THE PROBLEM AND PROMISE OF SCALE DEPENDENCY IN COMMUNITY PHYLOGENETICS

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Abstract. The problem of scale dependency is widespread in investigations of ecological communities. Null model investigations of community assembly exemplify the challenges involved because they typically include subjectively defined "regional species pools." The burgeoning field of community phylogenetics appears poised to face similar challenges. Our objective is to quantify the scope of the problem of scale dependency by comparing the phylogenetic structure of assemblages across contrasting geographic and taxonomic scales. We conduct phylogenetic analyses on communities within three tropical forests, and perform a sensitivity analysis with respect to two scaleable inputs: taxonomy and species pool size. We show that (1) estimates of phylogenetic overdispersion within local assemblages depend strongly on the taxonomic makeup of the local assemblage and (2) comparing the phylogenetic structure of a local assemblage to a species pool drawn from increasingly larger geographic scales results in an increased signal of phylogenetic clustering. We argue that, rather than posing a problem, "scale sensitivities" are likely to reveal general patterns of diversity that could help identify critical scales at which local or regional influences gain primacy for the structuring of communities. In this way, community phylogenetics promises to fill an important gap in community ecology and biogeography research.

Key words: community ecology; forest dynamics plot; phylogeny; scaling; species pool; tropical forest.

INTRODUCTION

The scale at which an ecological or evolutionary study is conducted determines which hypotheses the investigator will be able to address and how the results can be interpreted. Thus, scale dependency is not a new concept or challenge for biologists (Wiens 1989, Levin 1992). In community ecology research, where null models that involve subjectively defined "regional species pools" are commonplace, the issue of scale emerged early on as a problem because it clearly influenced how community structure could be interpreted (Colwell and Winkler 1984). The rapidly expanding field of "community phylogenetics" may be facing a similar challenge (Webb et al. 2002). Our objective is to establish the scope and nature of scale dependency in this field of research.

Community phylogenetics builds upon a long history of papers in community ecology that focused on questions regarding the nature of community assembly by using information on community taxonomic composition based on Linnaean ranks (e.g., Elton 1946, Simberloff 1970, Tokeshi 1991). By providing more accurate information regarding the degree of relatedness and diversity of species within a local assemblage, community phylogenetics offers a powerful tool for community ecologists, macroecologists, and biogeographers. The central methodology of community phylo-

genetics is to compare the phylogenetic dispersion of local communities to random species assemblages drawn from a more broadly defined species pool. If a local assemblage is found to be significantly phylogenetically overdispersed compared to the null distribution drawn from the species pool, then the evidence is considered consistent with the hypothesis that competition among closely related species helped structure the local community (Webb et al. 2002). If the local assemblage is significantly more phylogenetically clustered than the null distribution drawn from the species pool, then the evidence is considered consistent with the hypothesis that selective filters (e.g., environmental conditions) caused local assemblages to comprise closely related taxa, which tend to share similar traits (Webb et al. 2002). On the one hand, community phylogenetics offers a potentially powerful new way to address the old problem of determining the relative importance of the forces (biotic vs. abiotic) that structure local communities. On the other hand, there appear to be several limitations offered by current phylogenetic information. For example, if information regarding the comparative rates of evolution among clades is lacking community phylogenetics may have difficulty detecting whether communities are structured in response to evolutionary divergence and convergence in situ or by ancestral characteristics sorting out upon the environmental template (Grandcolas 1998). Further, for the purposes of this paper, there remain two important questions in regard to the above methodology: First, how does one

operationally define the spatial extent of the reference species pool, to which the local assemblage is compared (Colwell and Winkler 1984, Kembel and Hubbell 2006)? Second, are there general patterns of scale dependency which depend upon how one delineates the taxonomic scale of the local assemblage and the reference species pool (Cavender-Bares et al. 2006)?

The handful of studies that have used community phylogenetics in this context have provided mixed results concerning whether communities are phylogenetically clustered (Webb 2000), phylogenetically over-dispersed (Cavender-Bares et al. 2004), or show no phylogenetic structure (Kembel and Hubbell 2006). Recent evidence from Cavender-Bares et al. (2006) and N. G. Swenson, B. J. Enquist, J. Thompson, and J. K. Zimmerman (*unpublished data*) shows that the above studies are all prone to scale dependency. Specifically, as the local assemblage becomes more finely defined spatially, phylogentic overdispersion is common. At intermediate scales the community phylogenetic signal is generally random and at the largest spatial scales communities are typically phylogenetically clustered. Importantly, the conclusions of these studies may have changed had the size of the reference species pool been different (Kembel and Hubbell 2006), and had an alternative taxonomic scope been used (Cavender-Bares et al. 2004, 2006).

Here we perform phylogenetic analyses on three tropical forest dynamics plots across a range of taxonomic and species pool size scales in order to quantify the scope and generality of scale dependency in this emerging field. Specifically, we ask (1) Does the phylogenetic dispersion in multiple tree communities show scale dependency due to species pool spatial scale? (2) Does the phylogenetic dispersion in multiple tree communities show general patterns of scale dependency due to the taxonomic scale of the local assemblage consistent with those reported by Cavender-Bares et al. (2006)? and (3) If scale dependency is widespread, what are the implications for the rapidly expanding field of community phylogenetics? We show that both spatial and taxonomic scale can significantly influence one's conclusions about the relative influence of the forces that structure local diversity. However, importantly, we show that there may exist general patterns associated with the scale dependency of phylogenetic structuring.

Methods

Study locations

Tree community data from censuses of three forest dynamics plots (FDPs) were used for the study: (1) Barro Colorado Island (BCI) is a 50-ha FDP characterized as tropical lowland moist forest and located in Lake Gatun, Panama (Hubbell and Foster 1983, Condit et al. 1996); (2) San Emilio FDP (16 ha; see Plate 1) is located within the seasonally dry forest of northwestern Costa Rica (Enquist et al. 1999); (3) Luquillo FDP (16 ha) is characterized as a pre-montane moist forest, is located in the Luquillo Experimental Forest in Puerto Rico, and is part of the NSF Long-Term Ecological Research Program (Thompson et al. 2002). Census data used for the analyses were from 1996 for San Emilio and 1995 for Luquillo and BCI. During each FDP census, all free-standing woody stems 1 cm or greater (3 cm or greater at San Emilio) at 1.3 m from the ground were measured (Condit 1998).

Community phylogenetic analyses

Phylogenetic analyses of community structure require two main components. First, a phylogenetic tree representing the species pool must be generated. For all of the following analyses, a phylogenetic supertree representing the species pool was constructed by using the database Phylomatic (Webb and Donoghue 2005). A Nexus file was obtained from Phylomatic and was imported into the community phylogenetic software Phylocom Version 3.21 (*available online*).[4] The latest Angiosperm Phylogeny Group classification (Angiosperm Phylogeny Group II 2003; Phylomatic tree version R20031202) was used for the supertree backbone. The BLADJ algorithm was implemented inside Phylocom in order to calibrate each species pool supertree by applying known molecular and fossil dates (Wikstrom et al. 2001) to nodes on the supertree. Briefly, the BLADJ algorithm applies dates to "known" nodes on the supertree. Next, dates are applied to "unknown" nodes on the supertree by evenly spacing the dates between "known" nodes. It should be recognized that "known" dates used to calibrate the supertrees are crude estimates at best, but calibration of the supertree provides a substantial advantage over using nodal distances with all branch lengths set to one (Webb et al. 2002).

The second element required for community phylogenic analyses are local assemblages representing the focal communities. The local assemblages used in the present analyses were each derived from each individual FDP (BCI, Luquillo, and San Emilio). Using the community phylogenetic software Phylocom, observed phylogenetic relatedness (mean pairwise phylogenetic distance [MPD] and mean minimum phylogenetic distance [MMPD]) of co-occurring taxa in local assemblages was quantified. The metric MPD measures the pairwise phylogenetic distance between each species in the assemblage and ultimately reports the mean phylogenetic distance between all taxa. Thus MPD is generally considered a tree-wide, or basal, metric of the phylogenetic relatedness of co-occurring species (Webb 2000). The metric MMPD measures the phylogenetic distance between each species and it's nearest neighbor on the phylogenetic tree with which it co-occurs in the local assemblage and reports the mean nearest neighbor

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[4] ⟨http://www.phylodiversity.net/phylocom⟩

PLATE 1. A photograph of the San Emilio Forest (foreground) and the Santa Elena Peninsula (background) in Area de Conservacion Guanacaste, Costa Rica. This area was used for the "Region" scale species pool for the San Emilio FDP analyses. Photo credit: N. Swenson.

distance. Thus MMPD is generally considered to be a terminal metric of the phylogenetic relatedness of co-occurring species (Webb 2000).

The observed MPD and MMPD scores for each community were compared to the phylogenetic relatedness of taxa in 1000 randomly generated local assemblages (rndMPD and rndMMPD, respectively). All random local assemblages were generated using an independent swap method (Gotelli and Entsminger 2001) in Phylocom ensuring that the observed species diversity and abundance was maintained in the random assemblages.

A net relatedness index (NRI) and nearest taxon index (NTI) for each local assemblage was then calculated using the following formula (Webb et al. 2002):

$$NRI = -1 \times (MPD - rndMPD)/sdrndMPD$$

$$NRI = -1 \times (MMPD - rndMMPD)/sdrndMMPD$$

where sdrndMPD and sdrndMMPD are the standard deviation of the 1000 rndMPD and rndMMPD values, respectively. Negative values of NRI and NTI indicate higher mean phylogenetic distances than expected given the random assemblages and are indicative of phylogenetic overdispersion. Alternatively, positive NRI and NTI values indicate lower mean phylogenetic distances than expected and are indicative of phylogenetic clustering. To test for significant deviations of NRI or NTI from a null, or neutral, expectation (NRI or NTI = 0) we used a Wilcoxon test. Previous phylogenetic studies of FDPs have shown that the distribution of NRI and NTI scores from multiple equally sized quadrats is generally right skewed (Kembel and Hubbell 2006; N. G. Swenson, B. J. Enquist, J. Thompson, and J. K. Zimmerman, *unpublished data*) thereby making a nonparametric statistical test more appropriate.

Taxonomic scaling

To investigate the effect of taxonomic scale we divided each FDP into eight (BCI and San Emilio) or nine (Luquillo) taxonomic scales. First, each FDP was divided into individual 400-m^2 quadrats from which species composition was recovered. Second, the community phylogenetic dispersion of all species in each of the FDP quadrats was quantified. Next, we moved to

TABLE 1. The number of species in pools (*n*) at each scale utilized and the forest types included in the pool.

Location	0.36 ha		1 ha		FDP		Region		Country		Multiple countries	
	n	Forest types	*n*	Forest types	*n*	Forest types	*n*	Forest types	*n*	Forest types	*n*	Forest types
BCI†	118–144	moist	157–181	moist	301	moist	1270	dry, moist, wet forests	2446	cloud, dry, moist, wet forests	3435	cloud, dry, moist, wet forests
San Emilio	55–74	dry	85–88	dry	173	dry	197	dry forest	2261	cloud, dry, moist, wet forests	3435	cloud, dry, moist, wet forests
Luquillo	49–70	moist	71–87	moist	151	moist	281	cloud, moist, wet forests	738	cloud, dry, moist, wet forests	779	cloud, dry, moist, wet forests

† Barro Colorado Island.

the next most terminal node on the supertree (i.e., tracheophytes to angiosperms, angiosperms to eudicots, and so on) and measured the community phylogenetic dispersion of only those species terminal to that node (i.e., only angiosperms, only eudicots, and so on). This process was repeated until we came to the family level clade, Rubiaceae. The Rubiaceae were utilized as the smallest taxonomic scale because almost every 400-m^2 quadrat in each FDP has at least two species representatives from this family. Although taxonomic levels are admittedly artificial, we consider the hierarchical construct of taxonomy to be a useful heuristic tool in this analysis.

Species pool scaling

To determine the effect of spatial extent of the species pool used to assess the degree of local community phylogenetic relatedness and to quantify the degree to which community phylogenetic results vary along this scaling axis we performed an analyses using 30 randomly selected quadrats from each FDP that were 400 m^2 (0.04 ha) in size. These quadrats served as fixed local assemblages that were then compared to different sized species pools. This quadrat size (0.04 ha, i.e., local assemblage spatial scale) is a typical scale at which investigations of co-occurrence in trees and canopy height measurements in FDPs are performed. It is also the spatial scale at which FDPs typically measure abiotic variables such as elevation, slope, aspect, and soil type (Losos and Leigh 2004). It should be noted that previous scaling work in this field has shown that the phylogenetic dispersion of co-occurring species is also susceptible to scale dependency along a local assemblage spatial scaling axis (Cavender-Bares et al. 2006; N. G. Swenson, B. J. Enquist, J. Thompson, and J. K. Zimmerman, *unpublished data*). The general pattern shows increasing phylogenetic overdispersion with decreasing local assemblage spatial scale.

Six species pools of different sizes were generated separately for each of the three FDPs and each of the 30 local assemblages. The first species pool implemented was 3600 m^2 (0.36 ha). This was done by placing a 60 × 60 m species pool quadrat around the local quadrat (400

m^2) from which species composition could be determined. The second species pool size of 1 ha was determined for each local quadrat using the same methodology (i.e., placing a 100 × 100 m species pool quadrat around the local quadrat). The third species pool size used the species list from each FDP as the next largest species pool for all local quadrats. The fourth sized species pool for Luquillo used the species in the Luquillo Experimental Forest and for San Emilio the combined woody flora of Santa Rosa National Park and Palo Verde National Park (regional pool in Table 1 [Little et al. 1974, Chavarria et al. 2001, Enquist and Sullivan 2001]). The woody flora of the Panama Canal Watershed served as the next biggest pool for BCI (regional pool in Table 1 [Panama watershed tree atlas, *available online*]).[5] The fifth species pool scale used all woody shrub or tree species from the island of Puerto Rico for Luquillo, and for San Emilio and BCI the countries of Costa Rica and Panama (country pool in Table 1 [Little et al. 1974, Boyle 1996; neotropical tree species list, *available online*]).[6] Finally, we compiled species lists of all woody species from Puerto Rico, the U.S. Virgin Islands, and the British Virgin Islands (Little et al. 1974) for the Luquillo species pool and Costa Rica and Panama combined for the BCI and San Emilio FDPs (multiple countries pool in Table 1).

For each species pool generated across differing spatial scales, we constructed a phylogenetic supertree. Then, for each of the local quadrats, a measure of the phylogenetic relatedness of the co-occurring taxa, also described above, was measured. All local measures of phylogenetic relatedness were then compared to the phylogenetic composition of species randomly drawn from each of the species pools constructed at differing spatial scales. This process was repeated for each local quadrat for each species pool size. A breakdown of forest types and species richness in the pools utilized in this study can be found in Table 1.

[5] ⟨http://ctfs.si.edu/webatlas/maintreeatlas.html⟩
[6] ⟨http://ctfs.si.edu/neotropicaltree⟩
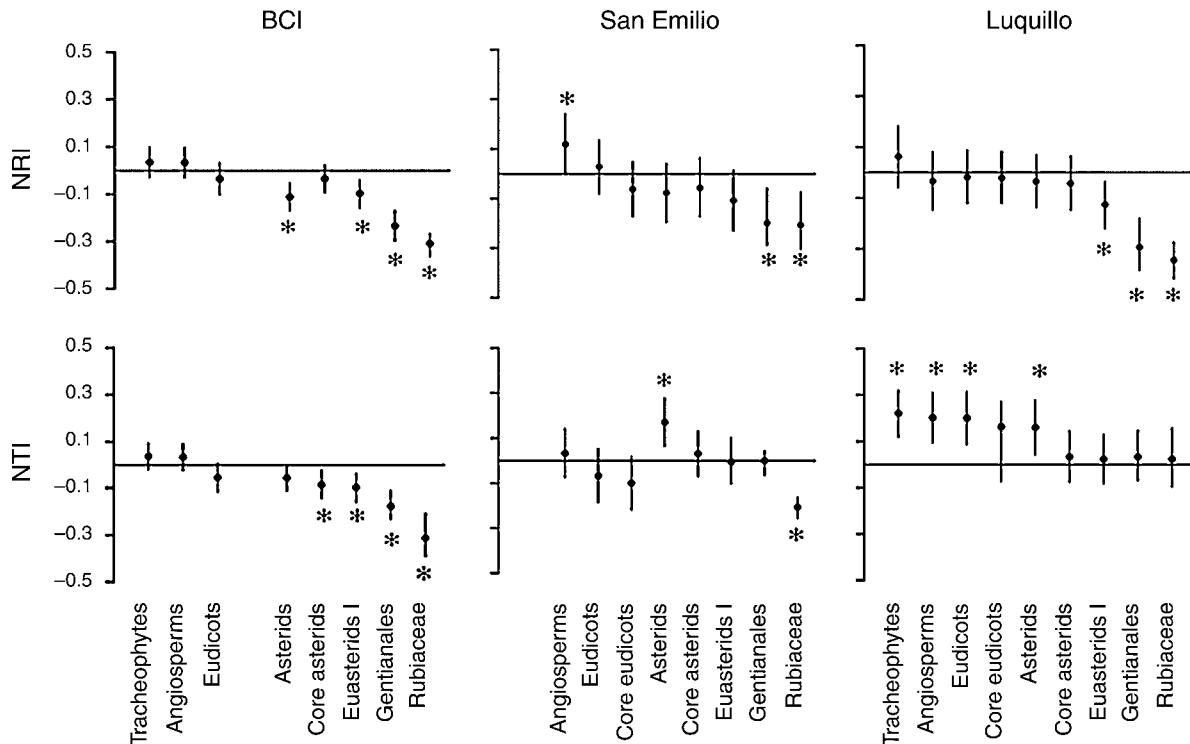
FIG. 1. The median net relatedness index (NRI) and nearest taxon index (NTI) scores for Barro Colorado Island (BCI), San Emilio, and Luquillo forest dynamics plots (FDPs) using eight or nine different taxonomic scales. Positive values indicate phylogenetic clustering, and negative values indicate phylogenetic overdispersion. The bars represent 95% confidence intervals. * $P < 0.05$ (Wilcoxon test).

RESULTS

Taxonomic scaling

Our taxonomic scaling analyses showed that as the taxonomic scale became finer the level of phylogenetic overdispersion increased (Fig. 1). In particular, the distribution of individual quadrat NRI scores was generally indistinguishable from neutral or clustered. In both BCI and Luquillo FDPs this pattern continued until the taxonomic scale of the Euasterid I clade was achieved. However, as taxonomic scale decreased from the Euasterid I clade to the Gentianales to the Rubiaceae clade the phylogenetic structure of the FDP communities became increasingly overdispersed.

All FDP communities, with the possible exception of San Emilio, showed a general pattern of a reduction of neutrality or clustering and a shift towards overdispersion as the taxonomic scale becomes finer (Fig. 1). Although the Luquillo, BCI, and San Emilio NTI scores all decreased with finer scales of taxonomy, the Luquillo NTI scores had a random pattern of phylogenetic dispersion at finer taxonomic scales in contrast to BCI and San Emilio.

Species pool scaling

The phylogenetic structure of 30 randomly sampled 400-m² quadrats from each FDP when analyzed as a whole did not deviate from the null expectation when the species pool changed from 0.36 ha to the entire FDP. As the species pool was scaled out to include the woody taxa from other forest types, other parts of the country or other parts of the continent the local quadrats became phylogenetically clustered when compared to the pool (Fig. 2).

DISCUSSION

Our results show that one's conclusions concerning the relative importance of the forces that structure local assemblages can be significantly altered by the influence of scale alone. Strong scale dependency was detected in each of the scaleable inputs: species pool and taxonomic scale. The taxonomic scaling analysis using the NRI revealed a general lack of evidence for phylogenetic structuring until a single order, Gentianales, or family, Rubiaceae, was included. Cavender-Bares et al. (2006) have also shown that the inclusion of other generic or higher level clades increased the level of phylogenetic clustering detected, but they were uncertain as to the generality of this finding. Our findings, from different tropical forest types, are consistent with the work of Cavender-Bares et al. (2006). Further, our results suggest that there may be a general pattern of scale dependency resulting from the taxonomic delineation of local assemblages where more finely taxonomically
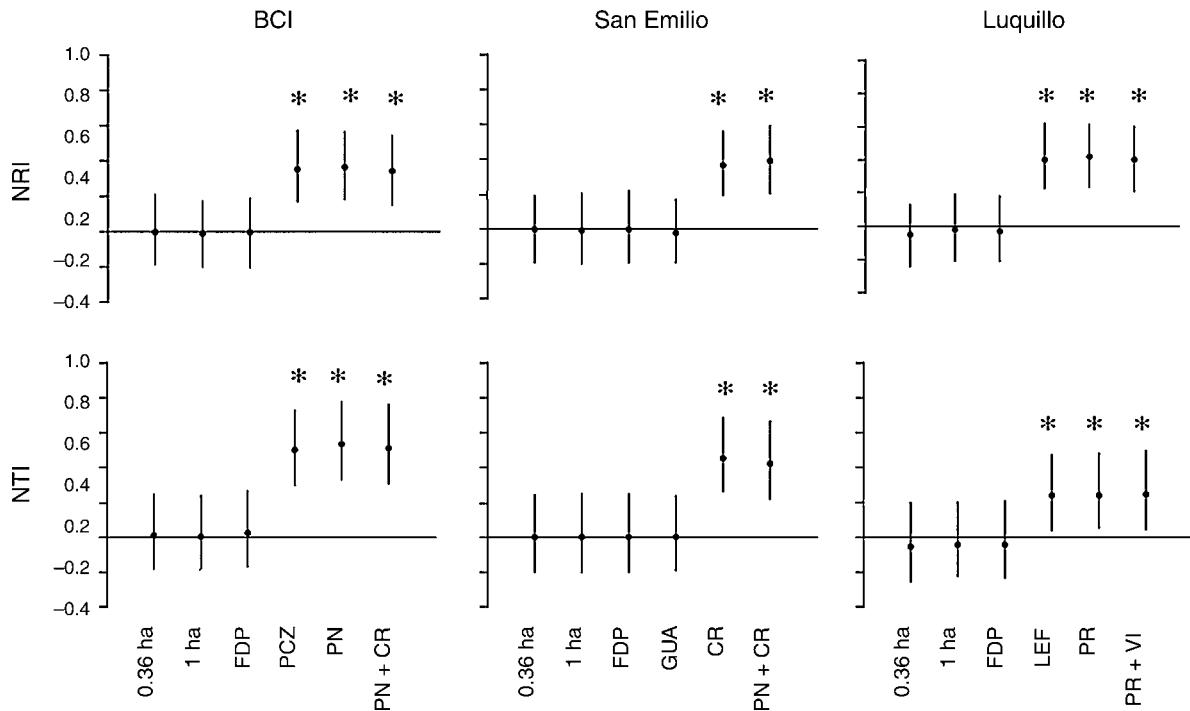
FIG. 2. The median NRI and NTI scores for BCI, San Emilio, and Luquillo FDPs using six different species pool sizes. Positive values indicate phylogenetic clustering, and negative values indicate phylogenetic overdispersion. The bars represent 95% confidence intervals. Key to abbreviations: FDP, forest dynamics plot; PCZ, Panama Canal Zone; PN, Panama; PN + CR, Panama and Costa Rica; LEF, Luquillo Experimental Forest; PR, Puerto Rico; PR + VI, Puerto Rico and the Virgin Islands; GUA, Santa Rosa and Palo Verde National Parks; CR, Costa Rica.

* $P < 0.05$ (Wilcoxon test).

defined communities are more likely to be phylogenetically overdispersed.

Our results also show that the conclusions of phylogenetic analyses of community structure are strongly dependent on species pool size. The present analyses found a large shift toward phylogenetic clustering in the 30 sample quadrats in each FDP when the species pool was increased to include all woody plant taxa in larger geographic regions containing different forest types (Table 1, Fig. 2). Thus, extending the species pool to include taxa residing in additional forest types was sufficient to change how the phylogenetic structure of local assemblages was interpreted. This is especially evident in San Emilio where the phylogenetic relatedness of species was not clustered using the "regional" scale species pool, which did not include other subjectively defined forest types, while clustering was found in all other forests using the "Regional" scale pools that did contain other forest types (Table 1, Fig. 2). However, further broadening of the species pool had little impact over the phylogenetic interpretation of the local quadrats, suggesting that influential clades were no longer being added to the pool. At the same time, phylogenetic clustering, indicative of abiotic filtering, is likely to result from processes occurring on larger spatial and temporal scales (Ricklefs 1987, Weiher and Keddy 1995, Webb et al. 2002).

The existence of widespread scale dependency in phylogenetic dispersion argues for either an explicit discussion of the spatial and taxonomic scale at which a given study was conducted or, preferably, scale sensitivity analyses. Scale dependency and the necessity for a scaling approach should not be considered a problem for phylogenetic investigations of communities. Instead a scaling approach should be seen as a standard methodology for gaining deeper insight from community phylogenetic analyses. Large changes in phylogenetic signals appear to be driven by scale, or shifts between scaling domains sensu Weins (1989). For instance, our species pool results all show a large jump towards phylogenetic clustering. Highlighting such scaling shifts could potentially indicate the spatial scale at which regional processes, biogeographic and/or evolutionary, gain primacy in the structuring of communities (Ricklefs 1987).

While there is no correct or natural scale for an ecological investigation, ecological and evolutionary phenomena are strongly dependent on scale (Levin 1992). A scaling approach reveals general scale dependent patterns that could be utilized in the future to better understand phylogenetic diversity in communities. In sum, our results underscore previous conclusions that community phylogenetics promises to fill an important gap in community ecological and biogeographic research.

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