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Latitudinal gradients of associations between beta and gamma diversity of trees in forest communities in the New World

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Abstract

Aims
We analyze two continental data sets of forest communities from across the New World to examine the latitudinal gradients of beta diversity after accounting for gamma diversity and the latitudinal gradient of gamma diversity after accounting for beta diversity.

Methods
Correlation and regression analyses were used to relate beta and gamma diversity to latitude along two latitudinal gradients in the New World (one including 72 forest sites located south of the equator and the other including 79 forest sites located north of the equator).

Important Findings
Beta diversity and gamma diversity were negatively correlated with latitude. Beta diversity was strongly and positively correlated with gamma diversity (Pearson's correlation coefficient: 0.783 for New World North and 0.848 for New World South). When beta diversity was regressed on latitude and gamma diversity, 69.8 and 85.7% of the variation in beta diversity were explained, respectively, for New World North and New World South. When gamma diversity was regressed on latitude and beta diversity, 81.8 and 84.3% of the variation in gamma diversity were explained, respectively, for New World North and New World South. After statistically removing the relationship between beta and gamma diversity, latitude has weak or no relationships with beta and gamma diversity. However, strong positive correlations between beta and gamma diversity may not be considered as evidence of one driving the other along a latitudinal gradient.

Keywords: β diversity • γ diversity • community composition • latitudinal diversity gradient • tree species richness

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INTRODUCTION

Understanding spatial variation in species diversity is one of the main goals in ecology. The latitudinal diversity gradient, which is defined as an increase in the number of species per unit area from poles toward the equator, is one of the most striking patterns of life on earth. However, the causes of the latitudinal diversity gradient remain poorly resolved (Mittelbach *et al.* 2007). Species diversity is often described with three components: alpha, beta and gamma diversity (Whittaker 1972). Alpha diversity measures species richness within local sampling units, gamma diversity measures total species richness in a region, which includes the local sampling units that quantify the alpha diversity of the region and beta diversity quantifies the variation in species composition among the local sampling units and thus represents the scalar that links alpha and gamma diversity and unifies local-regional diversity relationships (Ricklefs 1987). All the three components of species diversity generally decrease with increasing latitude (Chen *et al.* 2011; Qian and Ricklefs 2007). Understanding the origin and maintenance of the latitude diversity gradient is a major challenge to ecologists.

Kraft *et al.* (2011) conducted a global examination of the latitudinal gradient of beta diversity after accounting for gamma diversity. Specifically, they used a modified version of Whittaker's (1960) beta diversity index to quantify observed

beta diversity for each forest site, used a null model approach to determine expected beta diversity and related standard differences between the observed and expected values of beta diversity (i.e. standardized beta deviation) to absolute latitude (i.e., positive values for latitudes regardless of whether they are in the Northern Hemisphere or Southern Hemisphere). Because they found that standardized beta deviation is not linearly correlated with absolute latitude, they conclude that there is no need to invoke differences in the mechanisms of local community assembly in tropical and temperate regions to explain patterns of beta diversity. However, their null model, on which their conclusion is based, is not a valid null model for investigating beta diversity gradients driven by mechanisms of local community assembly because their null model incorporates species abundance distributions and because species abundance distributions are driven by mechanisms of local community assembly (Cheng *et al.* 2012) and in turn generate beta diversity gradients (Qian *et al.* 2013). Therefore, Kraft *et al.*'s (2011) conclusion is invalid. Furthermore, their approach considers the correlation between beta and gamma diversity as a result of the effect of gamma diversity on beta diversity. However, the correlation may be alternatively considered as a result of the effect of beta diversity on gamma diversity (Qian *et al.* 2005, 2013; Rodríguez and Arita 2004; Srivastava 1999; Willig *et al.* 2003).

Regardless of what factors result in the correlation between beta and gamma diversity, a necessary first step for understanding the correlation is to determine if one diversity (e.g. beta diversity) is still correlated with latitude after accounting for the other diversity (e.g. gamma diversity). In the present study, we analyze two continental data sets of forest communities from across the New World to examine the latitudinal gradients of beta diversity after accounting for gamma diversity and the latitudinal gradient of gamma diversity after accounting for beta diversity.

MATERIALS AND METHODS

Data used in this study were obtained from Gentry's data set located at www.wlbcenter.org/gentry_data.htm (the same data set is also available at www.mobot.org/MOBOT/Research/gentry/transect.shtml and salvias.net/Plots/index.php). The data set includes 197 forest plots that are 0.1 ha in size with ten 0.01-ha subplots (each being 50 m long). Because the ten 50-m-long subplots of each plot were placed in a random zig-zag pattern within the plot (Phillips and Miller 2002), spatial extent presumably varies among plots. However, there is no evidence that there is a latitudinal trend in the variation of spatial extent. These 197 plots were used in Kraft *et al.* (2011). Woody stems ≥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). Of the 197 Gentry's plots, 158 (80%) are located in the New World; the remaining 39 plots are scattered in the four continents of the Old World, and no meaningful latitudinal gradients can be assembled from the 39 plots. Thus, we assembled two latitudinal gradients from the New World plots: one includes all 72 plots located south of the equator and the other includes 79 plots located north of the equator and east of 100° W longitude (Fig. 1). We excluded a few plots in the western coast of North America because the same temperature at a latitude in eastern North America can be found at a latitude >20° further northern in western North America or temperature at the same latitude can differ by >15°C between eastern and western North America (Ahrens 2007). Information for latitude, longitude and elevation of each plot was obtained from Phillips and Miller (2002). The 72 plots in the New World South cover a latitudinal gradient of 40°, and the 79 plots in the New World North cover a latitudinal gradient of 47° (Fig. 1).

Elevation varies greatly among plots within each data set (ranging from 10 to 2940 m in New World North and from 20 to 2770 m in New World South) and there are significant relationships between the elevation and latitude of the plots (e.g. $r = -0.356$, $P < 0.05$, for the New World North data set), indicating that plots at lower latitudes tend to be higher in elevation. The average temperature lapse rate, at which the air temperature decreases with elevation, is ~6.5°C for every 1000-m rise in elevation (Ahrens 2007). An upward shift of 100 m is predicted to translate into a polarward shift of 100 km in the temperate zoon (Jump *et al.* 2009; Stephenson and Das 2011). Accordingly, we used latitudes after correcting for variation in elevation based on the converter of 100-m elevation for 100-km latitude (Qian *et al.* 2012).

We used the same approach as in Kraft *et al.* (2011) to quantify alpha, beta and gamma diversity for each plot.

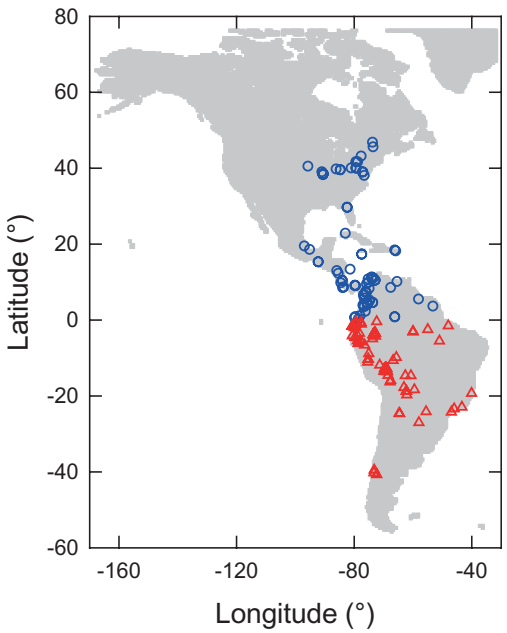

Figure 1: distribution of the 79 plots in the New World North (circle) and the 72 plots in the New World South (triangle).

Specifically, we define alpha diversity as the number of species in a single 0.01-ha subplot, gamma diversity of the plot as the total number of species in the 10 subplots of the plot and beta diversity as 1- alpha/gamma, where alpha is the average of the 10 alpha diversity values of the plot.

For each region, we used two statistical approaches to examine the relationship between beta diversity and latitude after accounting for gamma diversity and the relationship between gamma diversity and latitude after accounting for beta diversity. When examining the relationship between beta diversity and latitude after accounting for gamma diversity, we first conducted a series of partial regressions to partition the variation in beta diversity accounted for by (i) latitude, independent of gamma diversity, (ii) gamma diversity, independent of latitude, (iii) latitude and gamma diversity jointly and (iv) neither latitude nor gamma diversity (Legendre 2008); we then regressed beta diversity on gamma diversity and subsequently regressed the resulting residuals of the regression (i.e. residual beta diversity) on absolute latitude. This residual-based analysis approach has been commonly used in macroecological studies (Cadena *et al*. 2012; Hortal *et al*. 2008; Nogués-Bravo and Araújo 2006; Tuomisto *et al*. 2003). When examining the relationship between gamma diversity and latitude after accounting for beta diversity, we took the same two approaches outlined above but switched the positions of beta and gamma diversity in the regression analyses, i.e. treating gamma diversity as the dependent variable and beta diversity as an independent. To maximize the normality of regression residuals, we $\log_{10}$ transformed gamma diversity. We initially included both linear and quadratic terms of each independent variable in a regression. Because regressions with quadratic terms yielded nearly identical results to those without quadratic terms, our final regressions included only linear terms. To account for spatial autocorrelation in our analyses, we used MODTTEST (Legendre 2000) to recalculate *P* values for significance tests based on geographically effective degrees of freedom, which was determined according to Dutilleul's (1993) approach.

RESULTS

Latitude was negatively correlated with alpha, gamma and beta diversity (Pearson's $r = -0.747$, -0.740 and -0.724 for New World North; $r = -0.472$, -0.540 and -0.652 for New World South, respectively; Fig. 2). Beta diversity was strongly and positively correlated with gamma diversity (0.783 for New World North and 0.848 for New World South). These correlations were all significant ($P < 0.05$) after accounting for spatial autocorrelation.

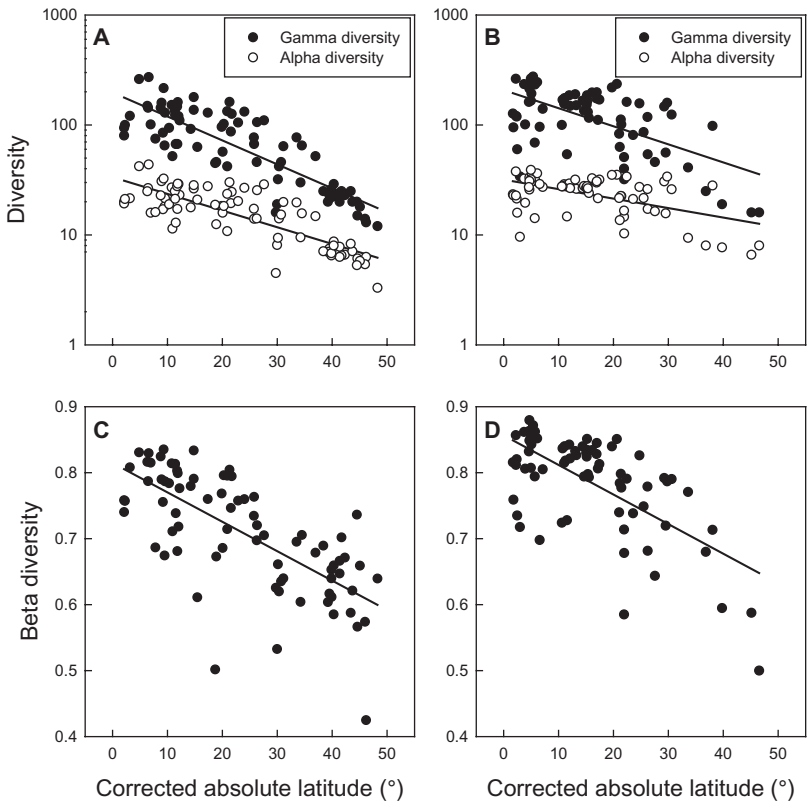

Figure 2: latitudinal gradients in alpha and gamma diversity (A and B; diversity on common log scale) and in beta diversity (C and D) for forest communities in New World North (A and C) and New World South (B and D).

When beta diversity was regressed on latitude and gamma diversity, 69.8 and 85.7% of the variation in beta diversity were explained, respectively, for New World North and New World South. For New World North, 52.1% of the variation in beta diversity was explained by latitude and gamma diversity jointly; 18.0% of the variation was explained by gamma diversity alone; and latitude did not independently explain any variation in beta diversity (Fig. 3A). For New World South, 40.5% of the variation in beta diversity was explained by latitude and gamma diversity jointly; 44.0% of the variation was explained by gamma diversity alone; and latitude explained only 1.2% of the variation in beta independently (Fig. 3A).

When gamma diversity was regressed on latitude and beta diversity, 81.8 and 84.3% of the variation in gamma diversity were explained, respectively, for New World North and New World South. For New World North, 59.2% of the variation in gamma diversity was explained by latitude and beta diversity jointly; 10.9% of the variation was explained by beta diversity alone; and 11.7% of the variation was explained by latitude alone (Fig. 3B). For New World South, 36.2% of the variation in gamma diversity was explained by latitude and beta diversity jointly; 48.3% of the variation was explained by beta diversity alone; and latitude did not independently explain any variation in gamma diversity (Fig. 3B).

When the relationship between beta and gamma diversity was statistically removed, the correlation between latitude and residual beta diversity was −0.028 and −0.238, respectively, for New World North and New World South, and the correlation between latitude and residual gamma diversity was −0.435 and −0.018, respectively, for New World North and New World South.

DISCUSSION

Previous studies on the latitudinal gradient of beta diversity have shown that beta diversity is generally greater at lower latitudes (Buckley and Jetz 2008; Chen *et al.* 2011; Lenoir *et al.* 2010; Qian 2009; Qian *et al.* 2009; Qian and Ricklefs 2007, 2012) and in areas with higher environmental energy (Qian and Xiao 2012). Several studies examined the latitudinal gradient of beta diversity at a local scale such as sampling areas smaller than 1 ha (Chen *et al.* 2011; De Cáceres *et al.* 2012;

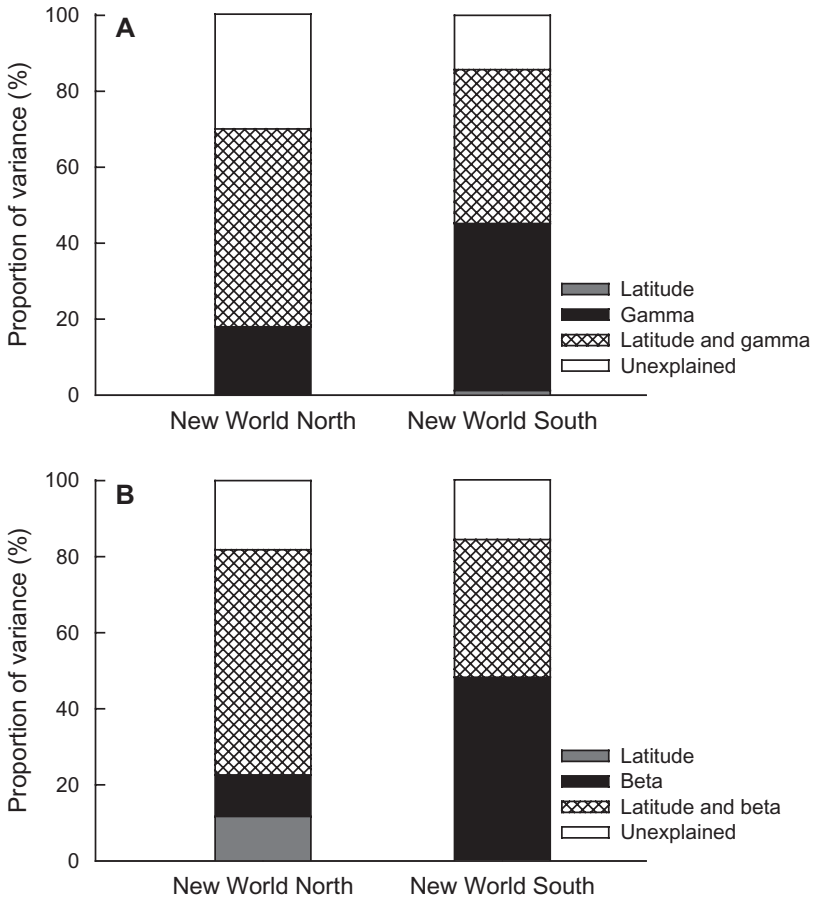

Figure 3: (A) variance in beta diversity explained only by latitude, only by gamma diversity or jointly by latitude and gamma diversity in forest communities. (B) variance in gamma diversity explained only by latitude, only by beta diversity or jointly by latitude and beta diversity in forest communities.

Kraft *et al*. 2011; Lenoir *et al*. 2010), but they did not examine the interrelationships between beta and gamma diversity along a latitudinal gradient except for Kraft *et al*. (2011), who used a null model approach to account for gamma diversity when they examined the latitudinal gradients of beta diversity. However, as Qian *et al*. (2013) point out, their null model is invalid because the null model preserves the same number of individuals in each subplot of the randomized data as in the subplot of the raw data. The numbers of individuals of each of multiple species in a community produce a species abundance distribution (Williamson and Gaston 2005), which results, at least in part, from mechanisms of community assembly (Andrewartha and Birch 1954; James and Rathbun 1981; Kolasa and Strayer 1988; McGill *et al*. 2007; Tokeshi 1999; Ugland and Gray 1982; Whittaker 1965). Because species abundance distributions drive the species-area relationship (He and Legendre 2002; Plotkin *et al*. 2000) and the slope of the species-area relationship is a measure of beta diversity (Cody 1975; Ricotta *et al*. 2002; Rosenzweig 1995), mechanisms that drive species abundance distributions also drive beta diversity within a local community. A null model that depends on species abundance distributions naturally incorporates mechanisms driving beta diversity and thus is invalid because, as Gotelli (2001, p. 337) points out, 'the null model strategy is to construct a model that deliberately *excludes* a mechanism being tested'. Consequently, Kraft *et al*.'s (2011) main conclusion, which is based on their null model, is invalid.

Beta diversity among subplots within a 0.1-ha plot decreases with increasing latitude in the New World. Although this trend at the fine spatial scale examined in the present study is consistent with that observed at broad spatial scales (Buckley and Jetz 2008; Qian 2009; Qian *et al*. 2009; Qian and Ricklefs 2007, 2012), the causes of the latitudinal gradient of beta diversity at the fine scale may completely differ from those generating the latitudinal gradient of beta diversity at a broad scale. At a broad scale, beta diversity strongly decreases with increasing spatial distance (due to dispersal limitation) and environmental distance (due to habitat filtering), and regional and historical processes, such as speciation, extinction and dispersal, and environmental heterogeneity between areas may play a key role in generating beta diversity between the areas (Buckley and Jetz 2008; Qian and Ricklefs 2007, 2012). In contrast, beta diversity among 0.01-ha subplots within a 0.1-ha plot may largely result from local community assembly processes and sampling constraints, rather than environmental heterogeneity within a plot. This is because each of Gentry's plots was sampled in such a way that a set of 10 subplots of the plot represented a relatively uniform segment of a forest community (Phillips and Miller 2002), environmental variation among the 10 subplots of the plot was therefore minimized. Furthermore, because the largest distance separating any two subunits of a plot is usually much <500 m, it is unlikely that variation in species composition among 10 subplots within a plot is due to dispersal barriers between the subplots. Thus, beta diversity between patches of a relatively homogeneous forest separated by such short distances is unlikely driven by environmental variation and dispersal limitation, although microhabitats certainly occur within the plot. Instead, the factors that determine distributions of seeds and seedlings around the parent trees (i.e. conspecific tree aggregation) may play a role in generating patterns of beta diversity within a plot. The latitudinal gradient of beta diversity at the local scale of the present study may largely result from the latitudinal gradient of species abundance distributions (Qian *et al*. 2013). For forest communities at a local scale such as 0.1 ha, distributions of microhabitats, dynamics of forest (light) gaps, density-dependent interactions and biotic interactions within a study site may also be among the factors influencing beta diversity within local communities (Comita *et al*. 2010; Lambers *et al*. 2002; Schupp *et al*. 2002).

At a fine scale such as the one examined in the present study, sampling constraints may also have played a role in generating the latitudinal gradient of beta diversity. In the present study, as well as in Chen *et al*. (2011) and Kraft *et al*. (2011), alpha diversity was measured based on each of ten 2-m by 50-m subplots within a plot. Because such small subplots each may only allow few individuals of mature trees to occupy, the number of species in each subplot may be, to some extent, constrained by the number of individuals of mature trees that can fit the size of a subplot. Because trees in tropical forests, which are usually 30–60 m tall, are generally larger than trees in temperate and boreal forests (Moles *et al*. 2009), the constraint to the number of individuals per subplot would presumably be greater in forests at lower latitudes than in forests at higher latitudes. As a result, the increase in the number of species from a higher latitude to a lower latitude would be slower at the 0.01-ha subplot scale than at the 0.1-ha plot scale, as shown in Fig. 2. This latitudinal gradient of sampling constraint would have partly generated the latitudinal gradient of the beta diversity observed in local forest communities.

Both beta and gamma diversity are strongly correlated with latitude. However, after statistically removing the relationship between beta and gamma diversity, latitude has weak or no relationships with beta and gamma diversity. Kraft *et al*. (2011) consider this as evidence for the influence of gamma diversity on beta diversity. Mechanisms that gamma diversity drives beta diversity are basically unknown. In contrast, previous studies have proposed mechanisms by which beta diversity can drive gamma diversity at a broad spatial scale (Qian *et al*. 2005, 2013; Rodríguez and Arita 2004). For example, if two contiguous areas each have a large proportion of unique species as a result of allopatric speciation or extinction and thus have high beta diversity between them, high gamma diversity of the two areas would be expected. However, at a local scale such as 0.1 ha, positive correlations between beta and gamma diversity may not be considered as evidence of one driving the other. There may be no causal relationship between beta and

gamma diversity at all. Instead, mechanisms of community assembly beyond the interaction between beta and gamma diversity may cause the relationship between them.

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