex traits that are difficult to measure (e.g., pathogen sensitivity; Webb et al. 2006b).

#### *Community and Pool Size*

We found that the size of the local community relative to that of the regional pool influenced the power of phylogenetic methods. When the size of the pool was held constant, the greatest power was observed for communities of intermediate size, ranging from approximately 30%–60% of the pool, depending on the assembly model and metric used (fig. 4). The loss of statistical power at com-

munity sizes that are very small or very close to the size of the entire pool may be due to simple probability theory—with a small number of species either included in the community or excluded by the assembly process, the probability of any given combination of taxa arising by chance in the null model is high. This reduces the statistical power of the phylogenetic test and increases Type II error rates. Caution should be taken in rejecting a hypothesis of filtering or limiting similarity in cases where the community is very species poor or constitutes a very large proportion of the pool.

The size of the regional pool (phylogenetic scope) has important implications for detection of phylogenetic structure, but the direction and magnitude of the effect are dependent on the assembly model and phylogenetic test statistic. At a constant community size, larger pool sizes reduce the power to detect patterns produced by limiting similarity but increase the power to detect filtering patterns (fig. 4). In the case of limiting similarity, we suggest that in circumstances with a larger phylogenetic scope, a greater number of clades will evolve similar trait values solely by chance. Thus, communities assembled from larger species pools often consist of distant relatives that competed (and excluded each other) more often than in communities assembled from small pools. This leads to larger communities being less evenly dispersed than small communities, creating the drop in power that we observed as phylogenetic scope increases.

The relative strengths of NRI and NTI with respect to pool and community size are complex (fig. 4), particularly in the case of our habitat filtering models. In general, when the pool size is large, NTI has more power (fig. 4B, 4C, 4E, 4F), while at small pool sizes, NRI performed better (figs. 2, 3; in part, fig. 4). We suggest that with small trees and a small number of taxa, filtering permits the success of members of a single clade. With larger trees containing more taxa, there is an increased probability that distantly related clades will converge to a similar trait values by chance. These groups of distant relatives could then both pass through the assembly filter and succeed in the same community. Because these groups of species in the community are distantly related, the power of a metric that measures the total relatedness of the community, such as NRI, will be decreased. On the other hand, a metric that focuses on closest relatives, such as NTI, will still find closest relatives (within each of the distantly related clades) to be closer than expected by chance. Communities subject to intense abiotic conditions composed of species-rich, distantly related clades may not be uncommon. For example, in the California chaparral, several plant species from distantly related clades in the Rosales and Ericales co-occur and share many similar trait values related to drought and disturbance (Ackerly 2004).

The choice of the proper group of species to include in a phylogenetic community analysis, particularly in the regional pool, is a difficult biological question because it is influenced by historical and ecological factors. Ultimately, this choice depends on the spatial and temporal scales of interest to the investigator. Our results add to the importance of this task for the empiricist interested in using phylogenetic community methods by illustrating how much the outcome depends on community and pool size. For example, our results suggest that we should be cautious in ruling out competition or limiting similarity on the basis of nonsignificant NRI and NTI values in large communities such as tropical forests, where signals of phylogenetic clustering are relatively common but signals of phylogenetic evenness are rare or absent (Webb 2000; Kembel and Hubbell 2006; N. J. B. Kraft, unpublished data).

#### *Future Directions*

Several areas deserve further exploration. Our models worked exclusively with the presence/absence of taxa within communities and simple models of ecological processes acting in isolation. A more realistic model would consider the abundance of taxa within the pool and the community as well as trait evolution patterns that include ecological interaction. It may be valuable to explore the effect of explicit correlations or trade-offs between evolving traits and traits evolving under directional selection. Because communities may be structured by a combination of several community assembly processes acting simultaneously or in sequence (Keddy 1992; Silvertown et al. 2006), it may be useful to explore the effect of multiple ecological processes on phylogenetic community structure. However, processes acting in opposing directions, such as limiting similarity and filtering, may act to remove any structure detectable with our current test statistics.

This study is part of a growing body of evidence demonstrating that phylogenies are a powerful tool for the study of community assembly and an important complement to traditional ecological experimentation. The power of these methods is greatest when traits are conserved, in large communities created by habitat filtering, and when the number of traits relevant to community assembly is large. Future studies should target systems that are amenable to phylogenetic study and ecological manipulation in order to strengthen our understanding of the connections between phylogenetic community structure, trait conservatism, and community assembly process.

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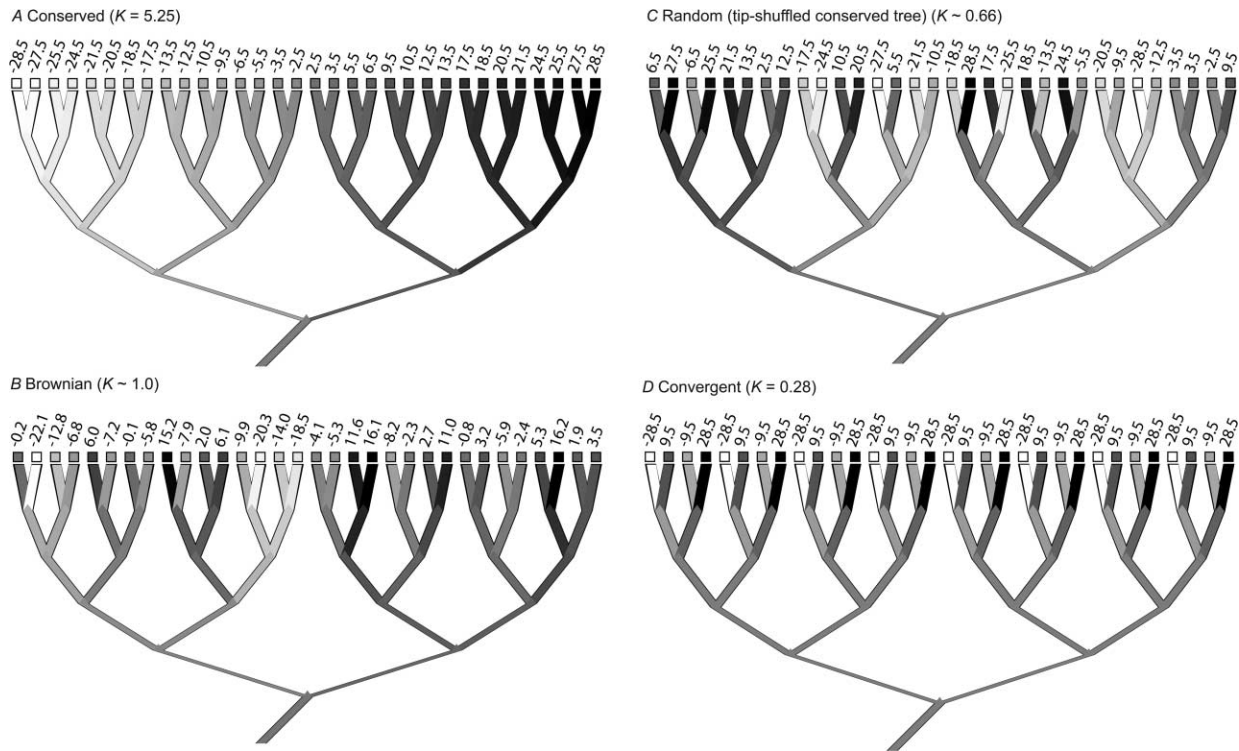
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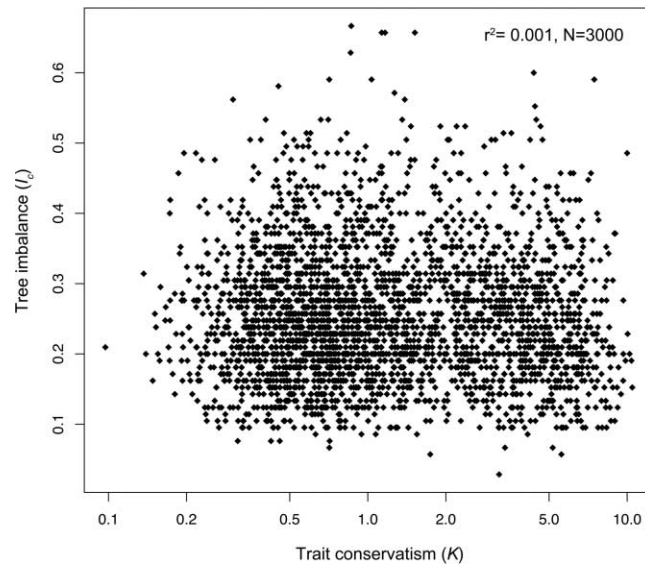
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# Appendix from N. J. B. Kraft et al., “Trait Evolution, Community Assembly, and the Phylogenetic Structure of Ecological Communities” (Am. Nat., vol. 170, no. 2, p. 271)

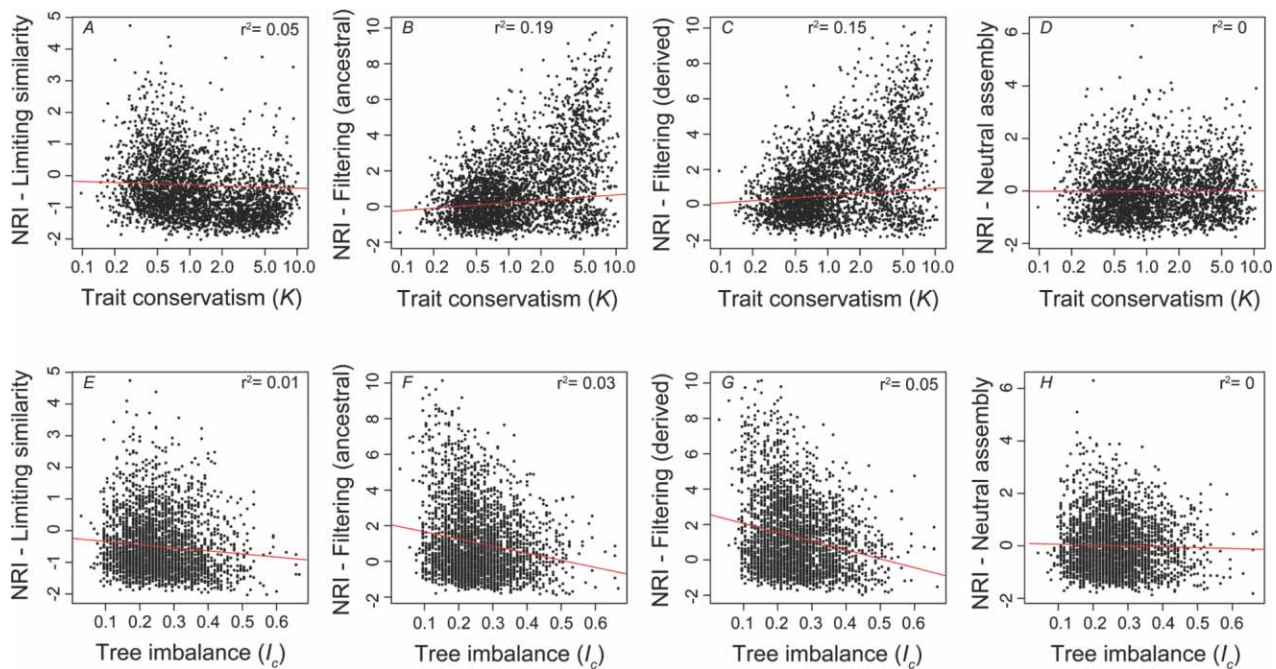
## Additional Figures



**Figure A1:** Trees used in simulation 1. We bracketed end points on the trait conservatism spectrum by generating trait patterns on balanced trees, including high trait conservatism with no convergence (A), moderately conserved traits generated by Brownian motion (B), random patterns of trait evolution generated by tip shuffling of the conserved tree (C), and a highly convergent pattern where traits repeatedly evolved across the phylogeny (D). Conservatism was described quantitatively using the  $K$  statistic:  $K = 1$  indicates that traits perfectly met a Brownian motion expectation, while  $K > 1$  indicates that traits are more conserved than that expectation. Cases where  $K < 1$  are less conserved (more convergent) than a Brownian expectation. A single pattern of trait evolution was constructed by hand for our conserved and convergent patterns (A, D), while 1,000 trait patterns were generated for the Brownian and random patterns (single examples are shown in B and C; average  $K$  values are reported). A parsimony-based reconstruction of ancestral states is indicated by branch shading for heuristic purposes. In preliminary studies, we found that the magnitude of trait values does not affect the observed phylogenetic community structure. For example, scaling the trait values in every simulation to a uniform range, such as from 0 to 1, did not alter the outcome of our study.

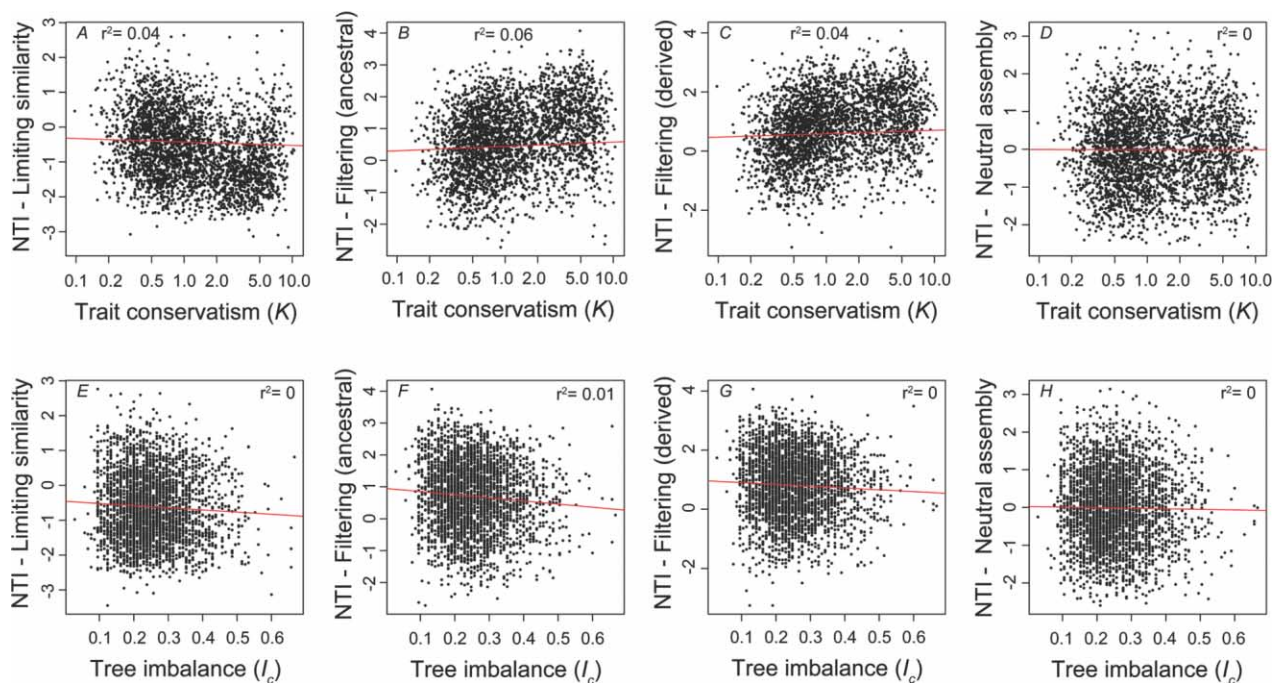


**Figure A2:** Relationship between trait conservatism ( $K$ ) and tree balance ( $I_c$ ) across the 3,000 16-taxon trees generated in simulation 2. See figure A1 for interpretation of  $K$ . An  $I_c$  of 0 indicates a perfectly balanced tree, while a value of 1 indicates a ladderlike tree. The value of  $K$  is bounded at 0.

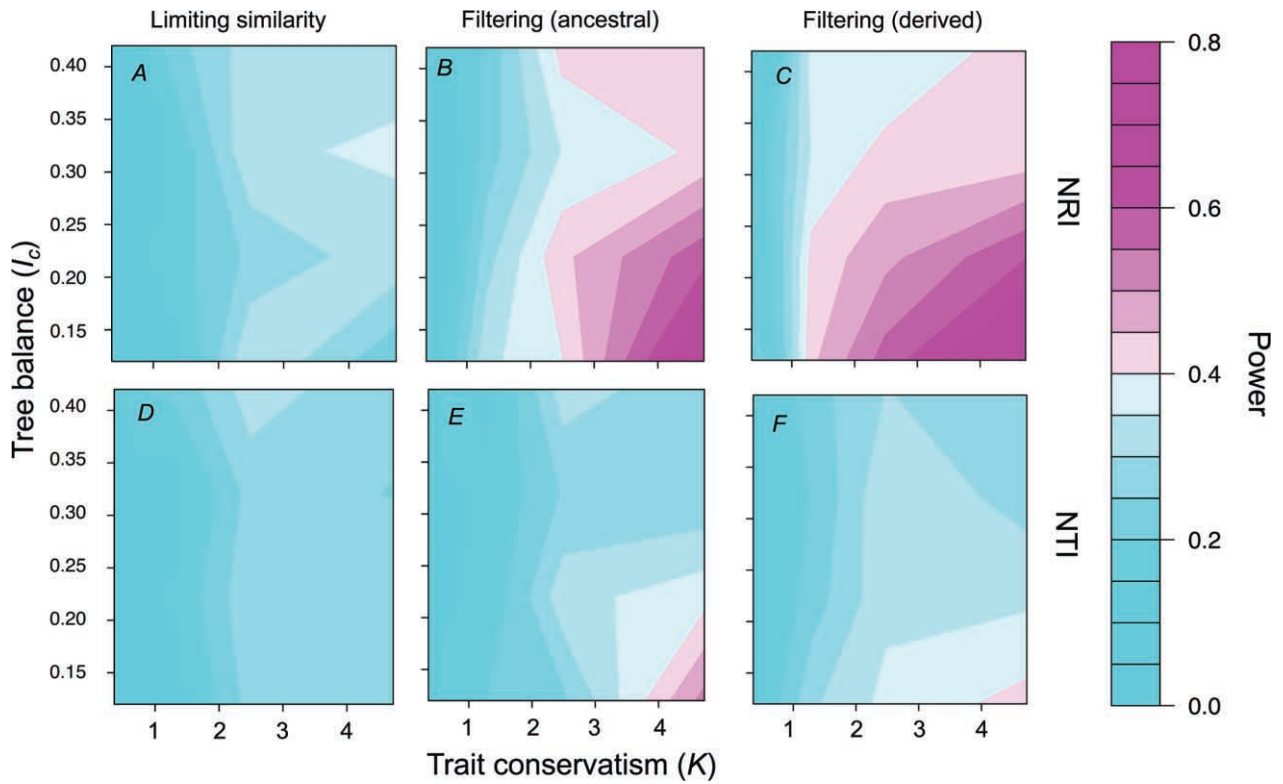


**Figure A3:** Relationship between net relatedness index (NRI) and trait conservatism ( $K$ ; A–D) and NRI and tree balance ( $I_c$ ; E–H) for the 3,000 16-taxon trees used in simulation 2. Positive NRI values indicate phylogenetic community clustering, while negative values indicate even dispersion. See legend to figure A2 for interpretation of  $K$  and  $I_c$ . Tree balance explains a small amount of variation in NRI for communities created by filtering and limiting similarity ( $r^2$  range = 0.01–0.05; E–G), though consistently less than is explained by trait conservatism (A–C).

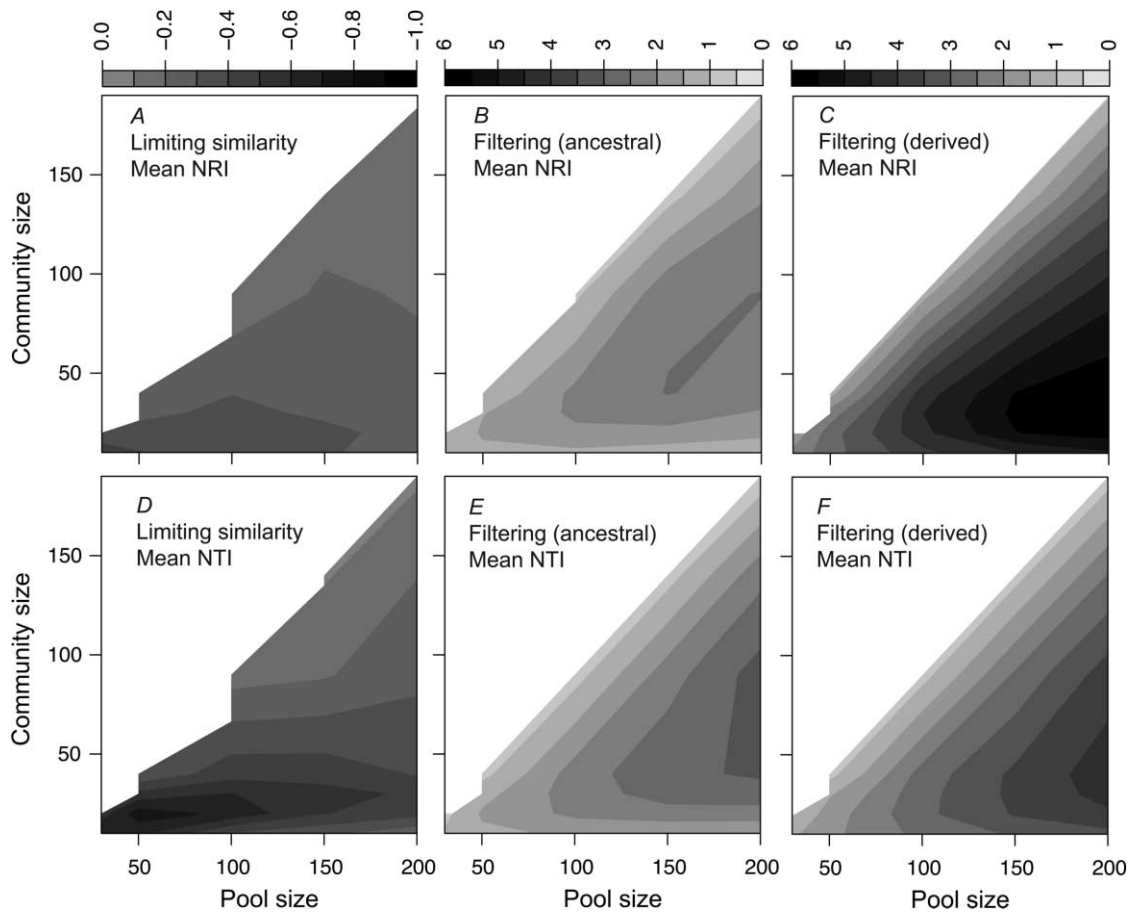




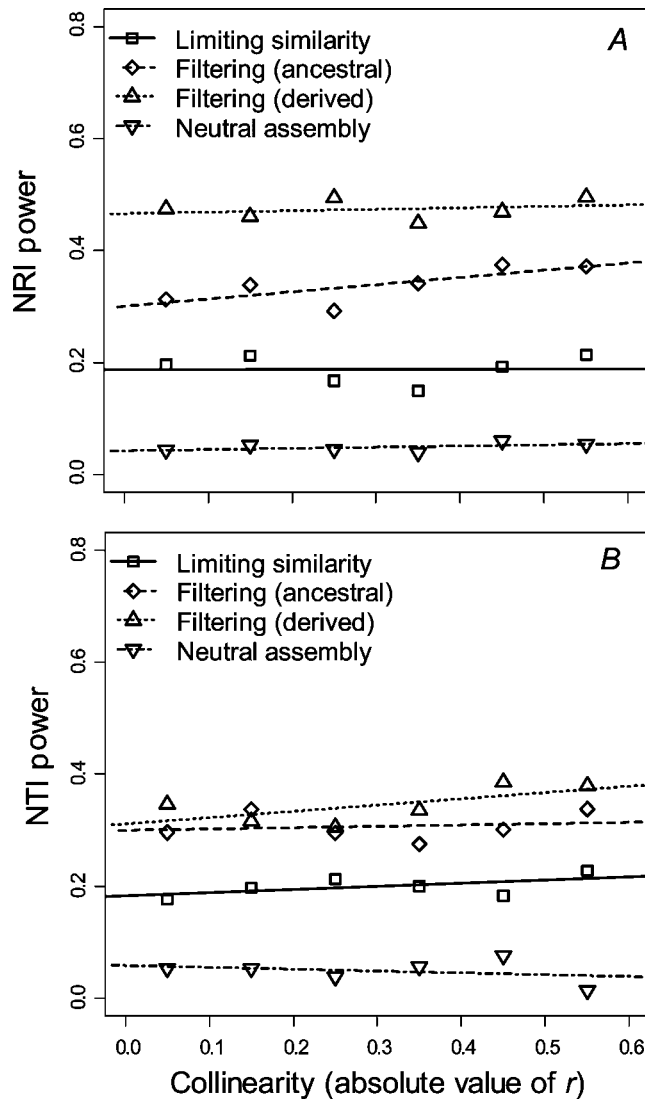
**Figure A4:** Relationship between nearest-taxon index (NTI) and trait conservatism ( $K$ ; A–D) and NTI and tree balance ( $I_c$ ; E–H) for the 3,000 16-taxon trees used in simulation 2. Positive NTI values indicate phylogenetic community clustering, while negative values indicate even dispersion. See legend to figure A2 for interpretation of  $K$  and  $I_c$ . Tree shape explained a small amount of variation in NTI for communities with a filter in the ancestral area of trait space ( $r^2 = 0.01$ ; F), though less than is explained by trait conservatism (B).



**Figure A5:** Relationship between trait conservatism ( $K$ ), tree balance ( $I_c$ ), and the power of net relatedness index (A–C) or nearest-taxon index (D–F) to detect phylogenetic community structure in the expected direction (table 1) for three different community assembly models for 3,000 16-taxon trees used in simulation 2. Trees have been placed into conservatism and balance bins of equal size to calculate power as the proportion of significant results in each bin. For interpretation of  $K$  and  $I_c$ , see legend to figure A2. Neutral (random) assembly is not predicted to produce phylogenetic structure, so two-tailed Type I error was calculated instead and was consistently at or below 0.05 in all areas of parameter space (not shown). In multiple regression models, the term describing the interaction between conservatism and balance was often significant, reflecting a reduced effect of trait conservatism on the power of phylogenetic methods as trees became more ladderlike, as can be seen clearly in B and C.



**Figure A6:** Additional results from simulation 4, showing the effect of variation in pool and community size on the detection of phylogenetic structure using one of three community assembly processes and a single trait evolving by Brownian motion. Mean values of net relatedness index (NRI; A–C) and nearest-taxon index (NTI; D–F) are plotted. For interpretation of NRI, NTI,  $K$ , and  $I_c$  see legends to figures A2 and A3. Pool and community sizes used to generate the contours are indicated in table 2. Gray-scale bars at the top of each column indicate mean values of NRI or NTI; note the smaller scale used for results from the limiting similarity model (A, D). Neutral (random) assembly yielded mean NRI and NTI values in the  $0 \pm 0.2$  range across all of parameter space (not shown).



**Figure A7:** Given the increase in power that we detected with additional traits for communities created by limiting similarity in simulation 3, it is reasonable to expect that simulations with multiple uncorrelated traits will show higher power than runs with traits that are highly correlated, since strongly correlated traits should behave more like a single trait. Even though traits evolved independently in our model, when we examined the 2,000 two-trait trees used in the simulation, we found that some runs produced traits that were strongly correlated by chance (mean  $r = 0 \pm 0.32$ , range  $-0.839$  to  $0.838$ ). Here we show the relationship between the collinearity of two independently evolving and the power of net relatedness index (NRI; A) and nearest-taxon index (NTI; B) to detect phylogenetic community structure in communities created with one of four community assembly models. Runs were sorted into equal-sized bins based on the absolute value of the correlation coefficient between the two traits in each simulation. Linear regressions were not significant for communities created with any model ( $P > .75$  in all cases); linear fits are shown for heuristic purposes. Linear fits between unbinned collinearity values and NRI or NTI also had very low explanatory power ( $r^2 < 0.002$  in all cases; data not shown).