

# Climatic correlates of phylogenetic relatedness of woody angiosperms in forest communities along a tropical elevational gradient in South America

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## Abstract

### Aims

This study assesses the relationship between phylogenetic relatedness of angiosperm tree species and climatic variables in local forests distributed along a tropical elevational gradient in South America. In particular, this paper addresses two questions: Is phylogenetic relatedness of plant species in communities related to temperature variables more strongly than to water variables for tropical elevational gradients? Is phylogenetic relatedness of plant species in communities driven by extreme climatic conditions (e.g. minimum temperature (MT) and water deficit) more strongly than by climatic seasonal variability (e.g. temperature seasonality and precipitation seasonality)?

### Methods

I used a set of 34 angiosperm woody plant assemblages along an elevational gradient in the Andes within less than 5 degrees of the equator. Phylogenetic relatedness was quantified as net relatedness index (NRI) and nearest taxon index (NTI) and was related to major climatic variables. Correlation analysis and structure equation modeling approach were used to assess the relationships between phylogenetic relatedness and climatic variables.

### Important Findings

Phylogenetic relatedness of angiosperm woody species in the local forest communities is more strongly associated with temperature-related variables than with water-related variables, is positively correlated with mean annual temperature (MAT) and MT, and is related with extreme cold temperature more strongly than with seasonal temperature variability. NTI was related with elevation, MAT and MT more strongly than was NRI. Niche convergence, rather than niche conservatism, has played a primary role in driving community assembly in local forests along the tropical elevational gradient examined. Negative correlations of phylogenetic relatedness with elevation and higher correlations of phylogenetic relatedness with elevation and temperature for NTI than for NRI indicate that evolution of cold tolerance at high elevations in tropical regions primarily occurred at recent (terminal) phylogenetic nodes widely distributed among major clades.

**Keywords:** angiosperm woody plants, community assembly, environmental filtering, niche conservatism, niche convergence, phylogenetic structure, tropical South America

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## INTRODUCTION

Species within any local community are necessarily assembled from the species pool of the region where the local community is located. It is broadly accepted that phylogenetic niche conservatism plays an important role in community assembly. Most of the ancestral clades of current species originated when the planet was predominately under tropical

environments (Behrensmeyer *et al.* 1992; Graham 1999), and cold climate tolerance evolved after the global cooling initiated in the early Eocene (~50 Mya; Graham 2011; Condamine *et al.* 2012), permitting some clades to persist in cold environments. Because ecological traits (e.g. cold tolerance) are phylogenetically conserved (Donoghue 2008) and because evolutionary events that yield novel functions are rare (Latham and Ricklefs 1993; Ricklefs 2006; Wiens and

Donoghue 2004), these evolutionary innovations are thought to have occurred in few clades (Ricklefs 2006). As a result, only a limited number of clades can spread into areas with cold climate in the process of environmental filtering. This process would result in a gradient of increasing phylogenetic relatedness with decreasing temperature. Empirical data from latitudinal gradients and temperate elevational gradients generally support this prediction (e.g. Algar *et al.* 2009; Giehl and Jarenkow 2012; Qian *et al.* 2013, 2014, 2015, 2016), and winter cold temperature has been found as a major driver of phylogenetic structure for these gradients (e.g. Hawkins *et al.* 2014; Qian *et al.* 2013).

However, species of distantly related clades might have evolved the same ecological traits to adapt a particular type of environment. Frequently cited examples of traits evolved to adapt particular environmental stresses include *Lophocereus schottii* and *Euphorbia spiralis*, which belong to distantly related families Cactaceae and Euphorbiaceae, respectively, and have converged on similar strategies to tolerate dry environmental conditions, including stem morphologies that reduce water loss (Gurevitch *et al.* 2002). Several studies have shown phylogenetic structure patterns that are opposite to the patterns predicted by niche conservatism hypothesis for plants in forest communities distributed along tropical elevational gradients. For example, phylogenetic relatedness of woody species decreases with increasing elevation in tropical Asia (Culmsee and Leuschner 2013; Qian and Ricklefs 2016) and tropical America (González-Caro *et al.* 2014; Qian and Ricklefs 2016). This pattern suggests that with increasing elevation and decreasing temperature, woody species in forest communities are more distantly related, suggesting that cold tolerance for plant species across elevations in the tropics evolved among distantly related clades through niche convergence, rather than niche conservatism (Qian and Ricklefs 2016).

Previous studies have examined the relationships between climatic variables and phylogenetic relatedness of angiosperms in local and regional assemblages for latitudinal gradients and elevational gradients in temperate regions, for which niche conservatism has played a key role in community assembly. However, few studies (e.g. Culmsee and Leuschner 2013; Qian 2014, 2017; Qian and Ricklefs 2016) have assessed the relationships for plant species in local forest communities assembled through niche convergence along elevational gradients in tropical regions. In the present study, I analyze a set of forest community samples along an elevational gradient in tropical South America. Qian and Ricklefs (2016) reported that phylogenetic relatedness of angiosperm woody plants in forest communities along this elevational gradient decreases with elevation but no studies have assessed the relationship between phylogenetic relatedness and climate for this tropical elevational gradient. Here, I assess the relation of phylogenetic relatedness of woody angiosperms with multiple climatic variables. In particular, I address the following two questions: (i) Are measures of phylogenetic relatedness of species in communities related to temperature variables more

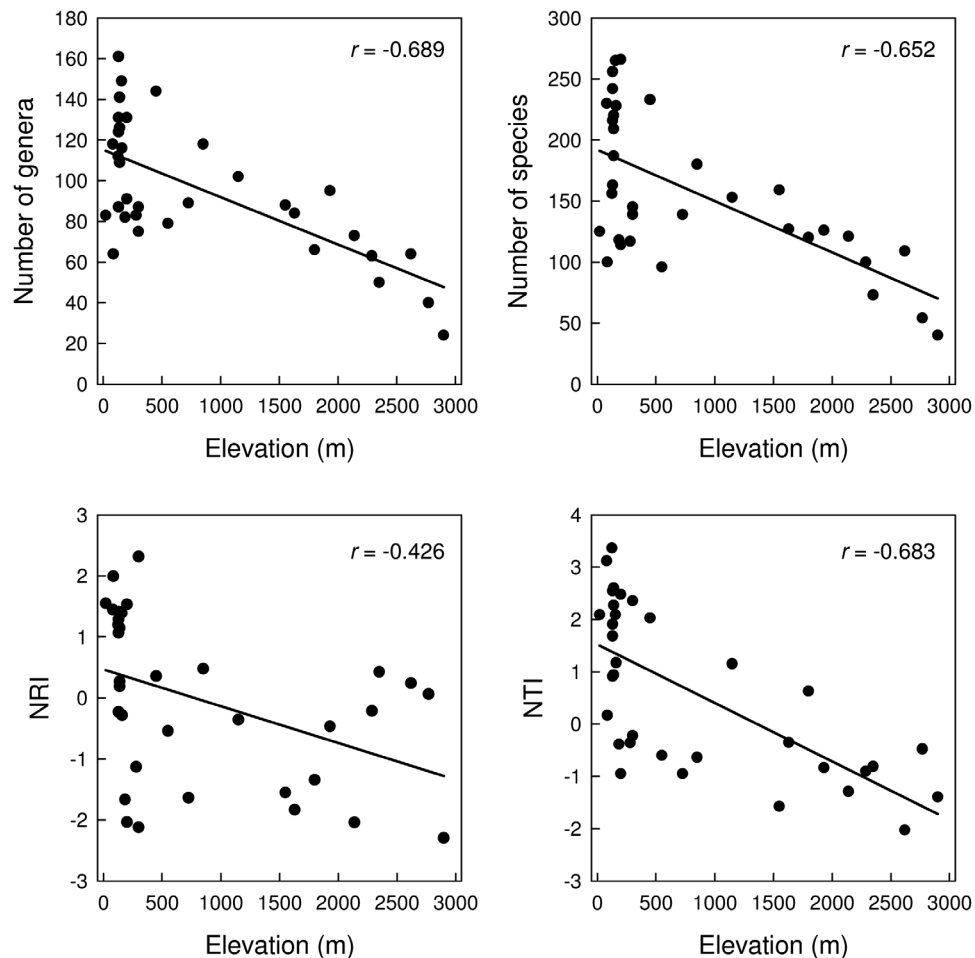
strongly than to water variables for the tropical elevational gradient, as observed in previous macroecological studies (e.g. Moles *et al.* 2014)? (ii) Is phylogenetic relatedness of species in communities driven by extreme climatic conditions (e.g. minimum temperature and water deficit) more strongly than by climatic seasonal variability (e.g. temperature seasonality and precipitation seasonality)? Based on findings of previous studies for other study systems (e.g. Wang *et al.* 2011; Qian *et al.* 2015, 2016), I predict that phylogenetic relatedness is more strongly related to temperature variables than to water variables, and is related more strongly with extreme climatic conditions than with seasonal climatic variability.

## MATERIALS AND METHODS

### The data

Species composition data for angiosperm woody plants used in this study were obtained by the late Alwyn H. Gentry and his coworkers (e.g. Gentry 1982, 1988; Phillips and Miller 2002). The dataset was carefully curated (Phillips and Miller 2002) and the full data set was made available online ([www.mobot.org/MOBOT/Research/gentry/transect.shtml](http://www.mobot.org/MOBOT/Research/gentry/transect.shtml), [www.salvias.net/pages/index.html](http://www.salvias.net/pages/index.html)). I selected a subset of the Gentry plots to include an elevational gradient in tropical South America, within a relatively narrow latitudinal range (between 5°S and 5°N). This included 34 forest communities, distributed from 20 to 2900 m above the sea level (as shown in Fig. 1 of Qian 2014), with the highest elevation just below the alpine tree-line (páramo; Hughes and Eastwood 2006). Because this is a long elevational gradient with great variation in climate, it is appropriate for investigating the relationships between phylogenetic relatedness and climatic variables for species in forest communities. Each sample is 0.1 ha in area with a homogeneous habitat. All woody stems equal to or greater than 2.5 cm diameter at breast height (at 1.3 m above ground) were measured and identified to species or morphospecies (Phillips and Miller, 2002). Botanical nomenclature was standardized according to The Plant List (version 1.1, [www.theplantlist.org](http://www.theplantlist.org)). The dataset included 1904 species in 637 genera.

I related phylogenetic relatedness of species in communities to the following six variables: mean annual temperature (MAT), temperature seasonality (TS), minimum temperature (MT; MT of the coldest month), annual precipitation (AP), precipitation seasonality (PS) and water deficit (WD; difference between annual potential evapotranspiration and annual actual evapotranspiration). These variables are considered major climatic variables driving community assembly of plants and animals (Culmsee and Leuschner 2013; Patrick and Stevens 2016; Qian *et al.* 2007, 2013). For each community, I obtained data for the first five variables from the WorldClim database (Hijmans *et al.* 2005; <http://www.worldclim.org>), which are, respectively, called BIO1, BIO4, BIO6, BIO12 and BIO15 in the WorldClim database, and obtained data for annual potential evapotranspiration and annual actual evapotranspiration from CGIAR-CSI's global aridity



**Figure 1:** relationships of elevation with the number of genera, the number of species, net relatedness index (NRI) and nearest taxon index (NTI).  $P < 0.05$  in all cases.

and PET database and global high-resolution soil-water balance database (Trabucco and Zomer 2009, 2010; <http://www.cgiar-csi.org/data>).

### Phylogeny reconstruction and phylogenetic metrics

I used an updated version of the phylogeny published in Zanne *et al.* (2014), the largest time-calibrated phylogeny of seed plants available to date (Qian and Jin 2016). It was built based on seven gene regions (i.e. ribosomal cluster regions: 18S rDNA, 26S rDNA, ITS, chloroplast genes: *matK*, *rbcL*, *atpB* and the chloroplast *trnL-F* intron) time-calibrated based on fossil data. All families of the angiosperm woody species in the 34 forest communities were resolved in the phylogeny. Of the 637 genera of angiosperm woody plants in the forest communities of the present study, 538 (84.5%) genera were resolved and included in this phylogeny. Because a reliable species-level phylogeny for the present study cannot be reconstructed due to lack of genomic data for most of the species, my analyses were based on a genus-level phylogeny, consistent with previous studies in the current literature (e.g. Culmsee and Leuschner

2013; Jansson *et al.* 2013; Lehtonen *et al.* 2015). I pruned the phylogeny to keep only the 538 focal genera. For the 99 genera found in the 34 forest samples but missing from the phylogeny, I added them to their respective families using Scenario 3 implemented in the S.PhyloMaker software (Qian and Jin 2016; available at <https://github.com/jinyizju/S.PhyloMaker>), which is analog to the approach of using Phylomatic and BLADJ to add unresolved tips (Webb *et al.* 2011). The 99 genera were present at both low and high elevations and the proportion of these genera in a forest plot was low, ranging from 3.6% to 17.5% (mean  $\pm$  standard deviation:  $8.7 \pm 2.7$ ).

Net relatedness index (NRI) and nearest taxon index (NTI) developed by Webb *et al.* (2002), which are the most commonly used indices to quantify phylogenetic relatedness of species in assemblages, were used in the present study. NRI quantifies the mean phylogenetic distance whereas NTI quantifies the mean minimum phylogenetic distance using all possible pairs of genera in a given community. Both indices are based on a null model approach. NRI was calculated as  $[-(\text{MPD}_{\text{obs}} - \text{MPD}_{\text{null}})/\text{sdMPD}_{\text{null}}]$ , where MPD is the mean pairwise phylogenetic distance between all genera within

a community,  $MPD_{obs}$  is the observed MPD,  $MPD_{null}$  is the expected MPD of randomized communities and  $sdMPD_{null}$  is the standard deviation of the MPD for the randomized communities. NTI was calculated using the same formula except that MPD was replaced with mean nearest phylogenetic taxon distance (MNTD). Each NRI or NTI value was calculated based on 999 randomized communities created using the independent swap algorithm (Gotelli and Entsminger 2003). For both NRI and NTI, a positive value indicates phylogenetic clustering, whereas a negative value indicates phylogenetic overdispersion. Species richness per genus was taken into account when calculating NRI and NTI (i.e. resulting values of NRI and NTI were abundance-weighted). NRI and NTI were calculated using Phylocom (<http://phylodiversity.net/phylocom>).

### Data analysis

The amount of the variation in a dependent variable that can be explained by an independent variable may partly depend on the variance of the independent variable; accordingly, I used coefficient of variation to examine the variation of each of the six environmental variables across the elevational gradient. I took two approaches to assessing the relationships between phylogenetic relatedness of species in communities and environmental variables. First, I used the Pearson correlation to quantify the bivariate relationships between variables. Second, I used path analysis (within structural equation modelling, 'SEM') to estimate the direct and indirect effects of environmental variables on phylogenetic relatedness. I used SYSTAT (Wilkinson *et al.* 1992) for traditional statistical analyses and the R package 'lavaan' version 0.5–20 ([cran.r-project.org/web/packages/lavaan](http://cran.r-project.org/web/packages/lavaan)) and R version 3.2.2 (R Core Team 2015) for SEM analyses.

## RESULTS

For the six environmental variables, coefficient of variation ranged from 0.190 to 1.657 for the 34 study forest communities along the tropical elevational gradient (Table 1). In

**Table 1:** coefficient of variation (CV) for each environmental variable and correlation coefficients ( $r$ ) between each environmental variable and elevation (ELEV), net relatedness index (NRI) and nearest taxon index (NTI)

Environmental variable	CV	ELEV	NRI	NTI
MAT	0.190	-0.962*	0.421*	0.712*
MT	0.264	-0.961*	0.402*	0.684*
TS	0.405	-0.452*	-0.098	-0.019
AP	0.317	-0.365*	-0.058	0.363*
PS	0.610	0.133	-0.377*	-0.438*
WD	1.657	0.068	-0.134	-0.293

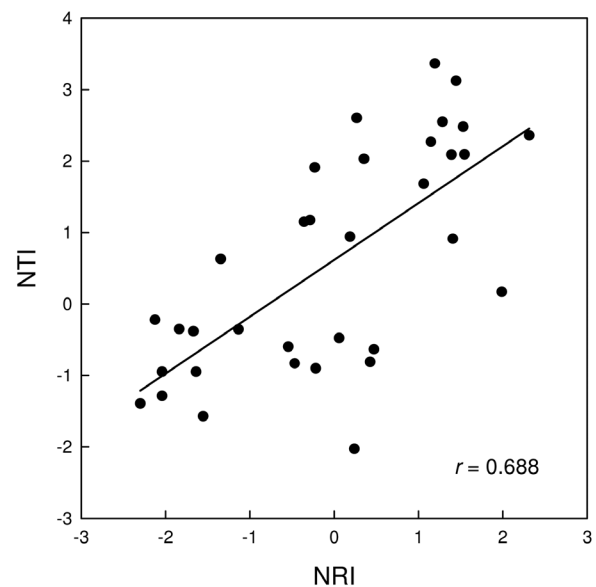
Significant correlations ( $P < 0.05$ ) were indicated with an asterisk. Environmental variables: AP = annual precipitation, MAT = annual mean temperature, MT = minimum temperature of the coldest month, PS = precipitation seasonality, TS = temperature seasonality, WD = water deficit.

general, water-related variables varied more strongly than temperature-related variables (e.g. variation in AP was 1.67 times greater than that of MAT; Table 1). MT was weakly correlated with TS ( $r = 0.402$ ,  $P < 0.05$ ; see online supplementary Appendix S1). MAT and MT were both strongly and negatively correlated with elevation ( $r = -0.962$  and  $-0.961$ , respectively,  $P < 0.05$  in both cases; Table 1). AP was weakly and negatively correlated with elevation ( $r = -0.365$ ,  $P < 0.05$ ; Table 1).

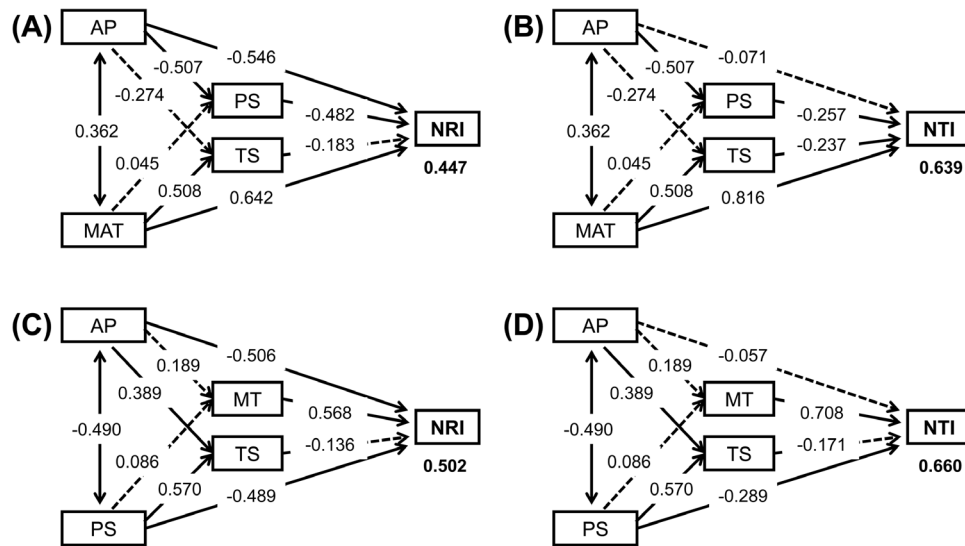
The number of genera and species of angiosperm woody plants in the forest communities was negatively correlated with elevation (Fig. 1). Phylogenetic relatedness also decreased with elevation regardless of whether it was measured using NRI or NTI (Fig. 1). The correlation between NRI and NTI was moderate but significant ( $r = 0.688$ ,  $P < 0.001$ ; Fig. 2).

Phylogenetic relatedness metrics NRI and NTI were most strongly correlated with MAT of the temperature-related variables ( $r = 0.421$  and  $0.712$ , respectively,  $P < 0.05$  in both cases; Table 1). NRI and NTI were most strongly correlated with PS among the three water-related variables ( $r = -0.377$  and  $-0.438$ , respectively,  $P < 0.05$  in both cases; Table 1). On average, temperature-related variables were more strongly correlated with phylogenetic relatedness than were water-related variables, and NTI showed a stronger correlation with environmental variables than did NRI (Table 1).

To simultaneously assess the effects of TS and PS on phylogenetic relatedness while accounting for MAT and AP, I built SEMs in which NRI or NTI was the response, MAT and AP were exogenous variables and TS and PS were endogenous variables. The SEM for NRI explained 44.7% of the variation and that for NTI explained 63.9% of the variation (Fig. 3A and B). The effect of PS was stronger than that of



**Figure 2:** the relationship between net relatedness index (NRI) and nearest taxon index (NTI).



**Figure 3:** structural equation models (SEM) showing relationships among annual precipitation (AP), precipitation seasonality (PS), mean annual temperature (MAT), minimum temperature (MT), and temperature seasonality (TS) in explaining variation in net relatedness index (NRI) and nearest taxon index (NTI) of angiosperm woody plants along the elevational gradient. Numbers on arrow lines are standardized path coefficients; numbers below boxes for NRI and NTI are  $R^2$  values. Path coefficients with dash lines are not significant ( $P > 0.05$ ).

TS regardless of whether NRI or NTI was considered (Fig. 3A and B). I also built SEMs to assess the effects of MT and TS on phylogenetic relatedness while accounting for precipitation. The SEM for NRI explained 50.2% of the variation and that for NTI explained 66.0% of the variation (Fig. 3C and D). The effect of MT was much stronger than that of TS regardless of whether NRI or NTI was considered (Fig. 3C and D). The effects of TS were not significant ( $P > 0.05$ ) in either model.

## DISCUSSION

In this study, I have explored the relationships between phylogenetic relatedness of angiosperm woody plants and environmental variables in local forest communities along a broad elevational gradient in tropical South America. I found that phylogenetic relatedness of angiosperm woody species in the local forest communities is more strongly related with temperature-related variables than with water-related variables, is positively correlated with MAT and MT and is related with extreme cold temperature more strongly than with seasonal temperature variability. The detected patterns are discussed below.

Temperature and precipitation are major determinants of patterns of species richness and composition (Ricklefs 2008). The niche conservatism hypothesis suggests they are major drivers of community assembly at a broad spatial scale (Latham and Ricklefs 1993; Wiens and Donoghue 2004). Here, I found that MAT and MT were associated with phylogenetic relatedness of species more strongly than was precipitation, even though precipitation varied across the study sites more strongly than did temperature (Table 1). Previous studies (e.g. Moles *et al.* 2014) also showed that temperature plays

a more important role than precipitation in shaping macroecological patterns of plants.

Environmental stress (tolerance) hypothesis has been considered as a major mechanism driving species richness and distribution (Latham and Ricklefs 1993); strong correlations between MT and species richness observed in empirical data (e.g. Qian *et al.* 2007; Wang *et al.* 2011) are consistent with this hypothesis. However, some studies (e.g. Wiens *et al.* 2006) have found that TS is more strongly correlated with species richness and distribution than MT, which is consistent with the environmental stability hypothesis. Because nearly all the studies that investigated the relative importance of MT and TS on species richness and distribution were conducted across latitudes and because MT and TS are strongly correlated along latitudinal gradients, the independent effect of each of the two variables cannot be determined for latitudinal gradients. In the present study, MT and TS were not strongly correlated ( $r = 0.402$ ). Phylogenetic relatedness of angiosperm woody plants was significantly correlated with MT ( $r = 0.402$  and  $0.684$ , respectively, for NRI and NTI; Table 1) but was unrelated with TS (Table 1), even in the case that TS varied more strongly than did MT among the study communities (Table 1). When the effects of MT, TS and PS on phylogenetic relatedness of species were assessed simultaneously in a structure equation model, MT was found to exert the strongest effect (Fig. 3C and D). Thus, the present study supports the notion that cold temperature extreme plays a more important role than climatic seasonality in driving phylogenetic relatedness of species in the elevational gradient examined here.

This study found that species in local communities are more distantly related with decreasing temperature (e.g. MAT, minimal temperature of the coldest month). This pattern is

contrary to the niche conservatism hypothesis but is consistent with the niche convergence hypothesis (Qian and Ricklefs 2016). The pattern found in this study is also consistent with patterns found in previous studies on plants for other tropical elevational gradients. For example, González-Caro *et al.* (2014) studied trees in forests across a broad Colombian elevation gradient (ranging from 200 to 3300 m). They showed that both NRI and NTI were positively correlated with temperature variables (including MAT and MT of the coldest month). Similarly, Culmsee and Leuschner (2013) showed that both NRI and NTI for trees in forests along an elevational gradient ranging from 650 to 3435 m in Malesia are positively correlated with MAT. The consistent relationship between phylogenetic relatedness and temperature found in all three studies suggests that the positive relationship between phylogenetic relatedness and temperature is a robust pattern for angiosperm woody plants in local forest communities along tropical elevational gradients. Qian and Ricklefs (2016) proposed a hypothesis to explain why phylogenetic relatedness of angiosperm woody plants increases with latitude but decreases with elevation in tropical regions. However, phylogenetic relatedness increases with increasing elevation (and thus with decreasing temperature) for animal communities in tropical South America [e.g. hummingbirds (Graham *et al.*, 2009), frugivorous birds (Dehling *et al.*, 2014) and moths (Brehm *et al.*, 2013)]. It is not clear why community assembly patterns would differ between animals and plants along elevational gradients in tropical regions.

This study found that NTI was more strongly correlated with elevation, MAT and MT than was NRI. This finding is again consistent with the finding of Culmsee and Leuschner (2013). NTI and NRI measure different evolutionary characteristics of communities. NTI is a measure of phylogenetic dispersion based on the relationships among branch-tips in a phylogenetic tree (i.e. nearest neighbors on branch-tips), regardless of the arrangement of higher-level lineages in the phylogenetic tree. Thus, NTI assesses fine-scale relatedness divergence (Webb 2000; Webb *et al.* 2002). In contrast, NRI is a measure of 'basal or tree-wide phylogenetic dispersion' (Webb *et al.* 2006). In principle, NTI and NRI may show different patterns for the same species assemblage. The positive relationship between NTI and NRI that was found in the present study suggests that evolution of the traits (e.g. cold tolerance) that determine the assembly of species in the species pool into different communities along the elevational gradient is consistent between deep and shallow nodes across the phylogenetic tree. Furthermore, negative correlations of phylogenetic relatedness with elevation and higher correlations of phylogenetic relatedness with elevation and temperature for NTI than for NRI indicate that evolution of cold tolerance at high elevations in tropical regions occurred at recent (terminal) phylogenetic nodes widely distributed among major angiosperm clades.

## SUPPLEMENTARY MATERIAL

Supplementary data are available at *Journal of Plant Ecology* online.

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