

Phylogenetic alpha and beta diversity in tropical tree assemblages along regional-scale environmental gradients in northwest South America

Sebastián González-Caro¹, María Natalia Umaña²,
Esteban Álvarez^{1,3,*}, Pablo R. Stevenson⁴ and Nathan G. Swenson²

¹ Ecosystem Services & Climate Change Lab, Botanical Garden of Medellín, Medellín, Antioquia 050001, Colombia

² Department of Plant Biology, Michigan State University, East Lansing, MI 48824, USA

³ Department of Ecology, Universidad de Alcalá, Alcalá, Madrid 28801, Spain

⁴ Department of Biological Sciences, Universidad de Los Andes, Bogotá 7495, Colombia

* Correspondence address. Medellín Botanical Garden, CL 73 No. 51D-14, Carrera 43 # 62 26, Medellín, Antioquia 050001, Colombia. Tel: +57-4-444-5500; Fax: +57-4-444-5500; E-mail: esalvarez3000@gmail.com

Abstract

Aims

Environmental gradients are drivers of species diversity; however, we know relatively little about the evolutionary processes underlying these relationships. A potentially powerful approach to studying diversity gradients is to quantify the phylogenetic structure within and between assemblages arrayed along broad spatial and environmental gradients. Here, we evaluate the phylogenetic structure of plant assemblages along an environmental gradient with the expectation that the habitat specialization of entire lineages is an important evolutionary pattern influencing the structure of tree communities along environmental gradients.

Methods

We evaluated the effect of several environmental variables on the phylogenetic structure of plant assemblages in 145 plots distributed in northwestern South America that cover a broad environmental gradient. The phylogenetic alpha diversity was quantified for each plot and the phylogenetic beta diversity between each pair of plots was also quantified. Both the alpha and beta diversity measures were then related to spatial and environmental gradients in the study system.

Important Findings

We found that gradients in temperature and potential evapotranspiration have a strong relationship with the phylogenetic alpha diversity in our study system, with phylogenetic overdispersion

in low temperatures and phylogenetic clustering at higher temperatures. Further, the phylogenetic beta diversity between two plots increases with an increasing difference in temperature, whereas annual precipitation was not a significant predictor of community phylogenetic turnover. We also found that the phylogenetic structure of the plots in our study system was related to the degree of seasonal flooding and seasonality in precipitation. In particular, more stressful environments such as dry forests and flooded forests showed phylogenetic clustering. Finally, in contrast with previous studies, we find that phylogenetic beta diversity was not strongly related to the spatial distance separating two forest plots, which may be the result of the importance of the three independent mountain ranges in our study system, which generate a high degree of environmental variation over very short distances. In conclusion, we found that environmental gradients are important drivers of both phylogenetic alpha and phylogenetic beta diversities in these forests over spatial distance.

Keywords: phylogenetic conservatism, habitat filtering, immigration, environmental gradient

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INTRODUCTION

Quantifying the drivers underlying the spatial distribution of biodiversity within tropical forests is a critical issue in ecology and conservation. Extensive studies have reported moderate to strong correlations between species richness and climatic variables such as temperature and precipitation (Clinebell *et al.* 1995; Gentry and Dodson 1987; Pitman *et al.* 2002; Ter Steege *et al.* 2005). Such work has highlighted the importance of the current ecological settings influencing the diversity, composition and assembly of tropical plant communities. However, our understanding about how biodiversity is distributed along gradients is incomplete because the evolutionary history underlying the spatial patterns is often ignored (Ricklefs 2006). For example, we do not know whether the turnover of species through space is actually the turnover of entire lineages or clades adapted to particular locations along a given gradient. Such a process would result in a high turnover in the phylogenetic composition of communities along an environmental gradient. An alternative scenario would be that closely related species have diverged in their coarse scale habitat preferences occupying different locations along the gradient (Fine *et al.* 2005). This process would result in relatively low phylogenetic beta diversity along an environmental gradient. Therefore, by investigating the phylogenetic structure of communities through space, we can assess the effect of evolutionary history on biodiversity patterns.

Phylogenetically based analyses appear to be a valuable approach to test the relative importance of the evolutionary imprint on present-day patterns of coexistence (Webb 2000; Webb *et al.* 2002). However coexistence mechanisms can be difficult to infer if the phylogenetic signal in trait data is not considered or when the abiotic environment is relatively homogeneous at local scales (Mayfield and Levine 2010). Therefore, phylogenetic information may be best used in ecology on very large scales to detect the non-random distribution of lineages in relation to spatial and environmental gradients.

This moves the phylogenetic approach to studying plant assemblages more toward analyzing the importance of historical or evolutionary processes that explain the vast majority of the variability in species distributions and away from simply analyzing the abiotic versus biotic or niche versus neutral dichotomies (Swenson 2013; Swenson and Umaña 2014).

Given our general understanding that regional-scale processes largely dictate present-day distributional patterns, additional work regarding the phylogenetic structure of assemblages along broad regional-scale gradients is needed. A proposed hypothesis regarding gradients in species richness presumes that species should be best adapted to the conditions where its lineage originated from and movements to other habitats would require evolutionary changes (Ricklefs 2006). Therefore, we would expect closely related species to occupy similar portions of regional-scale climatic gradients and particularly so in relatively stressful portions of those gradients. This mechanism would lead to a turnover of

entire lineages along regional-scale environmental gradients, thereby increasing the phylogenetic beta diversity in a system. Such a framework could be examined by simultaneously integrating phylogenetic alpha and beta diversity metrics for communities arrayed along broad environmental gradients in a region.

Here, we integrate information from 145 tree inventory plots established in a broad range of climatic conditions to assess the relationship between environmental factors and the phylogenetic composition within and between tree assemblages in a tropical region—northwest South America. This region is characterized by a variety of forest types arrayed along broad environmental gradients over short spatial distances (Gentry 1982). In this study, we evaluated several environmental variables associated with temperature, water seasonality and disturbance, which may represent different levels of stress for plant survival and have been strongly correlated with species richness in previous studies (Clinebell *et al.* 1995, Pitman *et al.* 2002). It is hypothesized that the large degree of environmental change over short geographic distances in our study system likely influences the occurrence of entire lineages. In particular, we expect that in lowland forests, characterized by less-stressful conditions and geologically older habitats, there will be assemblages composed of a mixture of distantly related lineages. Conversely, in montane forests that have a geologically younger substrate and more stressful environments, we are likely to see closely related species that have recently colonized these novel and stressful habitats. Given these predictions, we expect that the environment–space interaction will explain a great proportion of the variability in the phylogenetic composition within and between plots. We therefore asked the following specific questions: (i) How does the spatial variation in temperature and water availability influence the phylogenetic structure of tree communities? (ii) Does the phylogenetic structure of different forest types differ, thereby indicating the importance of differential sorting of lineages into specific forest types? and (iii) Does the phylogenetic beta diversity between tree communities turn over faster or slower than that expected given the species turnover along climatic gradients?

MATERIALS AND METHODS

We assembled a database of 145 tree inventory plots from our Colombian study region (Fig. 1). The plots are distributed across broad altitudinal (200–3300 m), edaphic, temperature (12–29°C) and precipitation (1100–8800 mm) gradients. Each inventory plot consisted of 1-ha plots, where all of the individuals with a diameter at breast height ≥ 10 cm were identified to the species. Thus, for each plot, we have a list of species, their sizes and abundances. Overall, we included a total of 4677 species, which account for 65% of the total; the remaining 35% were identified to morphospecies within genera.

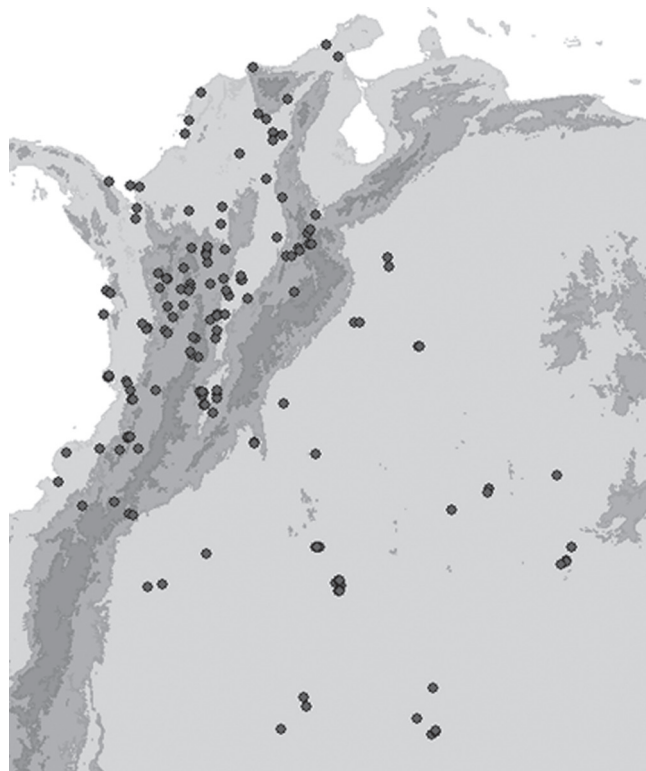


Figure 1: map showing Northwest South America and the distribution of the plots used in this study.

Abiotic variables

This study was focused on quantifying phylogenetic alpha and beta diversities along environmental gradients. To accomplish this, we evaluated six abiotic variables, which have been described as the most relevant factors influencing the patterns of plant species diversity and community dynamics (Currie 1991; Wright 1983). Specifically, we included annual mean temperature (AMT), minimum temperature (TMIN), maximum temperature (TMAX), annual precipitation (AP), minimum monthly precipitation (PMIN), maximum monthly precipitation (PMAX) and potential evapotranspiration (PET). Temperature and precipitation variables were extracted from the WorldClim database (Hijmans et al. 2005, www.worldclim.org) and PET from the Consortium for Spatial Information (www.csi-cgiar.org).

In addition to the continuous climatic variables described above, we used discrete habitat types based on precipitation seasonality, flooding and fragmentation. To accomplish this, we classified the inventory plots into one of three forest types according to their precipitation seasonality: dry, moist and wet, following the categories of Chave et al. (2005). Forests with a pronounced dry season, which imposes an important stress on plant communities, were classified as dry forests (<1500mm/year, >5 months dry season). Moist forests correspond to habitats where evapotranspiration exceeds rainfall during >1 month but <5 months (1–4 months with

1500–3500mm/year of rainfall). Finally, forests with rainfall >3500mm/year and no seasonality were classified as wet forests. Because seasonal flooding has also been shown to be a relevant variable explaining the phylogenetic composition of tropical forests (Umaña et al. 2012), we also classified our plots as *terra firme*, flooded forests with a short flooding season (<3 months/year) and flooded forests with a long flooding season (>3 months/year). Finally, we evaluated the effect of disturbance by classifying our plots into three categories: non-disturbed forests (N); low-disturbance forests (L) where landscape fragmentation occurs within a radius of at least 20 km from the plot; and high-disturbance forests (H) where the fragmentation occurs within a radius of 5 km from the plot.

Phylogenetic alpha diversity

A phylogeny for all species in our database was obtained by using the informatics tool Phylomatic (Webb and Donoghue 2004). Phylomatic uses the Angiosperm Phylogeny Group's APGIII consensus tree (R20120829) as a backbone onto which species are added based on their taxonomy. The phylogeny produced generally had little resolution within genera. Node ages were estimated using the *bladj* algorithm in Phylocom (Webb et al. 2008) and the estimated dates of Wikström et al. (2001). Nodes with no estimated dates in Wikström et al. (2001) were estimated by *bladj* as being equally spaced between two 'known' node dates (Webb et al. 2008). An image of the phylogenetic tree is available in the [online supplementary material](#).

To evaluate the phylogenetic alpha diversity of the tree plots, we calculated two commonly used metrics—the Net Relatedness Index (NRI) and Nearest Taxon Index (NTI) weighted by species abundances (Webb et al. 2008). The NRI index calculates the mean phylogenetic distances (MPDs) among all co-occurring individuals and it therefore indicates the 'basal' dispersion of the lineages within the community. The NTI index measures the mean nearest taxon distance (MNTD) among individuals and it therefore estimates the 'terminal' phylogenetic dispersion of the community. To standardize the observed MPD and MNTD to that expected given the species richness observed, we compared each metric with a null distribution of 1000 random communities constructed using the independent-swap null model (Gotelli 2000) in the software R (R Development Core Team 2012). The regional pool used in these randomizations included all the species occurring in the study plots. We multiplied the NRI and NTI results by -1 such that if the transformed values were >0 , then communities were phylogenetically clustered (closely related individuals co-occurring) and if the values were negative, then communities were phylogenetically overdispersed (distantly related individuals co-occurring).

Phylogenetic beta diversity

To quantify the phylogenetic beta diversity in our study system, we calculated two abundance-weighted metrics—betaNRI and betaNTI. These metrics are analogous to the NRI

and NTI alpha metrics, where the betaNRI calculates the mean phylogenetic distances for each pair of individuals between two communities. This metric has been shown to be equivalent to Rao's dissimilarity (Rao 1982; Swenson 2011) and has a long history of usage in community ecology. The betaNTI calculates the mean nearest phylogenetic neighbor among the individuals in two communities. This metric is similar mathematically and conceptually to traditional metrics of species turnover such as the Bray–Curtis Index (Swenson 2011). As with the alpha metrics NRI and NTI, the beta metrics used the independent-swap null model, and negative values of betaNRI and betaNTI indicate higher-than-expected phylogenetic turnover given the species turnover, meaning that each community generally contains distantly related individuals.

Conversely, positive values indicate lower phylogenetic turnover than expected given the species turnover, meaning that turnover between the two communities occurs between closely related individuals.

Statistical analyses

The central analytical goal of this work is to relate phylogenetic alpha and beta diversities to environmental gradients. Before conducting any of these analyses, we first checked to ensure the normality in our phylogenetic community structure results by performing Shapiro–Wilcoxon tests. Next, we evaluated the influence of continuous environmental variables on the NRI and NTI of a community using a generalized linear model (GLM). We constructed a GLM by including annual mean temperature (AMT), minimum temperature (TMIN), maximum temperature (TMAX), the annual precipitation (AP), minimum precipitation (PMIN), maximum precipitation (PMAX) and potential evapotranspiration (PET) as independent variables. We explored how much the variance (expressed as (null deviance – residual deviance)/null deviance) was explained by each of the environmental variables and by their interacting effects.

In doing so, we selected the best environmental predictors based on the Akaike Information Criterion (AIC) and AIC weight (AICw). To evaluate categorical variables such as forest type (i.e. rainfall seasonality, flooding period and level of disturbance), we performed a *T*-test. In addition, we calculated the percentage of NRI and NTI values that indicated significant clustering (values >1.96) or significant overdispersion (values <–1.96).

To evaluate the relationship between environmental variables and the phylogenetic beta diversity, we used multiple regressions on distance matrices (MRM) available in the 'ecodist' package in R (Lichstein 2007). Because predicted variables are usually correlated with geographic distance, we performed the MRM test controlling for spatial distance. To quantify the spatial distance, we calculated the great circle distance between each pair of plots by using geographic coordinates from each plot and the 'fossil' package in R (Vavrek 2011). In addition, we determined the contribution of each variable to the total variance explained by removing each variable from the full model and calculating the R^2 . We did

not include the values of TMAX, TMIN, PMAX and PMIN in these analyses because the variance explained by these variables was insignificant. This analysis allowed us to determine which independent variables were the best predictors of phylogenetic beta diversity in our study system.

RESULTS

Phylogenetic alpha diversity

The phylogenetic alpha diversity was characterized using the NRI and NTI metrics. Although these metrics do not necessarily co-vary (Webb 2000), they are similar in this study. In general, the results obtained from the GLM showed that NRI and NTI were both positively correlated with temperature variables and PET. Specifically, the AICw scores indicated that the model with annual mean temperature (AMT) was the best at explaining the NRI values and that maximum temperature (TMAX) was the strongest predictor of NTI (Table 1; Fig. 2). In other words, phylogenetic clustering of closely related species increased with temperature and evapotranspiration. However, we found a weak correlation between NRI and NTI with AP (Table 1; Fig. 2C). Finally, we found that the NRI and NTI values in dry forests were on average more phylogenetically clustered than those in wet and moist forests, indicating that lower precipitation levels lead to the co-occurrence of closely related species (Table 2; Fig. 3).

The one instance where the NRI and NTI results were not consistent was when we compared flooded and *terra firme* forests. Specifically, these forests differed in their NTI

Table 1: the results of the GLM for NRI and NTI with the environmental variables

Variable	Coefficient	Pseudo- R^2	AIC	AICw
NRI				
PET	0.56	0.22	483.24	4.34E–03
AMT	0.62	0.26	473.61	5.36E–01
TMIN	0.58	0.23	480.3	1.89E–02
TMAX	0.62	0.26	474	4.41E–01
AP	0.2	0.02	518.85	8.04E–11
PMIN	0.19	0.02	519	7.46E–11
PMAX	0.2	0.02	518.9	7.84E–11
NTI				
PET	0.37	0.12	465.88	0.268
AMT	0.37	0.11	466.63	0.184
TMIN	0.33	0.09	470.65	0.025
TMAX	0.38	0.12	464.54	0.523
AP	0.19	0.03	481.22	0.000
PMIN	0.2	0.03	481.61	0.000
PMAX	0.19	0.03	481.54	0.000

Regression coefficients are standardized to compare the effect of variables. Pseudo- R^2 values are calculated as: (null deviance – residual deviance)/null deviance. Bold numbers represent the best models explaining the NRI and NTI values.

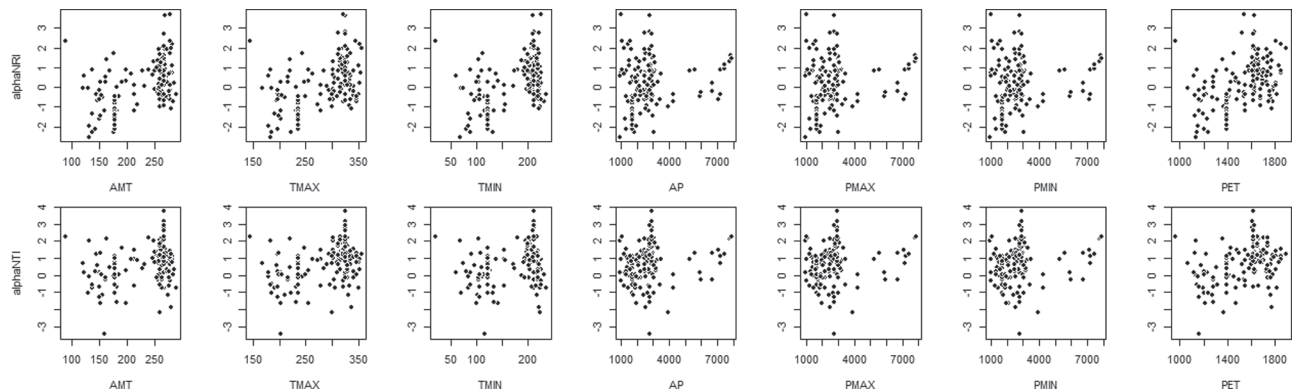


Figure 2: correlation between environmental variables and phylogenetic alpha diversity indexes (NRI or NTI). Environmental variables abbreviations: AMT = annual mean temperature, AP = annual precipitation, PET = potential evapotranspiration, PMAX = maximum precipitation, PMIN = minimum precipitation, TMAX = maximum temperature and TMIN = minimum temperature.

Table 2: the results of the *T*-tests between NTI and NRI values and the discrete environmental variables rainfall seasonality, flooding period and level of disturbance

Variable	Category	Mean	<i>t</i>	DF	<i>P</i> value	Clustered (%)	Overdispersed (%)
NRI							
Rainfall seasonality	Dry	1.28	4.54	18	0.0002	25	0
	Moist	−0.03	−0.009	3	0.92	0	0
	Wet	−0.07	−0.71	120	0.47	12	5
Flooding period	<i>Terra firme</i>	0.02	0.21	117	0.82	14	5
	Flooded	0.5	2.84	18	0.01	4	0
	Swamp	0.33	0.71	6	0.49	10	0
Level of disturbance	None	−0.7	−0.57	76	0.56	15	3
	Low	−16	−0.79	29	0.43	2	8
	High	7	3.33	36	0.002	17	2
NTI							
Rainfall seasonality	Dry	0.85	4.48	18	0.0002	35	0
	Moist	0.13	0.29	3	0.78	9	0
	Wet	0.68	6.56	120	0	26	7
Flooding period	<i>Terra firme</i>	0.62	6.06	117	0	16	0.5
	Flooded	1.09	5.17	18	0	33	4
	Swamp	0.77	1.56	6	0.16	20	10
Level of disturbance	None	0.98	8.49	76	0	29	0
	Low	0.12	0.56	29	0.58	5	5
	High	0.53	3.26	36	0.002	7	2

Percentage values represent the proportion of sites that were significantly clustered and overdispersed assemblages per category. Abbreviations: DF: degrees of freedom

values but not necessarily in their NRI values (Table 2; Fig. 3). Specifically, we found that the NTI values in flooded forests (i.e. floodplains and swamp forests) were on average more phylogenetically clustered than the same in *terra firme* forests, but for the NRI analyses, only floodplain communities were phylogenetically clustered (Table 2; Fig. 3). Finally, communities with high levels of local disturbance were more phylogenetically clustered using both metrics (Table 2; Fig. 3).

Phylogenetic beta diversity

The correlation analyses found that AMT was strongly correlated with PET ($r = 0.51$, $P = 0.001$) and PET was correlated with AP ($r = 0.37$, $P = 0.01$), but AMT and AP were not correlated ($r = -0.12$, $P = 0.067$). These variables were not correlated with spatial distance (AMT-SD: $r = 0.054$, $P = 0.018$; PET-SD: $r = 0.056$, $P = 0.088$; AP-SD: $r = -0.042$; $P = 0.81$) likely due to the cordillera bisecting our study region.

The correlation analyses between phylogenetic beta diversity and the environmental variables had similar results when using either the ‘basal’ (betaNRI) or ‘terminal’ (betaNTI) metrics of phylogenetic beta diversity, although the correlations with betaNTI were slightly stronger (Table 3; Fig. 4). Specifically, we found that betaNRI and betaNTI were negatively correlated with AMT and positively correlated with AP (Table 3; Fig. 4). PET was negatively correlated with betaNTI

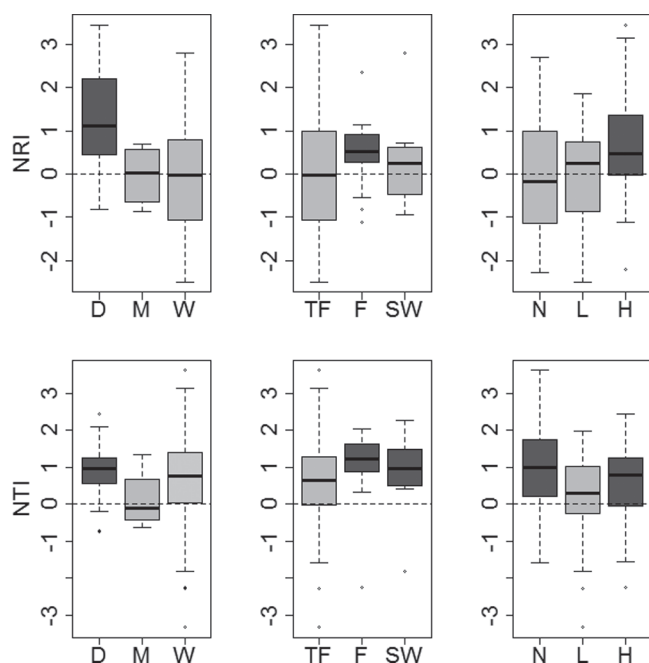


Figure 3: boxplot of phylogenetic alpha diversity indexes distributed on discrete environmental variables and phylogenetic alpha diversity indexes (NRI or NTI). Black boxes represent grouping factors different from zero. Environmental variables abbreviations: D = Dry, F = flood-plains, H = high disturbance, L = low disturbance, M = moist, N = no disturbance, S = swap, TF = *terra firme*, W = wet.

Table 3: the results of the multiple regression analyses on distance matrices (MRM) among beta diversity metrics (betaNRI and betaNTI), environmental factors (AMT, PET and AP) and geographic distance (GEO)

Variable	Coefficient	R^2	Explained variance
Full	—	0.152	—
GEO	4.57E-02	—	0.12
AP	4.67E-05	—	0.04
PET	9.90E-04	—	0.09
AMT	-1.02E+00	—	0.56
Full	—	0.126	—
GEO	4.57E-02	—	0.14
AP	4.67E-05	—	0.04
PET	-9.10E-03	—	0.08
AMT	-1.21E-02	—	0.58

and weakly positive correlated with NRI. Thus, the phylogenetic composition of communities turns over faster than expected given the species turnover along AMT and PET gradients, but more slowly than expected along the AP gradient. In addition, we found a weak correlation between phylogenetic turnover metrics and spatial distance, suggesting that dispersal limitation of entire lineages or closely related species is not influential in this system (Table 3; Fig. 5). Finally, the results showed that environmental variables were more strongly correlated with betaNRI and betaNTI than with spatial distance (Table 3).

DISCUSSION

The present research aimed to investigate the relationship between environmental variables and the phylogenetic structure within and between plant assemblages in a diverse tropical region. Although a few studies in tropical forests have evaluated the role of historical and environmental factors underlying patterns of species composition, a great deal of additional research is needed to fully integrate the evolutionary history into ecological analyses (e.g. Graham and Fine 2008). Here, we evaluated the phylogenetic diversity of plant species within and between inventory plots arrayed along broad environmental and spatial gradients. Our results show that the phylogenetic structure of communities in the study region is best predicted by temperature gradients. Specifically, cool high elevations had higher-than-expected phylogenetic alpha diversity and lowland warm forests tended to have lower-than-expected or not-different-from-expected phylogenetic alpha diversity. This pattern is consistent with previous studies of plant assemblage phylogenetic structure, where highlands had a higher phylogenetic overdispersion and lower-elevation habitats had phylogenetic clustering (Bryant *et al.* 2008).

Several processes may explain the phylogenetic alpha diversity results. First, lower temperatures are associated with high elevations where a combination of conditions such as low solar radiation and freezing also represent strong habitat filters. Such demanding environments are expected to result in repeated convergent adaptation as those observed in Paramo flora. The high-elevation plots in our study are located in three different, but parallel, mountains ranges that emerged at different points in the geological history of the region. Each of these ranges has a distinct gradient in habitat from the lowlands to the highlands. It is likely that separate lineages have converged on the stressful high-elevation habitats, thereby creating a pattern of phylogenetic overdispersion. An alternative plausible hypothesis is that some plant species already adapted to cold conditions (i.e. temperate clades) occupy high-elevation habitats in our study system and these clades are distantly related to other tropically derived lineages found at these same elevations. For example, *Quercus* and *Juglans* are common genera in our high-elevation plots and these taxa represent the contribution of completely novel lineages to the high-elevation assemblages (Van der Hammen 1974).

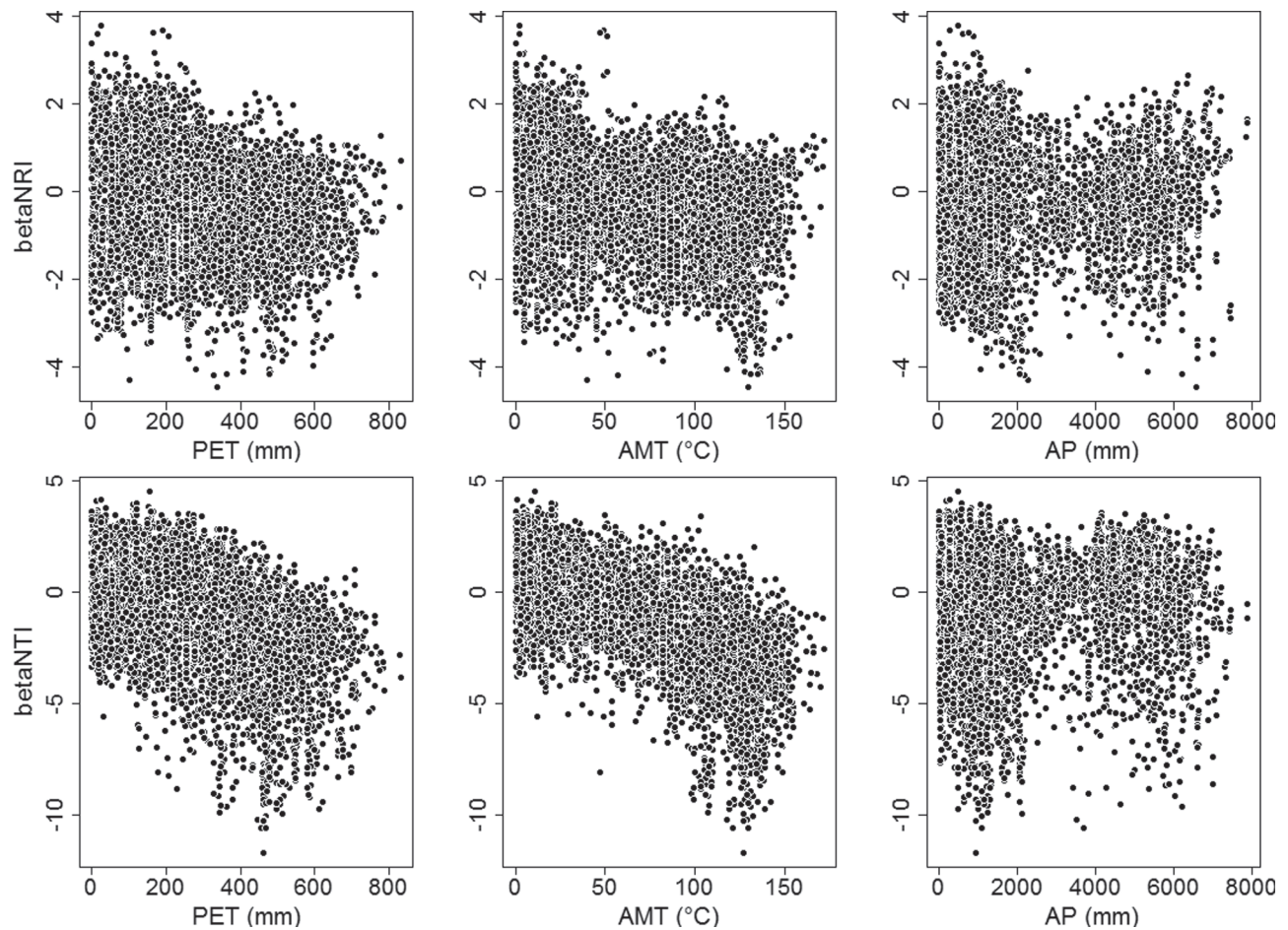


Figure 4: plot depicting correlation between phylogenetic beta diversity metrics and environmental variables. Environmental variables abbreviations: AMT = annual mean temperature, AP = annual precipitation and PET = potential evapotranspiration.

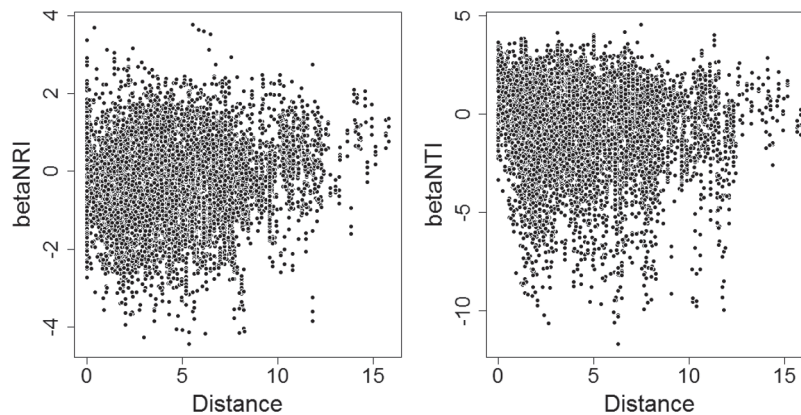


Figure 5: plots depicting correlation between phylogenetic beta diversity metrics and spatial distance.

Overall, both the hypotheses described above are not mutually exclusive and may be responsible for the phylogenetic overdispersion pattern in high-elevation assemblages.

Climatic variables such as annual precipitation (AP) were not significantly correlated with the phylogenetic structure

of the assemblages we studied, but we did find that seasonality in the form of flooding was significantly related to the phylogenetic dispersion of an assemblage. Specifically, the most demanding habitats (dry forests and floodplains) were phylogenetically clustered. Both dry and flooded forests

present substantial hydraulic challenges for tree species and are expected to filter out many lineages not adapted to such stressful habitat types, leaving those that can tolerate the abiotic template to colonize and radiate. For example, recent research has reported that plant clades with particular adaptations to dry forest habitats are the result of recent evolutionary radiations, which would lead to patterns of phylogenetic clustering (Pennington *et al.* 2009).

The level of disturbance is another variable that has been shown to be strongly related to the phylogenetic structure of plant assemblages (e.g. Letcher 2010; Norden *et al.* 2012). The present study found that plots with high disturbance were more likely to be phylogenetically clustered. This result is consistent with previous research and the expectation that disturbance filters out all but a few lineages that can tolerate disturbed conditions (Letcher 2010; Norden *et al.* 2012).

We also evaluated whether the phylogenetic beta diversity between pairs of forest plots was related to their environmental and spatial distances. As expected, we found that environmental variables associated with temperature were strongly associated with the patterns of phylogenetic turnover. That is, sites with lower differences in temperatures had lower phylogenetic compositional turnover than expected, whereas plots with higher differences in temperatures exhibited higher phylogenetic turnover. These results are consistent with the alpha diversity results that suggest that temperature is strongly associated with the within-plot phylogenetic composition. Ultimately, these results may suggest that species tend to conserve their ancestral environmental distributions and limit their movements to other environmental ranges (Eiserhardt *et al.* 2013; Silvertown *et al.* 2006).

Surprisingly, we found that the spatial distance separating two assemblages was not strongly related to their phylogenetic similarity. Many plots used in our analyses are located in high-elevation habitats that are distributed among three mountain ranges that originated independently. Thus, environmental distance is not linearly related to spatial distance in the study system, thereby making pure environmental effects on the phylogenetic composition much clearer than in study systems where environmental and geographic distance strongly co-vary.

In summary, we have found that at higher temperatures, species are closely related and the communities exhibit low turnover, but at lower temperatures, distantly related species co-occur and there is a high phylogenetic turnover among plots. The high-elevation result is likely due to the mixing of tropical and temperate lineages and dispersal limitation of lineages from one mountain range to the next. The lower-elevation results are consistent with a group of tropical clades dominating the community composition and the general lack of any clades typically thought of as temperate. Hence, our results indicate the long-lasting evolutionary imprint on the present-day composition of plant assemblages arrayed along broad environmental gradients in our study region.

Caveats and limitations

The phylogeny used in this analysis presents some limitations due to the low resolution in the terminal branches. Therefore, we could not explore mechanisms such as allopatric or parapatric speciation and distributions of sister species. However, the analyses presented are useful in that they clearly demonstrate the non-random sorting of entire lineages in the study system.

SUMMARY

Based on our findings, we conclude that there is a distinct phylogenetic imprint on the composition of species assemblages in relation to temperature gradients in our study system. From our evidence, we infer that habitat specialization by entire lineages has an important role in structuring tropical tree communities and underlies many distributional patterns in the Andes. Thus, we emphasize that not only contemporary but primarily historical factors also influence the structure of northern South American forests and this can be detected through the integration of phylogenetic alpha and beta diversities along environmental gradients.

SUPPLEMENTARY MATERIAL

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