



Phylogenetic community structure and phylogenetic turnover across space and edaphic gradients in western Amazonian tree communities

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Ecological and evolutionary processes influence community assembly at both local and regional scales. Adding a phylogenetic dimension to studies of species turnover allows tests of the extent to which environmental gradients, geographic distance and the historical biogeography of lineages have influenced speciation and dispersal of species throughout a region. We compare measures of beta diversity, phylogenetic community structure and phylobetadiversity (phylogenetic distance among communities) in 34 plots of Amazonian trees across white-sand and clay terra firme forests in a 60 000 square kilometer area in Loreto, Peru. Dominant taxa in white-sand forests were phylogenetically clustered, consistent with environmental filtering of conserved traits. Phylobetadiversity measures found significant phylogenetic clustering between terra firme communities separated by geographic distances of <200–300 km, consistent within recent local speciation at the watershed scale in the Miocene-aged clay-soil forests near the foothills of the Andes. Although both distance and habitat type yielded statistically significant effects on both species and phylogenetic turnover, the patterns we observed were more consistent with an effect of habitat specialization than dispersal limitation. Our results suggest a role for both broad-scale biogeographic and evolutionary processes, as well as habitat specialization, influencing community structure in Amazonian forests.

The turnover in species composition across space results from the interaction between ecological and evolutionary processes. Dispersal limitation, environmental heterogeneity, interspecific competition, and interactions among trophic levels can influence the spatial distribution of species at multiple spatial scales (Harms et al. 2001, Condit et al. 2002, Fine et al. 2004, Gilbert and Lechowicz 2004). However, the historical biogeography of lineages and the evolution of traits that confer habitat specialization over large time scales also play an important role in determining community composition (Chave et al. 2007, Hardy and Senterre 2007, Chave 2008). Processes such as speciation, extinction, and long-distance dispersal determine which lineages inhabit a particular region, and as such, influence community composition and turnover between communities (Ricklefs and Schluter 1993, Ricklefs 2004, ter Steege et al. 2006, Emerson and Gillespie 2008, Vamosi et al. 2009).

At small spatial scales, community composition is often considered to be a result of processes such as environmental filtering and competitive interactions that sort species from a larger pool (Weiher and Keddy 1999, Webb et al. 2002). This approach typically focuses on small spatial and short time scales and assumes that the pool is fixed, ignoring evolutionary processes. However, at larger scales, the diverse biogeographic history of different areas within a region and

different lineages may also shape patterns of species diversity and turnover (Raven and Axelrod 1974, Harrison and Grace 2007). In addition, features of the environment may drive speciation itself (Hughes and Eastwood 2006) and may cause completely different origination histories and dynamics within regions (Forest et al. 2007).

In order to test the importance of different processes driving patterns of species diversity and turnover within a region, one would ideally transplant each species into every habitat type found within a geographic region and experimentally manipulate all of the abiotic and biotic factors that influence range limits for each species in every community. At the same time, one would also want to know the age of each species, where it speciated, and the dispersal history of its populations. Given the impossibility of gathering all of these data, we can instead take a three-pronged approach to describe patterns of diversity within and among communities.

First, by investigating the patterns of phylogenetic relatedness within communities we can gain a richer understanding of the processes that influence community assembly at both local and regional scales (“phylogenetic community structure”: Webb et al. 2002, Cavender-Bares et al. 2009). However, patterns of community phylogenetic structure have been found to be highly scale-dependent and analyses undertaken at different spatial, taxonomic and

environmental scales result in conclusions that suggest completely different interpretations regarding the relative importance of biotic interactions and environmental filtering in community assembly (Cavender-Bares et al. 2006, Swenson et al. 2006, Kraft et al. 2007, Vamوسي et al. 2009). Second, to address these issues of spatial and environmental scaling, the turnover in species composition among and within habitats can be quantified, and the relative importance of spatial distance and environmental variables can be examined within a Mantel test framework using taxonomic beta diversity (“beta diversity”: Tuomisto et al. 1995, Phillips et al. 2003). Third, we can study how community phylogenetic signal changes across scales, distances, and environments (“phylobetadiversity”: Graham and Fine 2008). By adding this phylogenetic dimension to studies of species turnover, one can test the extent to which environmental gradients and historical biogeography of lineages have influenced speciation, extinction, and dispersal of species throughout a region (Graham and Fine 2008).

Tree communities associated with different soil types in the lowland Amazon basin afford an excellent opportunity to explore how phylogenetic relatedness influences community composition and species turnover across space. Amazonian forests contain the most diverse flora in the world, and understanding the turnover between habitat types in this biome may yield clues towards a fuller understanding of the mechanisms driving the origin and maintenance of such extraordinary species diversity. In the Amazon, the most distinctive edaphic habitat is nutrient-poor white-sand forests which contain an endemic flora and fauna (Alvarez and Whitney 2003, Fine et al. 2010). The tree communities found in white-sand forests are, by Amazonian standards, of extremely low diversity, with

common white-sand endemic species accounting for a great majority of all individual stems (Fine et al. 2010). White-sand forests have very short canopies (some as short as four meters tall) and appear in the landscape as habitat islands and archipelagos, surrounded by other non-flooded, “terra firme forests” growing on other, more fertile soil types (Fig. 1). These forest mosaics are visible from satellite images, and appear as dark spots surrounded by lighter-colored greens that represent high-canopy rain forests growing on clays, loams and brown sands (“terra firme forests”) (see Vriesendorp et al. 2006 for color images). White sands (WS) and (non white-sand) “terra firme” (TF) soils in the Peruvian Amazon have different histories. White sands are derived from Pre-Cambrian sediments and are extremely nutrient poor and have been present in South America for over 200 million yr, thus are older than the oldest angiosperms (Hoorn 1993, 1994, Fine et al. 2005). By contrast, the fertile clay soils of the western Amazon have only been present since the Miocene (<20 million yr); they contain a much higher nutrient availability (Hoorn 1993, 1994, Fine et al. 2005, Frasier et al. 2008) There is very little overlap in species composition between white-sand forests and forests growing on other terra firme soils (Fine et al. 2010).

In the present study we combine analyses of beta diversity, phylogenetic beta-diversity, and community phylogenetic structure of lowland Amazonian tree communities. Each of the processes in Table 1 is associated with a unique combination of predictions for the three analyses with respect to geographic distance and habitat type. By simultaneously considering community phylogenetic structure, beta diversity and phylobetadiversity, we argue that a more complete picture emerges about the relative importance of these processes (Table 1). We use this new

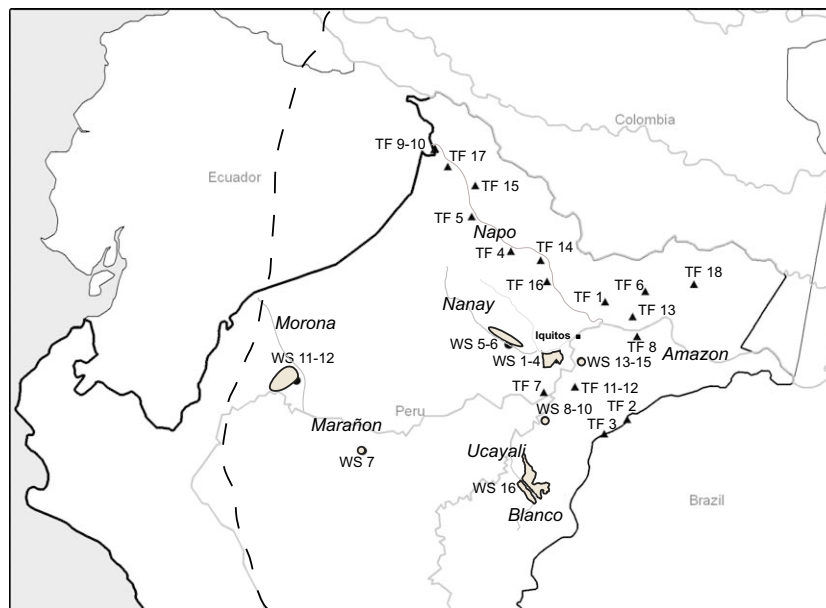


Figure 1. A map showing the locations of the white-sand plots (gray shapes, labeled WS 1–16), and the terra firme plots (triangles, labeled TF 1–18) in northeastern Peru. Rivers are labeled in italics. Dashed line approximates the limit of the Amazonian lowlands (< 500 m a.s.l.). White-sand areas depicted on this map are all of the known ones in the Dept of Loreto, Peru and are drawn to approximate their extent on the landscape (modified from Vriesendorp et al. 2006), with the exception of WS 1–4, which details the boundaries of the Allpahuayo-Mishana National Reserve (of which ca 25% of its area is covered by white-sand forests). See Supplementary material Table S2 for names and coordinates of all plots.

approach to evaluate the relative importance of dispersal, habitat specialization, and speciation in the assembly of tree communities in white-sand and terra firme forests of the Peruvian Amazon.

Methods

Data sets and morphospecies

White-sand and terra firme forests were sampled throughout the Dept of Loreto, Peru (Fig. 1). The region receives >3000 mm of rain annually, with no distinct dry season (Marengo 1998). Nigel Pitman and colleagues provided data for terra firme forest plots (Fig. 1; Supplementary material Table S1, S2). These plots are 1 ha tree inventories including all trees >10 cm diameter at breast height (dbh) of 18 terra firme sites, and none of them sample white-sand forests. Terra firme plots contained 1820 species and morphospecies, out of 10 867 individuals, and averaged 251.7 species per plot. Soil texture analyses (% sand/clay/silt by mass) were performed for the terra firme communities (Pitman et al. 2008).

Because white-sand forests are structurally so much smaller than terra firme forests, it was necessary to modify standard sampling methods developed for terra firme forests to obtain representative samples of white-sand forests. Most inventories of terra firme rain forests in the last few decades have been conducted at the scale of 1 ha, with a dbh cutoff of 10 cm. This protocol allows researchers to sample all of the trees of the midcanopy and canopy and most of the understory tree species. In white-sand forests, trees grow very slowly yet reach reproductive size with trunks smaller than 10 cm dbh (and in the extremely stunted forests, the

great majority of individuals will never approach 10 cm dbh); thus a smaller cutoff is necessary to sample trees in white-sand forests. Another discrepancy is that some white-sand patches are smaller than 1 ha. To overcome these limitations, we sampled white-sand forests in two different ways, trying to sample comparable numbers of individuals as the terra firme plots. For “high-canopy” white-sand forests (canopies at approximately 10–20 m, (n = 13)), 0.1 ha plots were used with dbh cutoffs of 5 cm to obtain a sample of ca 300 individuals per plot. Three of the white-sand plots (WS 6, 10 and 15 in Fig. 1) consisted of stunted forest with 99% of the trees <10 m tall, with most around 5 m in height. To make a representative sample in these forests we made plots of 10 × 25 m (0.025 ha) and inventoried all stems >2.5 cm dbh. In total, 16 white-sand forest plots in seven geographical locations in the state of Loreto, Peru were inventoried by P. Fine and colleagues, during 2001–2004 (Fig. 1, Supplementary material Table S2; see also Fine et al. 2010). White-sand plots contained 221 taxa, out of 3631 individuals, and averaged 36.4 species per plot. Representatives of all species encountered were collected at each site, and voucher specimens from both WS and TF plots are deposited in the Herbario Amazonense (AMAZ) at the Univ. Nacional de la Amazonía Peruana in Iquitos, Peru; WS vouchers are also deposited at the Field Museum of Natural History Herbarium in Chicago, IL (F).

The difference in sampling criteria between white-sand and terra firme forests did not have a large effect on the analyses of phylogenetic community structure or phylobetadiversity, because both sampling schemes exhaustively sampled adult trees in plots of each habitat type, and all samples recorded similar numbers of individuals. The differences in species diversity, and dominance of common

Table 1. Predictions of phylogenetic community structure, beta-diversity, and phylobetadiversity for different processes that influence community assembly of tree communities in the western Amazon. Predictions for phylogenetic community structure are for average patterns found in white-sand (WS) and terra firme (TF) habitats in Fig. 1. Predictions for beta diversity and phylobetadiversity are given for both paired plots of divergent habitat (WS-TF) or same habitat type (WS-WS, TF-TF). The reference pool for the total phylogeny is made of all tree taxa (and individuals) found in WS 1-16 and TF 1-18.

Process	Phylogenetic community structure	Beta diversity	Phylobetadiversity
Dispersal limitation	No prediction ¹	High beta-diversity values across space	Non-random patterns between plots separated by large distances (high phylobetadiversity if close relatives are spatially clumped)
Frequent dispersal among plots	Random patterns	Low beta-diversity values across space	Random patterns with respect to space
Habitat specialization	Non-random patterns within WS and TF plots ²	High beta-diversity between WS and TF plots	Non-random patterns between habitat types (high phylobetadiversity if clustering occurs – low if evenness occurs within habitat types)
Habitat generalization	Random patterns with respect to habitat type	Low beta-diversity across habitat types	Random patterns between habitat types
Frequent (allopatric) speciation within the region	Phylogenetic clustering in a geographically delimited subset of the plots	High beta-diversity between putative radiation center(s)	Low phylobetadiversity if paired sites are within area of in-situ radiation, high if between radiation centers
Infrequent speciation within a region	Random patterns	No prediction	Random patterns

¹Unless there is a phylogenetic component to dispersal ability that covaries with geography in Fig. 1.

²Phylogenetic clustering if traits that promote habitat specialization are phylogenetically conserved; phylogenetic evenness if traits that promote habitat specialization are convergent.

species is a strong pattern, not an artifact introduced by sampling differences, as illustrated by the higher species richness per number of individuals sampled in terra firme habitats versus white-sand habitats (Supplementary material Fig. S1). Nevertheless, it is a fact that fewer individuals per plot were sampled in white-sand forests relative to terra firme forests. To test for an effect of the lower number of individuals in white-sand forests on our results, we rarefied the numbers of individuals in all plots to 200 and recalculated phylogenetic alpha and beta diversity. Rarefied phylodiversity estimates were strongly correlated with non-rarefied estimates (Supplementary material Table S2).

Fine et al. (2010) as well as Pitman et al. (2008) compared dried specimens to mounted vouchers at AMAZ, F, the Missouri Botanical Garden (MO) and the New York Botanical Garden (NY). Specimens that were unable to be identified to species were left as “morphospecies”, but these were always identified to family, and often to genus (Supplementary material Table S1). These were included in the data set with their family, genus (if known) and morphospecies number. Unidentified morphospecies were visually compared to other unidentified species and standardized both within and between plots. We have confidence that very few (if any) of the white-sand unidentified morphospecies are in fact, named TF species or vice versa, because four of the authors from Pitman et al. 2008 and Fine et al. (2010) have worked on the identification of both datasets.

Nevertheless, working with unidentified species does present problems. A complication that could artificially inflate taxonomic beta diversity change with distance is the fact that in the terra firme dataset, there are hundreds of unidentified morphospecies. These morphospecies are generally identified to the level of genus; and we have high confidence (given the expertise of the many botanists involved in these plots) that at any given site, morphospecies diversity very closely matches actual species diversity; yet morphospecies between sites may indeed be the same species but count as separate species. A phylogenetic approach to measuring diversity is not affected by this large number of morphospecies that were encountered in terra firme habitats because morphospecies can be ascribed to their proper genus or family within the phylogeny.

Phylogenetic hypotheses

We assembled a phylogenetic tree by grafting the 1972 taxa present in the community dataset onto a backbone phylogenetic hypothesis using Phylomatic (Webb and Donoghue 2005). The backbone of the tree was the Phylomatic backbone tree version R20070607, based primarily on the APG II phylogenetic classification of angiosperms (Angiosperm Phylogeny Group 2003). Within-family phylogenetic relationships were resolved to the genus level by hand based on information in published phylogenetic trees (Supplementary material Table S4), and branch lengths in the tree were adjusted to match clade age estimates reported by Wikstrom et al. (2001) using the BLADJ algorithm (Webb et al. 2008a). Genera remained polytomies within families, and morphospecies were grafted onto the tree based on the best taxonomic information

available (i.e. a morphospecies identified to genus would be grafted onto the tree at the node containing that genus), while maintaining the age of named nodes on the unresolved tree. To determine the effect of incomplete resolution on measures of phylogenetic diversity, we repeated all analyses on both the tree resolved to the genus level (Fig. 2), and the incompletely resolved tree which was resolved only to the family level. The resolved and unresolved trees were identical with the exception that within-family phylogenetic relationships were collapsed to a polytomy at the crown age of the family in the unresolved tree, maintaining the number of taxa on the phylogeny (1972) but changing the number of internal nodes from 438 to 345. Results from both the resolved and unresolved trees were very similar (Supplementary material Table S5, S6). We used the resolved tree for the analyses reported here.

Phylogenetic community structure

We used two metrics to analyze phylogenetic distances for community structure and phylobetadiversity. The first metric was based on the mean pairwise phylogenetic distances (MPD) among unique taxa (αMPD_i) and individuals (αMPD_i) within communities. The second metric, the mean nearest taxon distance, was defined as the mean phylogenetic distance to closest relative for distinct taxa (αMNTD_i) and individuals (αMNTD_i) within communities.

All of these metrics summarize the average phylogenetic distance among distinct individuals (αMPD_i , αMNTD_i) or taxa (αMPD_t , αMNTD_t) in a local community. Intraspecific phylogenetic distances were assumed to be zero. Observed patterns of each metric were compared to the patterns expected under a null model in which taxa labels were shuffled across the tips of the tree 999 times to generate randomized phylogenetic relationships among taxa while maintaining the observed phylogenetic tree, species abundance distribution, and community structure. Measures of standardized effect size were then calculated for each metric in each community:

$$\begin{aligned} \alpha\text{NRI}_i &= (\text{Mean}(\alpha\text{MPD}_{i \text{ Random}}) - \alpha\text{MPD}_{i \text{ Observed}}) / \text{SD}(\alpha\text{MPD}_{i \text{ Random}}) \\ \alpha\text{NRI}_t &= (\text{Mean}(\alpha\text{MPD}_{t \text{ Random}}) - \alpha\text{MPD}_{t \text{ Observed}}) / \text{SD}(\alpha\text{MPD}_{t \text{ Random}}) \\ \alpha\text{NTI}_i &= (\text{Mean}(\alpha\text{MNTD}_{i \text{ Random}}) - \alpha\text{MNTD}_{i \text{ Observed}}) / \text{SD}(\alpha\text{MNTD}_{i \text{ Random}}) \\ \alpha\text{NTI}_t &= (\text{Mean}(\alpha\text{MNTD}_{t \text{ Random}}) - \alpha\text{MNTD}_{t \text{ Observed}}) / \text{SD}(\alpha\text{MNTD}_{t \text{ Random}}) \end{aligned}$$

where $\text{Mean}(x)$ and $\text{SD}(x)$ are the mean and standard deviation of phylogenetic distances across 999 randomizations. We refer to patterns of communities containing closely related species (NRI or $\text{NTI} > 0$) as phylogenetic clustering and communities containing distantly related species (NRI or $\text{NTI} < 0$) as phylogenetic evenness (Webb 2000). Phylogenetic alpha diversity tests were calculated using the `ses.mpd` and `ses.mntd` functions in `picante` ver. 0.7 (Kembel et al. 2010).

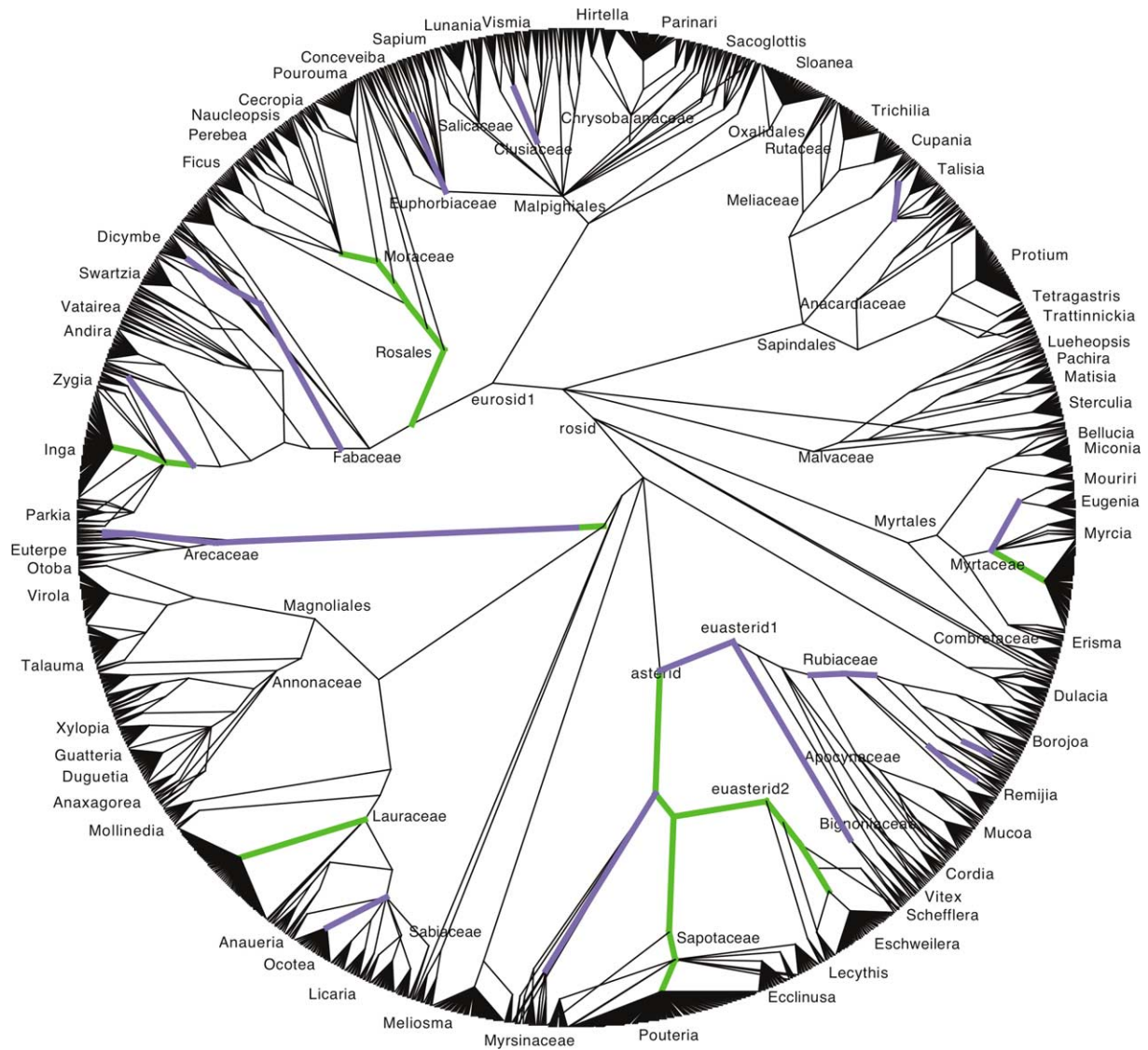


Figure 2. The resolved phylogenetic tree linking 1972 taxa in Amazonian terra firme and white-sand habitats. Edges are shaded to indicate edges descendant from nodes with more descendant taxa in terra firme (green) and white-sand (blue) habitats than expected by chance, versus a null model of 999 randomizations of taxa labels across the tips of the phylogeny including all taxa from both habitats. Shaded edges were in the top 5% of the distribution of numbers of taxa descended from each node obtained from the randomizations. See Supplementary material Table S7 for a complete list of the genera that were found to have significant patterns of association with habitat.

We argue that it is important to analyze community structure and phylobetadiversity focusing on phylogenetic distances both among individuals and among taxa. Calculating phylogenetic distances among individuals and also among taxa in a community allows comparisons of community structure with the influence of rare species on community-wide measures of diversity becoming effectively down-weighted by methods that measure phylogenetic relatedness among individuals. Previous studies have largely measured phylogenetic community structure based on the presence of taxa, rather than incorporating abundance or measuring phylogenetic relatedness among individual organisms (Vamosi et al. 2009). Including both taxon- and individual-based analyses adds an important dimension to studies of phylogenetic diversity, as it allows the separation of effects of ecological dominance versus composition per se

on community structure. While extremely common species or differences in numbers of individuals or taxa among communities could, in theory, overwhelm patterns of phylogenetic structure, we accounted for these factors by comparing observed patterns to a null model that held the number of species or individuals in each community constant while randomizing phylogenetic relationships among taxa or individuals.

Diversification and nodal significance tests

To allow a comparison of diversification patterns between habitats, we identified clades in the phylogenetic tree whose descendants were overrepresented within habitats using the nodesig function in the Phylocom software (Webb et al. 2008a), which compares the total observed number of taxa

or individuals across all communities in each habitat descended from each of the 438 internal nodes in the phylogenetic tree, to the number expected under a null model of shuffling taxa labels across the tips of the entire phylogeny 999 times. Clades whose observed number of descendant taxa or individuals were in the top 5% ($\alpha = 0.05$) of the null distribution in a habitat were considered significantly overrepresented in that habitat.

Beta diversity and phylobetadiversity

Beta diversity was measured based on comparing shared taxa across taxa and individuals in pairs of communities, using the Bray–Curtis distance (Legendre and Legendre 1998) to estimate compositional dissimilarity among samples. Phylobetadiversity was measured in a way analogous to the measurement of phylogenetic community structure. We calculated the mean pairwise phylogenetic distance separating a pair of taxa (betaMPD_t) or individuals (betaMPD_i) drawn from each of two communities, and the mean phylogenetic distance to closest relative in a paired community for all taxa (betaMNTD_t) and individuals (betaMNTD_i) in those communities.

Observed phylobetadiversities were compared to the patterns expected under a null model of random shuffling of taxa labels across the phylogeny, and measures of standardized effect size analogous to the alpha phylogeny measures were computed:

$$\begin{aligned} \text{betaNRI}_i &= (\text{Mean}(\text{betaMPD}_{i \text{ Random}}) - \text{betaMPD}_{i \text{ Observed}}) / \text{SD}(\text{betaMPD}_{i \text{ Random}}) \\ \text{betaNRI}_t &= (\text{Mean}(\text{betaMPD}_{t \text{ Random}}) - \text{betaMPD}_{t \text{ Observed}}) / \text{SD}(\text{betaMPD}_{t \text{ Random}}) \\ \text{betaNTI}_i &= (\text{Mean}(\text{betaMNTD}_{i \text{ Random}}) - \text{betaMNTD}_{i \text{ Observed}}) / \text{SD}(\text{betaMNTD}_{i \text{ Random}}) \\ \text{betaNTI}_t &= (\text{Mean}(\text{betaMNTD}_{t \text{ Random}}) - \text{betaMNTD}_{t \text{ Observed}}) / \text{SD}(\text{betaMNTD}_{t \text{ Random}}) \end{aligned}$$

Negative values of betaNRI and betaNTI indicate high phylogenetic turnover (above the species level) between pairs of communities; positive values indicate that communities contain closely related pairs of taxa or individuals. Beta phylogeny tests were calculated using the comdist and comdistnt functions in Phylocom ver. 4.1 (Webb et al. 2008a). All beta and phylobetadiversity metrics were compared to spatial distances separating plots using a Mantel test (Legendre and Legendre 1998), and to soil texture distances separating plots (% soil texture dissimilarity) for terra firme plots.

We defined communities in this study as co-occurring tree individuals and taxa from the angiosperm clade, an enormous lineage that includes >100 million yr of evolutionary history and hundreds of thousands of species. As a result there are very different inferences that can be drawn from different phylogeny measures. MPD and NRI tend to be more sensitive to tree-wide distributions of lineages, while MNTD and NTI are more sensitive to the distribution of lineages close to the tips of the tree (Webb et al. 2002). Here we refer to phylogenetic diversity

measured using MPD and NRI as “tree-wide” clustering and evenness, and phylogeny measured using MNTD and NTI as clustering and evenness “towards the tips of the tree”. Processes including dispersal, habitat specialization and speciation have very different predicted effects on phylogenetic diversity depending on how it is measured (Table 1). Non-random patterns of MPD/NRI would imply that these processes have occurred in the distant past, i.e. affecting the entire clade of angiosperms, while significantly non-random patterns of MNTD/NTI imply more recent processes, within the past several million years.

Results

Phylogenetic community structure, diversification and nodal significance tests

White-sand forests contain species distributed randomly with respect to the entire tree, but the dominants in white-sand forest are found in just a few clades clustered on the phylogeny (mean alphaNRI_i > 0; Fig. 3). Individual white-sand communities tended to be dominated by a few representatives of each of these clades, leading to phylogenetic evenness towards the tips of the tree (mean alphaNTI_i and alphaNTI_t < 0; Fig. 3). Terra firme forests also contained species distributed randomly with respect to the entire tree, but dominants in terra firme forests were distributed evenly across the entire tree (mean alphaNRI_i < 0), and individual terra firme communities were phylogenetically clustered towards the tips of the tree (mean alphaNTI_i and alphaNTI_t > 0), containing numerous dominant species from closely related groups of species (Fig. 3). These patterns of non-random phylogenetic community structure are consistent with habitat specialization being an important process in community assembly (Table 1). Nodes whose descendants were overrepresented in white-sand and terra firme habitats were found to have significant patterns of association with habitat in 67 of 438 internal nodes (Fig. 2; Supplementary material Table S7).

Beta diversity and phylobetadiversity

Across all communities, plots that were closer together in space were more similar in species composition (Mantel test, Bray–Curtis distance vs spatial distance; Table 3). Similar patterns were seen among terra firme communities and among white-sand communities, with the spatial turnover of species within both habitats stronger when abundance data was used. Comparing observed patterns of phylobetadiversity between communities versus those expected under a null model of permuting taxa labels across the tips of the tree including all species in both habitats, we tested both whether the average standardized phylobetadiversity among communities differed from the null expectation, and for relationships between spatial distance and standardized phylobetadiversity between communities. Pairs of white-sand communities that were closer together in space were more clustered phylogenetically tree wide (Mantel test: betaNRI vs spatial distance; Table 3, Fig. 4), and the average pair of white-sand communities was

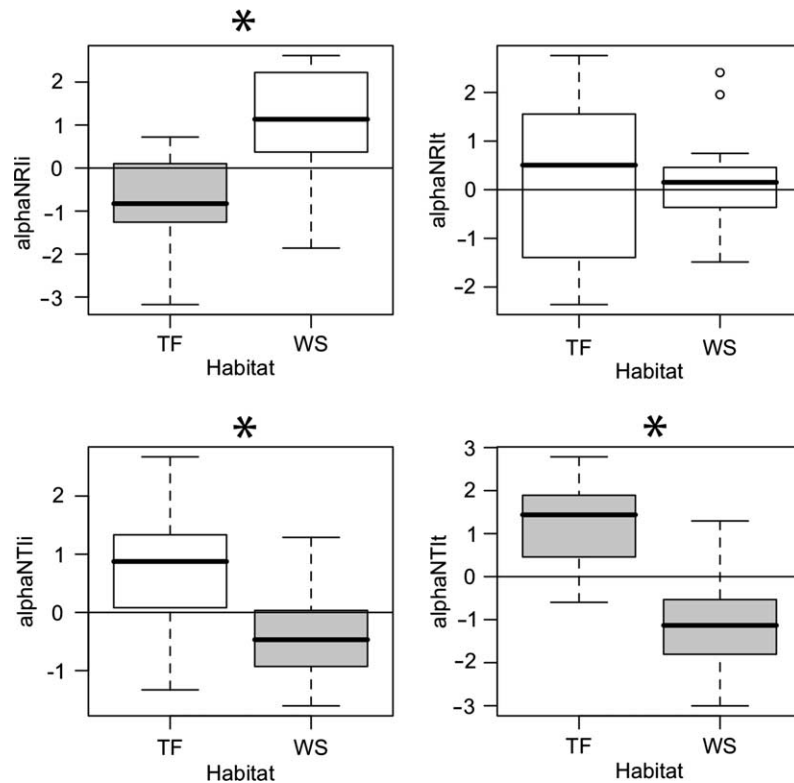


Figure 3. Phylogenetic community structure (alphaNRI and alphaNTI) of communities in terra firme (TF) and white-sand (WS) habitats. Positive values indicate phylogenetic clustering, and negative values indicate phylogenetic evenness, relative to a null model of random shuffling of taxa labels across the tips of the phylogenetic tree including all taxa in both habitats. Shaded bars indicate that phylogenetic structure in that habitat differed from the random expectation (t-test versus expected value of zero, $p < 0.05$). An asterisk symbol indicates that habitats differed from one another in phylogenetic structure (t-test, $p < 0.05$).

phylogenetically clustered tree wide and phylogenetically even towards the tips of the tree.

Taxa in pairs of terra firme forests closer together in space were more phylogenetically clustered tree wide than expected (Mantel test; $\beta\text{a}\text{NRI}_t$ vs spatial distance; Table 3) and dominants were more clustered towards the tips (Mantel test; $\beta\text{a}\text{NTI}_i$ vs spatial distance; Table 3). The average pair of terra firme communities were phylogenetically clustered towards the tips (mean $\beta\text{a}\text{NTI}_i$ and $\beta\text{a}\text{NTI}_t > 0$; Table 2) and dominants in the average pair of terra firme communities were phylogenetically even tree wide (mean $\beta\text{a}\text{NRI}_i < 0$; Fig. 4). The significantly clustered pairs of communities were largely separated by geographic distances of $< 200\text{--}300$ km (Fig. 4), and generally on the same side of the Amazon River (Fig. 5). Among terra firme communities (for which soil texture data were available), soil texture distances among communities were correlated with beta diversity and $\beta\text{a}\text{MNTD}$, indicating that terra firme communities with similar soil texture contained taxa that were phylogenetically clustered towards the tips of the tree (Table 3). Pairs of white-sand and terra firme communities that were closer together in space were phylogenetically clustered tree wide ($\beta\text{a}\text{NRI}$) and phylogenetically even towards the tips ($\beta\text{a}\text{NTI}$) (Fig. 4, 5). Species and individuals in the average pair of communities from contrasting habitats (WS vs TF) were phylogenetically even relative to the null expectation by all measures except $\beta\text{a}\text{NRI}_t$ (Table 2, Fig. 5).

Discussion

What is the relative importance of dispersal limitation and habitat specialization and how do they interact to influence ecological sorting and community phylogenetic structure?

Dispersal limitation and habitat specialization are two factors that are thought to most influence species abundances and distribution in tropical forests (Phillips et al. 2003, Chave 2008). While both are likely to be occurring simultaneously, these two factors are often presented as competing explanations because of the assumptions of neutral theory. According to neutral theory, species are functionally equivalent. Thus habitat specialization to soil type (as well as to any other habitat type) should not be occurring and influencing species distributions; instead, the pattern of aggregated groups of conspecifics is thought to result simply from dispersal limitation alone, given that most seeds of a mother plant will be dispersed to nearby sites (Hubbell 2001). At small scales, such as within 50 ha, this theory has been surprisingly effective in predicting species abundances (Harms et al. 2001, Hubbell, 2001, 2008). However, it is difficult to gauge the importance of dispersal limitation at scales > 50 ha, because other theories (including niche theory) predict that variables such as soil heterogeneity also predict aggregation of conspecifics, and most studies have not disentangled geographic distance and environmental heterogeneity to adequately test neutral

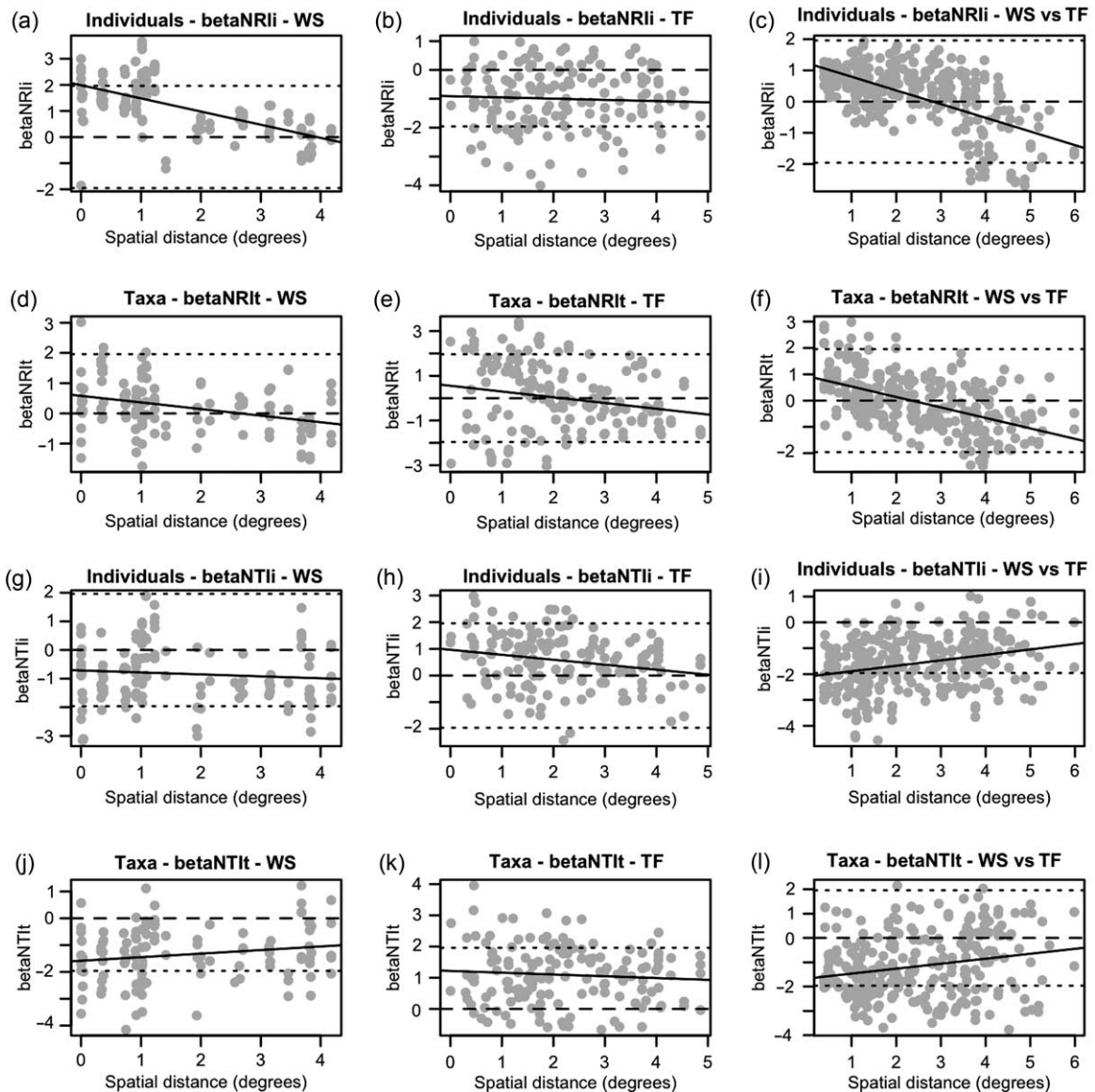


Figure 4. Standardized effect size of phylobetadiversity (betaNRI and betaNTI) versus spatial distance (degrees latitude/longitude) separating communities in terra firme and white-sand habitats. The solid line indicates best fit from regression of betaNRI/betaNTI vs spatial distance. The dashed line represents the expectation under a null model of random shuffling of taxa across the tips of the phylogenetic tree including all species in both habitats (betaNRI/betaNTI = 0), and the dotted lines indicate 95% confidence intervals around the null expectation (mean $\pm 1.96SD$). Positive values indicate phylogenetic clustering, negative values indicate phylogenetic evenness. Pairs of communities outside the 95% confidence interval are significantly more clustered or even with respect to one another than expected. For example, the significant phylogenetic clustering between pairs of TF plots (panels e, h and k) occur above the dotted line mostly between 0–3 degrees of latitude (i.e. in plots located within 0–300 km of each other).

theory (Tuomisto et al. 1995, 2003, Condit et al. 2002, Phillips et al. 2003, Fine et al. 2010).

We find support for species-neutral dispersal limitation in our results. Consistent with predictions from neutral theory (Table 1), we found non-random patterns of species turnover (beta diversity) with spatial distance, irrespective of habitat type (Mantel tests; Table 3). In addition, these patterns were stronger when considering patterns of phylogenetic relationships among individual trees versus collapsing individuals into taxa, consistent with dispersal limitation causing common species to be abundant only in a subset of the plots, but present at low densities at many other plots (Table 3). Yet patterns of spatial turnover in

phylobetadiversity between white-sand and terra firme plots were generally stronger than within-habitat turnover (Table 3). Thus, regarding the relative importance of dispersal limitation and habitat specialization, we propose that dispersal limitation may well explain species abundance dynamics within major habitat types (such as in white-sand forests, nutrient-rich clay soil forests, flooded forests, etc.), but that different assemblages of species are likely to dominate in each habitat type, due to specific adaptations to particular habitats (Pitman et al. 2001).

Taken together, our results provide strong evidence for habitat specialization influencing patterns of tree diversity in western Amazonian forests (see predictions in Table 1).

Table 2. Mean values of standardized phylobetadiversity (betaNRI and betaNTI) in terra firme and white-sand habitats. Positive values of these indices indicate phylogenetic clustering, negative values indicate phylogenetic evenness, relative to a null model of shuffling tip labels across the phylogenetic tree including all taxa in both habitats. Symbols indicate statistical significance of a t-test comparing observed values versus expected value of zero for random data (* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$).

Variable	Habitat	Mean
betaNRIi	WS-WS	1.12 ***
	TF-TF	-1.00 ***
	WS-TF	0.17 **
betaNRIt	WS-WS	0.21 *
	TF-TF	-0.01
	WS-TF	-0.03
betaNTIi	WS-WS	-0.83 ***
	TF-TF	0.56 ***
	WS-TF	-1.59 ***
betaNTIt	WS-WS	-1.36 ***
	TF-TF	1.09 ***
	WS-TF	-1.18 ***

Besides the taxonomic and phylogenetic turnover between white-sand and terra firme plots, we found non-random patterns of phylogenetic community structure in white-sand and terra firme forests (Fig. 3; Table 2). Habitat specialization and environmental filtering lead to phylogenetic clustering when traits that provide advantages in a particular environment are phylogenetically conserved (Table 1). For example, the significant phylogenetic clustering of individuals in white-sand forests ($\alpha\text{NRIi} > 0$; Fig. 3) could result from environmental filtering of lineages that possess traits that lead to dominance in white-sand habitats such as ectomycorrhizal associations (Singer and Araujo 1979, Smith and Read 1997) or other specialized adaptations to counter the extreme nitrogen stress of white-sand forests (Medina and Cuevas 1989, Coomes 1997, Coomes and Grubb 1998).

Alternatively, if traits that promote habitat specialization evolve convergently, one would expect environmental filtering to cause phylogenetic evenness. For example, white-sand communities exhibited significantly non-random patterns of phylogenetic evenness toward the tips (NTIi and NTIt, Fig. 3). Any number of traits that provide an advantage in white-sand forests that are also phylogenetically convergent could interact with environmental filtering to produce these patterns (Table 1). For example, white-sand plants have low foliar N, long-lived leaves, and slow growth rates. Plant species from throughout the angiosperm phylogeny have independently evolved long-lived and short-lived leaves with higher and lower N (Reich et al. 1997, Wright et al. 2004); thus convergent evolution of leaf traits may be interacting with environmental filtering to produce phylogenetic evenness towards the tips in white-sand communities (Fig. 3). Furthermore, because nutrients are so limiting in white-sand forests, it is more difficult for plants to replace tissues that are lost to herbivores and pathogens, thus driving selection for greater investment in plant defenses (Janzen 1974, Fine et al. 2006). Species that are endemic to white-sand forest were found to have significantly higher defense allocation than their congeners that inhabit terra firme forests, providing strong evidence

that total defense investment is a convergent trait for the six tree genera included in the study (Fine et al. 2006).

The non-random phylogenetic community structure patterns we find in our data suggest a role for niche-based community assembly in these forests (Table 1), and we believe that the white-sand–terra firme mosaic found in the western Amazon is an ideal study system to pursue experimental studies about the ecological processes that influence community assembly. However, trait data are not yet available for the thousands of taxa living in these forests. Processes including competition and attack by natural enemies are likely to be important in tropical tree communities, and are best studied by experimental manipulation (Fine et al. 2006, Gilbert and Webb 2007) and at scales smaller than the plot network considered here (Cavender-Bares et al. 2009). Thus, many of the patterns we observed will require trait data and experimental manipulations in order to distinguish among the difference processes that structure these forests (Table 1), and to fully understand the evolution of traits and habitat associations (Fine et al. 2005, Agrawal and Fishbein 2006) and relationships between trait, phylogenetic, and taxonomic diversity along environmental gradients (Kraft et al. 2008, Kraft and Ackerly 2010).

Regional and biogeographic influences on phylodiversity: speciation, dispersal and ecological sorting at large scales

White-sand and terra firme forests of the western Amazon have very different biogeographic histories. Even though the forests are immediately adjacent to each other today, the nutrient-rich clays are Cretaceous sediments that were laid down in the Miocene at the earliest (<20 million yr old; Hoorn 1993, 1994). By contrast, there is ample evidence that similar edaphic environments to current white-sand forests were widespread throughout South America long before Andean uplift, including the northwestern corner which is now called the “western Amazon”, and probably predate the angiosperms (Kubitzki 1990, Struwe et al. 1997, Frasier et al. 2008). How might the variation in age of the habitats influence phylogenetic patterns of community structure in white-sand and clay forests? If there were phylogenetically conserved traits that caused differential colonization of habitat types throughout millions of years, we would expect to find non-random patterns in white-sand or terra firme forests tree-wide (Table 1). This was not the case, as we find little evidence for significant patterns of tree-wide phylogenetic clustering of taxa (NRIi) in either white-sand or terra firme forests (Fig. 3). Clustering patterns tree-wide at large scales are argued to result from in-situ radiations within regions or continents (Table 1; Hardy and Senterre 2007, Webb et al. 2008b). The absence of this pattern suggests dispersal and mixing of angiosperm lineages throughout time within our study region due to frequent connections between rainforest areas on different continents in the last 55 million yr (Davis et al. 2002, Weeks et al. 2005) and the prevalence of long-distance dispersal (Lavin et al. 2004, Pennington and Dick 2004). For rainforests, perhaps the NRI of community

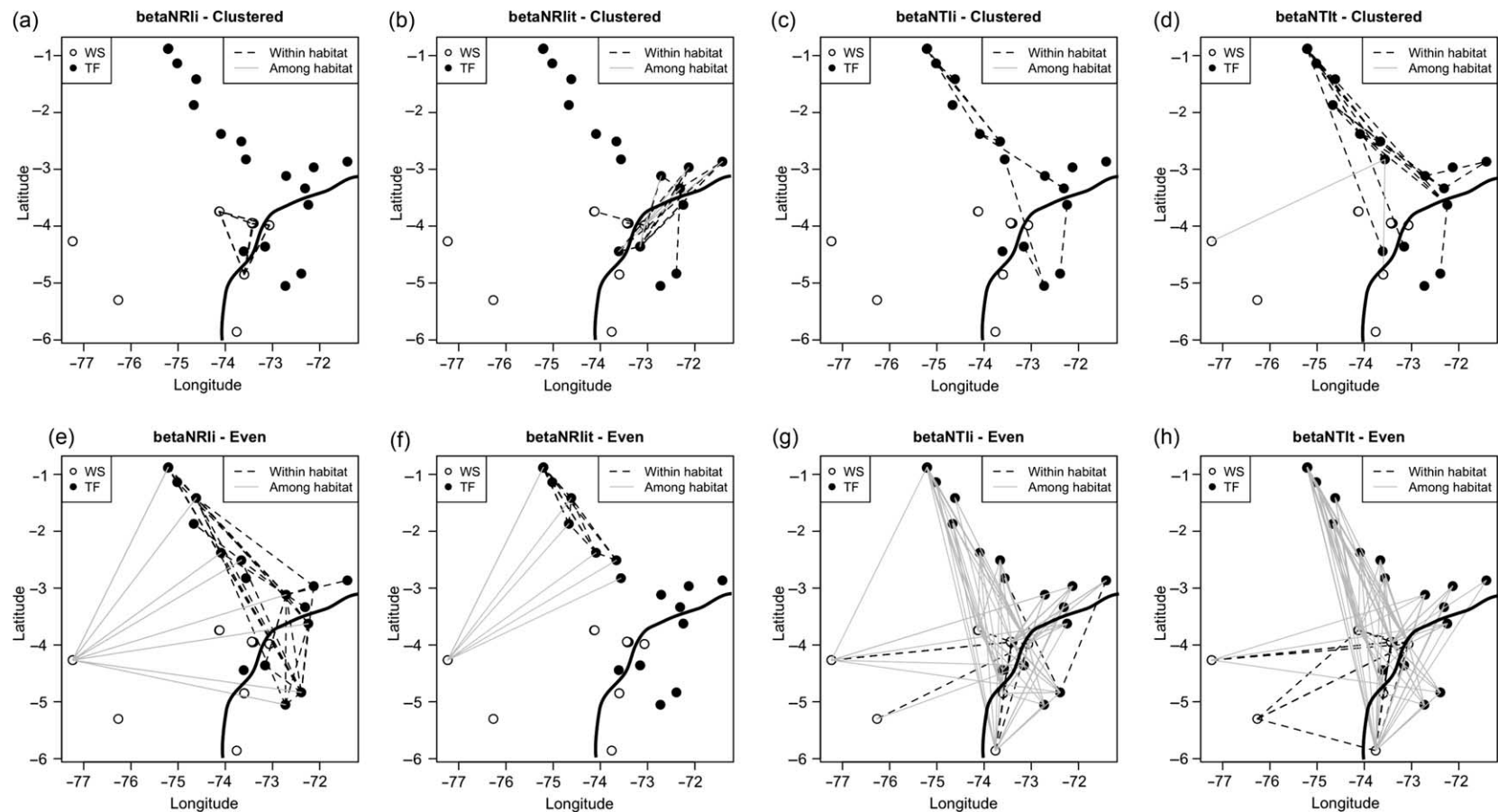


Figure 5. A map of phylobetadiversity comparisons with lines connecting communities whose pairwise phylobetadiversity measured using betaNRIi, betaNRIit, betaNTIi, or betaNTIt were significantly phylogenetically clustered (value > 1.96 , $\alpha = 0.05$, panels a–d) or phylogenetically even (value < -1.96 , $\alpha = 0.05$, panels e–h) relative to the null expectation from a null model of shuffling tip labels across the entire phylogeny. See Fig. 1 to match the points in Fig. 5 to localities; the Amazon-Ucayali River is overlaid over the points (solid black line). The left half of Fig. 5 shows the results of betaNRI (tree-wide phylogenetic patterns of communities) and the right half shows the results of betaNTI (phylogenetic patterns of communities towards the tips). Differences in patterns for NRI and NTI using individuals (which gives more weight to the dominant taxa in a community) vs taxa (all taxa in a community receive equal weight) can be compared between panels a–b, c–d, e–f, and g–h. For example, the north-eastern WS forest plots share dominant taxa (panel a); these four locations contain individuals that are more closely related than expected. The community phylogenetic similarity among these same WS communities is weaker when the dominants are down-weighted (panel b). At the same time, these panels indicate that TF forests in the south-east exhibit phylogenetically significantly similar communities with NRIit, but not with NRIi. Conversely, panels g and h indicate that most of the WS and TF plots are more distantly related (towards the tips) than expected. This pattern is evident whether analyzed with NTIi or NTIt, suggesting that similar processes are simultaneously occurring in the dominant taxa and in the community as a whole.

Table 3. Results of Mantel tests of beta diversity (Bray–Curtis distance) and phylobetadiversity (betaNRI and betaNTI) versus the spatial distance (degrees latitude/longitude) and soil texture distance (% soil/sand/clay texture dissimilarity) separating individuals and taxa from distinct communities in terra firme and white-sand forests. Because the null model used to standardize phylogenetic diversity is based on randomizing the tips of the phylogeny including all taxa from both habitats, soil texture correlations (calculated within TF habitats only) are presented as unstandardized phylogenetic diversity. Symbols indicate the statistical significance of a Mantel test (* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$).

Variable 1	Variable 2	Correlation		
		Comparison	Individuals	Taxa
Beta diversity (Bray–Curtis)	Spatial distance	All	0.22 ***	0.19 ***
		TF-TF	0.26 **	0.19
		WS-WS	0.32 **	0.25 **
		TF-WS	−0.25 ***	−0.17 **
Standardized phylobetadiversity (betaNRI)		All	0.16 **	−0.20 *
		TF-TF	−0.15	−0.26 *
		WS-WS	0.35 *	0.25 *
		TF-WS	−0.60 ***	−0.53 ***
Standardized phylobetadiversity (betaNTI)		All	−0.01	−0.10
		TF-TF	0.24 *	0.24 *
		WS-WS	0.15	−0.06
		TF-WS	0.28 ***	0.22 ***
Beta diversity (Bray–Curtis)	Soil texture distance	TF-TF	0.37 ***	0.36 ***
		Phylobetadiversity (betaMPD)	0.17	−0.23
		Phylobetadiversity (betaMNTD)	0.39 ***	0.40 ***

phylogenetic samples will always yield random patterns at large spatial scales (Webb et al. 2008b).

The fact that white-sand and terra firme soils of the northwestern Amazon have such different histories suggests that patterns towards the tips (NTI) of community phylogeny samples or phylobetadiversity may tell us more about events that have occurred more recently. Different clades toward the tips of the phylogeny dominate different geographic areas within the terra firme forest habitat within our study region. For terra firme forests, communities separated by <2–3 degrees latitude/longitude (~200–300 km) showed the strongest patterns of phylobetadiversity clustering (Fig. 4, 5). Several processes could explain this pattern.

First, there may be some kind of ecological sorting across the terra firme plots related to edaphic properties. Within-habitat phylobetadiversity in terra firme forests was significantly correlated with soil texture and the spatial distance separating communities (Table 3). Phillips et al. (2003) compared tree composition in Holocene and Pleistocene soil deposits in southern Peru, and found results very similar to the ones we report: subtle, though consistent relationships of tree species being associated with one of two soil types (and similar to the terra firme plots in our study, their plots differed in percent clay and percent sand). Pitman et al. (2008) also report a sharp discontinuity in species composition between terra firme plots near the Peru-Ecuador border, corresponding to a shift in soil texture.

A second possibility is that the forests in this region are still recovering, or have recently (in tree generations) recovered from some sort of ancient, catastrophic disturbance. This could include climatological, geological and human-influenced events, for example upheaval from rivers changing course, volcanic eruptions, fires, or flooding events caused by failures of natural dams (Pitman et al. 2005, 2008, Frasier et al. 2008). Pitman et al. (2005) documented a low diversity forest north of our study area that likely was still showing the effects from a catastrophic

flooding event that happened over 500 yr ago. If different plots have recovered from such disturbances at different rates, there may be lineages of plants that successfully compete more strongly in different successional sequences, and that may influence the pattern of phylogenetic clustering towards the tips between different plots.

A third possibility is that the spatial and/or habitat heterogeneity within the terra firme forests in the western Amazon has promoted recent speciation. Gentry (1986) wrote about “explosive” speciation that may have resulted from isolated populations in the Andean cloud-forests responding to local selective pressures. Similarly, during the Pleistocene and/or Pliocene, climate change may have caused forests to become fragmented near the foothills of the Andes (Haffer 1969, Haffer and Prance 2001), resulting in speciation that could have a distinct spatial signature in many areas, especially if climate change caused the forest to become fragmented into dozens of small, isolated forest patches throughout the western Amazon. This refuge theory remains controversial, and many paleoecologists do not agree that the evidence supports a western Amazonian forest landscape that was divided up into many small refuges (Colinvaux and De Oliveira 2001; see review in Frasier et al. 2008). Nevertheless, the phylogenetic clustering of terra firme forests towards the tips of the tree (Table 2) and the large number of (presumably) recently differentiated taxa in those forests both suggest the recent origin of many lineages in the terra firme forests, and an increased diversification rate in terra firme forests relative to white-sand forests since the Miocene, ca 10–20 million yr ago (Antonelli et al. 2009). A majority of the phylogenetically clustered terra firme communities are spatially close together and on the same side of the Amazon River (Fig. 5), thought to be an important biogeographic barrier for other Amazonian taxa (i.e. birds, Capparella 1992, Hayes and Sewlal 2004). Thus, riverine barriers and other factors that cause dispersal limitation may slow recently evolved tree species from expanding their ranges to encompass all of the sites in our study area, even after substantial time.

The three possibilities detailed above are not mutually exclusive, and together they likely contribute to the patterns we find of high phylobetadiversity turnover between terra firme sites. Our results here could be extended by increasing the scale of sampling and bolstering our measurement of soil variables, in order to find out exactly where on the landscape phylogenetic turnover is occurring, and which soil variables might be most important. Phylogeographic studies could be employed to test whether species are undergoing population expansion consistent with either recovery from disturbance or recent speciation combined with dispersal limitation. Moreover, regional clustering within the western Amazon consistent with recent speciation might be detectable in future studies that have the data to expand our scope by including other regional floras (Central America, the Chocó, eastern and central Amazon, the Guianas, southeastern Brazil; even West Africa). For example, phylogenetic analyses of various groups of non-volant mammals have found that western Amazonian species radiated more recently than taxa from the Central Amazon, the Guianas, or southeastern Brazil (Patton and da Silva 1998).

We observed phylogenetic clustering of individuals at white-sand sites, but phylogenetic evenness at terra firme sites (Fig. 3). These divergent phylogenetic structure patterns may relate to the timing of origin and colonization of the white-sand and terra firme habitats in the western Amazon (ter Steege et al. 2006). If the number of individual conspecifics is positively correlated with the age of a species (Hubbell 2001), perhaps differential age could contribute to an explanation of the extremely strong dominance patterns in white-sand forests. Consistent with this notion, we note that all of the over-represented nodes in the white-sand community phylogeny (Fig. 2; Supplementary material Table S7) belong to families present in South America prior to Andean uplift in the Miocene (Romero 1993). Yet, are white-sand endemics necessarily old species? Fine et al. (2005) found that the five species of *Protium* (Burseraceae) found in white-sand forests had independently been derived from older terra firme lineages. However, these five species are not extremely dominant in white-sand forests, leaving open the possibility that dominant species such as *Dicymbe uiaparaensis* (Fabaceae), *Pachira brevipes* (Malvaceae), and several dominant white-sand endemics from the Clusiaceae are extremely old and represent basal species within their respective lineages (such as *Potalia* (Gentianaceae), Frasier et al. 2008).

Conclusions

Our results suggest that the biogeographic history of different habitats along with habitat specialization drives high beta diversity and patterns of phylogenetic community structure both among and within habitats. At the same time, a role for dispersal limitation is suggested by the finding that beta diversity increases with spatial distance, although it is not as strong as the effect of habitat type. Moreover, our results suggest that the influence of biogeographic and evolutionary processes on community phylogeny can interact with the effect of local processes such as habitat specialization and dispersal limitation,

necessitating both phylogenetic community structure and phylobetadiversity measures to understand the relative importance of these processes (Table 1). Phylobetadiversity is a necessary extension of studies of community phylogenetic structure because many of the biogeographic and dispersal-related processes we are interested in studying only make testable predictions about the differences among communities or turnover of phylogeny in space, rather than about the pattern of relatedness in any one local community. This approach places traditional community phylogenetic structure analyses within a framework that can be simultaneously investigated at multiple scales, for both spatial distance and environmental variables (Graham and Fine 2008). Moreover, significant patterns of phylogenetic turnover can be visualized on a map (Fig. 5), affording new insights into particular areas within a region that are most likely to be driving evolutionary processes (Graham et al. 2009). Given the intractability of experimental approaches to resolve these broad-scale biogeographic questions, the approach we have used provides a way to test the relative importance of local and regional processes in generating phylogenetic diversity and influencing the assembly of forest communities within regions.

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