A Journal of Macroecology

Global Ecology and Biogeography

Phylogenetic beta diversity of angiosperms in North America

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ABSTRACT

Aim Ecologists have generally agreed that beta diversity is a key component of global patterns of species richness. Incorporating phylogenetic information into the study of beta diversity allows researchers to identify the degree to which the shared evolutionary histories of species explain ecological patterns observed today. For example, phylogenetic analyses can determine whether closely related species tend to occupy similar positions along broad climatic gradients and whether this explains the compositional turnover along these gradients. Despite the promise of phylogenetic beta diversity analyses, few continental-scale investigations exist. Here, we quantify the phylogenetic beta diversity and taxonomic beta diversity of the angiosperm flora across North America. We relate these metrics to one another and to geographical and environmental distances to uncover the phylogenetic signal underlying species compositional turnover.

Location North America.

Method Seventy-one regional floras were used and assigned into five latitudinal zones and two longitudinal bands. The Sørensen index and PhyloSor index were used to quantify taxonomic similarity and phylogenetic similarity, respectively, between floras, and were related to geographical and environmental distances.

Results Phylogenetic similarity between floras is strongly correlated with taxonomic similarity, is higher in eastern North America than in western North America, and increases strikingly with latitude. Geographical and environmental distances together explained on average about 76% of the variation in phylogenetic beta diversity with environmental distance explaining more variation in phylogenetic similarity in three of the four latitudinal bands examined.

Main conclusions The results show that phylogenetic beta diversity is consistently lower than taxonomic beta diversity, which suggests that the spatial turnover of species in the study system is predominantly the spatial turnover of closely related species and not distantly related species. Thus, the turnover of angiosperm floras in North America is best explained by small divergences along environmental axes for closely related species and a gradual turnover of lineages through space.

Keywords

Distance decay of similarity, environmental gradient, latitudinal diversity gradient, phylobetadiversity, species turnover, taxonomic beta diversity.

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INTRODUCTION

Understanding the underlying mechanisms that drive geographical variation in species diversity across the globe is a central theme in ecology and biogeography (Mittelbach *et al.*, 2007). Species diversity is often described with three compo-nents: alpha, beta and gamma diversity (Whittaker, 1972). Alpha and gamma diversity both measure species richness within an area, but they focus on different spatial scales. Gamma diversity measures total species richness in a larger area comprised of many smaller subunits in which alpha diversity, the species richness in a subunit, is measured. Beta diversity quantifies the

variation in species composition among the subunits; thus beta diversity represents a scalar linking alpha diversity and gamma diversity. While it has traditionally received less attention, ecologists have generally agreed that beta diversity is a key component of global patterns of species richness (e.g. Stevens, 1989; Koleff *et al.*, 2003; Qian & Ricklefs, 2012).

Previous studies on beta diversity at a broad scale have generally focused on taxonomic beta diversity (species turnover between localities) with respect to geographical and ecological distances. For example, at a regional or continental scale, McKnight *et al.* (2007), Diniz-Filho *et al.* (2009) and Melo *et al.* (2009) examined spatial turnover of species in some groups (e.g. amphibians, birds and mammals) of vertebrates in the New World, and Qian & Ricklefs (2012) examined spatial turnover of vascular plant species in North America. On a global scale, several studies (e.g. Gaston *et al.*, 2007; Buckley & Jetz, 2008; Qian & Ricklefs, 2012) have examined spatial turnover of species in different groups of vertebrates. While taxonomic beta diversity can effectively provide information about the degree of overlap of species between sites, it does not incorporate information regarding the evolutionary non-independence of the species in the study system. Specifically, because all species are treated equally in taxonomic beta diversity, it does not provide information about how deep in evolutionary time clades of these species have been separated (e.g. Chave *et al.*, 2007; Graham & Fine, 2008). Incorporating information regarding the phylogenetic non-independence or relatedness between species in studies of beta diversity may substantially advance our understanding of the ecological and evolutionary mechanisms structuring communities (Ives & Helmus, 2010). For example, consider three hypothetical communities A, B and C each of which has a unique set of five species, and all species in communities A and B belong to the same family, whereas the five species in community C belong to five different families which are deeply diverged in a phylogenetic tree. Because these communities have no species in common, taxonomic beta diversity between each pair of the three communities is one when taxonomic beta diversity is quantified with Sørensen dissimilarity index (i.e. the maximum amount of species turnover between communities). However, because all species in communities A and B belong to the same family, it is reasonable to conclude that communities A and B are phylogenetically more similar, compared with community C, and thus they likely share similar environmental requirements or experience biotic and abiotic forces in the same way (Cavender-Bares *et al.*, 2009). An obvious example of this type of situation is found in north temperate tree assemblages across continents. Specifically, these assemblages share little-to-no species but share the majority of their genera and families. In other words, the species beta diversity in this system is largely reflecting dispersal limitation of individual species, but the phylogenetic beta diversity is low reflecting the shared biogeographical and evolutionary history that has structured these assemblages.

The use of phylogenetic information is increasingly common in ecological and biogeographical studies exploring the role of ecological and historical processes in structuring communities (Webb *et al.*, 2002; Graham & Fine, 2008; Cavender-Bares *et al.*, 2009). The past decade has witnessed a rapid development in formulating phylogenetic metrics that quantify phylogenetic information within communities (e.g. phylogenetic alpha diversity; e.g. Faith, 1992; Webb, 2000; Cadotte *et al.*, 2010) and between communities (e.g. phylogenetic beta diversity; e.g. Lozupone & Knight, 2005; Chave *et al.*, 2007; Swenson, 2011). Analogous to taxonomic beta diversity, which measures change in species composition across space, phylogenetic beta diversity measures how phylogenetic relationships among species change across space (Graham & Fine, 2008). If sites under comparison include a high proportion of small ranged species belonging to clades that on average diverged at a time that is later than expected average divergence time, one would expect to find high taxonomic beta diversity but low phylogenetic beta diversity between the sites. In contrast, if two sites under comparison include a high proportion of small ranged species belonging to clades that on average diverged at a time that is earlier than expected average divergence time, it is expected that one would find both high taxonomic beta diversity and high phylogenetic beta diversity between the sites, a pattern indicating that communities in the sites contain species that belong to lineages with long-standing and disparate evolutionary histories (Graham & Fine, 2008). Thus, patterns observed with measures of phylogenetic beta diversity may or may not be consistent with those observed with measures of taxonomic beta diversity. When related with both geographical and environmental gradients, phylogenetic beta diversity provides an evolutionary approach to evaluate how community structure changes as a function of geographical and environmental gradients (Chave *et al.*, 2007; Swenson, 2011; Hardy *et al.*, 2012).

North America (north of Mexico) is one of the few continental regions that has a wide longitudinal span from relatively low (ca. 30°N) to high (> 80°N) latitudes, transected by similar north–south oriented physiographic features – the Appalachian Mountains in the east and the American Cordillera in the west. This continental region is ideal for investigating the relative roles of geographical and environmental distances on phylogenetic structure (including phylogenetic beta diversity) of floras and faunas because more than half of North America (north of Mexico) was covered by massive ice sheets only 14,000 years ago (FAUNMAP Working Group, 1994), and thus nearly all species which currently occur in the northern half of North America are immigrants primarily from the southern part of North America. Furthermore, for much of the southern North America where ice sheets were absent during the Last Glacial Maximum, species in the current floras are largely immigrants from further southern areas after the glaciation. If physiological tolerances (such as freezing tolerance) evolve differentially among phylogenetic clades, northerly re-colonization of species after the glaciation may generate phylogenetic patterns through environmental filtering and species sorting processes (Wiens & Donoghue, 2004). In particular, one would expect that there is a latitudinal gradient in phylogenetic beta diversity because the phylogenetic structure of biological assemblages are expected to be more clustered towards higher latitudes, as predicted by the tropical

niche conservatism hypothesis (Wiens & Donoghue, 2004). The two south-north-trending mountain systems are ideal systems for investigating phylogenetic turnover along strong spatial and environmental (particularly temperature) gradients. A latitudinal gradient in phylogenetic beta diversity may also be expected if there is an interaction between phylogenetic relatedness and post-glacial dispersal. If closely related species have dissimilar post-glacial dispersal then phylogenetic beta diversity may be low with latitude, whereas if major (i.e. basal) lineages differed in their dispersal phylogenetic beta diversity may be high with latitude.

This study addresses the following questions: (1) How does taxonomic similarity between floras vary among major phylogenetic clades (lineages) of angiosperms? (2) How closely is phylogenetic similarity related with taxonomic similarity in angiosperm floras in North America and is phylogenetic beta diversity higher than taxonomic beta diversity? (3) Is there a strong latitudinal gradient of distance decay in phylogenetic similarity, i.e. phylogenetic similarity decreases with increasing geographical or environmental distance, as observed in taxonomic similarity (Qian & Ricklefs, 2007)? (4) Is phylogenetic beta diversity related with geographical distance more strongly or less strongly than with environmental distance? (5) Do the relationships of phylogenetic beta diversity with geographical and environmental distances differ between latitudinal and longitudinal bands across North America?

MATERIALS AND METHODS

Floras used in this study are state/province-level floras of North America (north of Mexico). We divided California and Ontario each into southern and northern parts in order to make boundaries of latitudinal zones more consistent across longitudes and split Texas into sections to make areas of floras more similar (Fig. S1). We distinguished Labrador and the island of Newfoundland.

We assembled angiosperm (flowering plant) species lists for each of the state and province-level geographical units from Kartesz's (1999) North American plant database, except for the subunits of California, Texas and Ontario, for which we used CalFlora (http://www.calflora.org/), Hatch *et al.* (1990), and other botanical sources. Species exotic to North America were excluded. A total of 15,589 angiosperm species were included in this study. We assigned the species to the following eight groups based on Angiosperm Phylogeny Group (2009): magnoliids plus Chloranthales (71 species), monocots without commelinids (970), monocots with commelinids only (2106), fabids (3059), malvids (1272), lamiids (2504), campanulids (2821) and others (2785).

We assigned each species to a family of Angiosperm Phylogeny Group (2009). We used Phylomatic (Webb & Donoghue, 2005) and a maximally resolved supertree of angiosperms (available at http://www.phylodiversity.net), which is based on Angiosperm Phylogeny Group (2009), to assemble the species list into a phylogeny for the angiosperm flora of

North America (i.e. the continental species pool phylogeny). Branch lengths were estimated with the BLADJ algorithm (Webb *et al.*, 2008) based on family ages in a dated version of megatree of Davies *et al.* (2004) implemented in phylomatic. Given the scarcity of comprehensive, time-calibrated phylogenies within families and genera, we followed previous studies (e.g. Hardy *et al.*, 2012) to treat genera as polytomies within families and species as polytomies within genera.

For each pair of floras, we calculated a taxonomic similarity index and a phylogenetic similarity index. Because Sørensen index (Sørensen, 1948) is one of the most commonly used taxonomic similarity indices, and PhyloSor (Bryant *et al.*, 2008) is one of the most commonly used phylogenetic similarity indices; and because PhyloSor is phylogenetic analog of Sørensen index (Bryant *et al.*, 2008; Swenson, 2011; Feng *et al.*, 2012), we used these two similarity indices in this study. They are defined as (Bryant *et al.*, 2008):

$$\text{Sørensen} = \frac{2 \times S_{ij}}{S_i + S_j}$$

and

$$\text{PhyloSor} = \frac{2 \times BL_{ij}}{BL_i + BL_j},$$

where S_{ij} is the number of species shared between localities i and j, S_i and S_j are the numbers of species in localities i and j, respectively; similarly, BL_{ij} is the total length of the branches shared between localities i and j, BL_i and BL_j are the total branch lengths in localities i and j, respectively. Values of both Sørensen index and PhyloSor index range from 0 (no similarity) to 1 (complete similarity). Taxonomic dissimilarity (i.e. 1 – Sørensen) and phylogenetic dissimilarity (i.e. 1 – PhyloSor) are considered as measures of taxonomic beta diversity and phylogenetic beta diversity, respectively, in this study. Both Sørensen and PhyloSor indices may be decomposed into the turnover and nestedness components of beta diversity (Baselga, 2010; Leprieur *et al.*, 2012). Because our goal is to compare overall taxonomic and phylogenetic beta diversity in the same set of sample units, we did not use the decomposing methods.

We related PhyloSor to geographical distance and environmental distance. Geographical distance between localities was measured between their midpoints. Environmental distance between localities was measured by principal components from a principal component analysis based on seven environmental variables: (1) mean annual temperature (an indicator of ambient energy); (2) mean coldest month (January) temperature (related to frost and freezing tolerance); (3) difference between mean January temperature and mean July temperature (temperature seasonality); (4) annual precipitation (water availability); (5) summer precipitation (water availability during the north temperate growing season – May through August); (6) actual evapotranspiration (AET, a measure of productive energy); and (7) potential evapotranspiration (PET, a measure of ambient energy). These variables have been commonly used

to characterize regional environments in macroecological studies. We obtained temperature and precipitation data from New *et al.* (1999) and evapotranspiration data from Ahn & Tateishi (1994). We subjected the seven environmental variables to a principal component analysis based on their correlation matrix. The first three principal components (PCs) accounted for a very high amount (97.1%) of the variation in the seven environmental variables (Table S1). As a result, we used the three PCs to represent the seven environmental variables. We calculated difference on each PC axis between each pair of floras, and calculated an overall distance as the Euclidean distance based on all the three PC axes. Because the results of analyses using the three individual PC distances are nearly identical to those with the Euclidean distance resulting from the three PCs, we used the Euclidean distance of the three PCs as a measure of environmental distance in final analyses. We also used raw temperature and precipitation data in some analyses.

Area and elevation range both vary among study localities. Larger areas and elevation ranges tend to include more types of habitats. To determine whether differences in area and elevation range between localities should be included as additional environmental variables, we first regressed PhyloSor simultaneously on geographical and environmental distances and then added differences in area and elevation range between localities to the regression model. Then we compared adjusted coefficients of determination between the two models. We did this for different latitudinal and longitudinal bands (see below). Because differences in area and elevation range between localities only explained, on average, additional 1.3% of the variation in PhyloSor beyond the variation explained by geographical and environmental distances, they were excluded from further analyses.

We regressed PhyloSor against geographical and environmental distances simultaneously and compared their standardized coefficients (i.e., standardized regression slopes; Legendre & Legendre, 1998) from the regression to determine their relative effects on phylogenetic beta diversity. Standardized regression coefficients were obtained through applying regression to standardized variables. We also conducted a series of partial regressions (Legendre & Legendre, 1998) to partition the variance in PhyloSor into four fractions: uniquely explained by geographical distance, uniquely explained by environmental distance, explained jointly by geographical and environmental distances and explained by neither distance.

Because of the non-independence in pairwise data, the number of degrees of freedom can increase the rate of the Type I error, and thus the significance of tests based on traditional *P* values can be inflated. Although the main goal of our study is to detect the trend in changes of phylogenetic beta diversity along a latitudinal gradient and relative strengths of the effects of geographical distance and environmental distance on phylogenetic beta diversity, rather than statistical inference test, we provided *P* values derived based on a randomization approach in case some readers are interested in statistical significance in our analyses. We performed a random permutation ($n = 999$) for each regression analysis. We obtained error probabilities by using the *z* standard deviate, where $z = \text{abs}((\text{observed coefficient}$
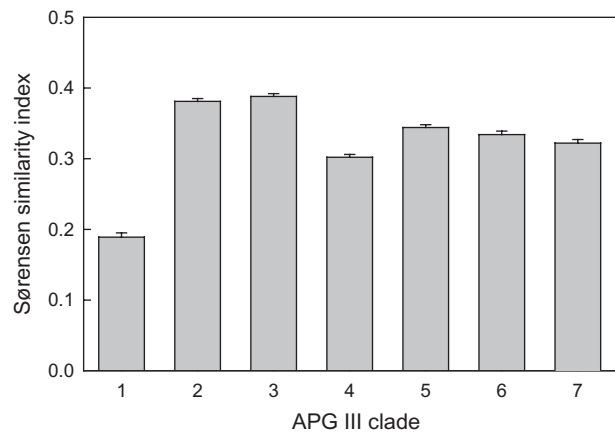

Figure 1 Taxonomic (Sørensen) similarity (mean ± se) among angiosperm floras in North America by clade of Angiosperm Phylogeny Group (2009) (1: magnoliids plus Chloranthales; 2: monocots without commelinids; 3: monocots with commelinids only; 4: fabids; 5: malvids; 6: lamiids; 7 campanulids). The number of flora pairs is 2407 for clade 1 and 2485 for clades 2 through 7.

– mean of permuted coefficient)/standard deviation of permuted coefficient) (Crawley, 2002). The *z* standard deviate is normally distributed (Crawley, 2002) so that the error probability can be assessed from statistical tables or appropriate curves or functions (e.g. a *z*-score > 1.96 translates into a *P*-value < 0.05 for a two-tailed test). The same or a similar randomization approach has been commonly used in previous studies (e.g. Kühn & Klotz, 2006; Qian *et al.*, 2008). Randomizations were performed with R (R Development Core Team, 2009).

We conducted most analyses according to relatively narrow latitudinal and longitudinal bands. We divided North America north of Mexico, southern Texas and Florida into five latitudinal zones as shown in Fig. S1 (Bands A through C comprising the contiguous USA; D, Canada south of 60°; and E, the rest of Canada, Alaska and Greenland). Longitudinally, we conducted two sets of analyses, each for one major mountain system. Our analysis for eastern North America included states (USA) and provinces (Canada) which are primarily located in or nearby the Appalachian Mountains, and our analysis for western North America included states and provinces located in a great mountain system which includes Rocky Mountains, Brooks Range, Cascades and Sierra Nevada (Fig. S2).

RESULTS

The average of taxonomic similarity (Sørensen index) for the 2485 pairs of the 71 floras is 0.342, ranging from 0.002 to 0.877. Of the seven phylogenetic clades of Angiosperm Phylogeny Group (2009), Sørensen index is lowest for clade magnoliids plus Chloranthales and highest for the two monocot clades (Fig. 1).

Phylogenetic similarity (PhyloSor) between floras is strongly correlated with taxonomic similarity (Sørensen index)
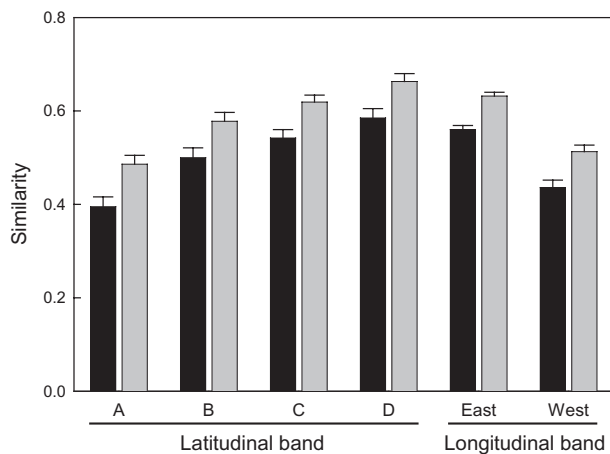
Figure 2 Comparisons of taxonomic similarity (Sørensen index, black) and phylogenetic similarity (PhyloSor, gray) (mean ± se) among latitudinal and longitudinal bands in North America (see Materials and Methods). Pairwise localities separated by over 3500 km were excluded from the comparisons (see text).

Table 1 Standardized regression coefficient (slope) and adjusted coefficient of determination from the multiple regression of phylogenetic beta diversity (i.e. 1 – PhyloSor) against geographical distance (Geo.dist) and environmental distance (Env.dist).

Band	n	Geo.dist	Env.dist	R^2_{adj}
Latitude A	136	0.301*	0.611*	0.751*
Latitude B	153	0.403*	0.615*	0.934*
Latitude C	153	0.322*	0.630*	0.857*
Latitude D	45	0.808*	-0.021**	0.630*
Longitude East	435	0.586*	0.421*	0.901*
Longitude West	136	0.426*	0.327*	0.489*

*$P < 0.05$; **$P > 0.10$.

Table 2 Standardized regression coefficient (slope) and adjusted coefficient of determination from the multiple regression of ln(PhyloSor) against absolute differences in mean annual temperature (TEM.diff) and annual precipitation (PREC.diff) between localities.

Band	n	TEM.diff	PREC.diff	R^2_{adj}
Latitude A	136	−0.151*	−0.691*	0.550*
Latitude B	153	−0.222*	−0.423*	0.324*
Latitude C	153	0.059***	−0.767*	0.580*
Latitude D	45	0.069***	−0.238**	0.008**
Longitude East	435	−0.919*	0.019***	0.831*
Longitude West	136	−0.696*	−0.095***	0.481*

*$P < 0.05$; **$P < 0.10$; ***$P > 0.10$.

($r = 0.997$), and the former is on average higher than the latter by 9.7%. At the continental scale, they are on average 0.439 and 0.342, respectively. The lengths of latitudinal and longitudinal bands vary with the shortest length being in latitudinal band A (~3500 km). To compare phylogenetic and taxonomic similarities among latitudinal and longitudinal bands, we only used pairwise localities separated by a distance of 3500 km or shorter. Phylogenetic similarity is higher than taxonomic similarity for all latitudinal and longitudinal bands (Fig. 2). Both similarity metrics strikingly increase with latitude. Phylogenetic and taxonomic similarities are higher in eastern North America than in western North America (Fig. 2).

Geographical and environmental distances together explained on average about 76% of the variation in phylogenetic beta diversity (i.e. 1 – PhyloSor) across the six latitudinal or longitudinal bands, ranging from 49% for the western longitudinal band to 93% for latitudinal band B (Table 1). The standardized coefficient for environmental distance was much larger than that for geographical distance in three of the four latitudi-

nal bands (Table 1), indicating that environmental differences between localities have played a much larger role than geographical distances in driving patterns of phylogenetic beta diversity in these three bands. In contrast, the standardized coefficient for geographical distance was much higher than that for environmental distance in latitudinal band D (Table 1), indicating that geographical distance has played an overwhelming role in driving phylogenetic beta diversity in this latitudinal band. Geographical distance influenced phylogenetic beta diversity more strongly than environmental distance in both longitudinal bands (Table 1).

When PhyloSor was related to differences in temperature and precipitation between localities, the standardized regression slope (coefficient) of precipitation is much steeper than that of temperature in the four latitudinal bands (Table 2). In contrast, in the two longitudinal bands, the standardized slope of temperature is much steeper than that of precipitation. These patterns indicate that the precipitation gradient played a more important role than the temperature gradient in generating the entire environmental gradient of a latitudinal band, whereas the relative roles of precipitation and temperature in generating an environmental gradient within a longitudinal band are reversed.

A strong gradient in distance decay of phylogenetic similarity along a latitudinal gradient was observed (Fig. 3): the slope of the relationship between phylogenetic similarity measured as ln(PhyloSor) and geographical distance decreased from −0.533 in latitudinal band A through −0.450 and −0.258 in latitudinal bands B and C, respectively, to −0.124 in latitudinal band D (Fig. 3). In other words, the slope was more than four times steeper in band A than in band D. For the two longitudinal bands, the slope was much steeper in the eastern North American band than in the western North American band (−0.428 vs. −0.223; Fig. 4). This is in agreement with the pattern of the slopes of the relationships between phylogenetic similarity and environmental distance in the two longitudinal bands (−0.219 for eastern North America vs. −0.179 for western North America; Fig. 4).

Variation partitioning analyses showed that most of the variation in phylogenetic similarity that was explained by geographical and environmental distances was not distinguishable
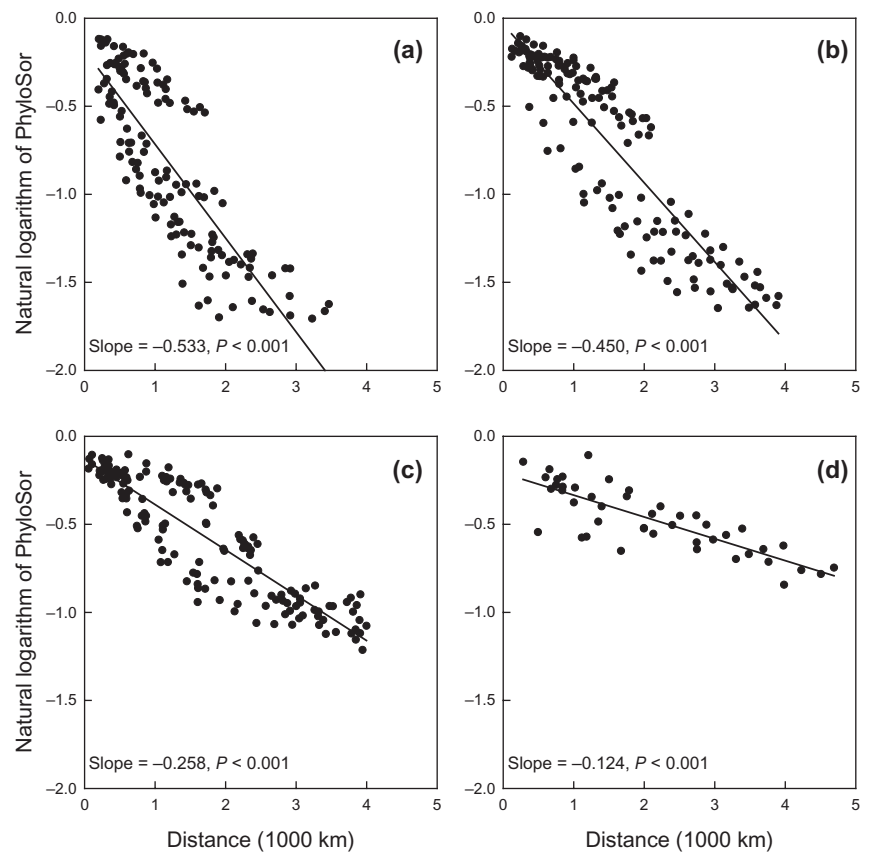
Figure 3 Relationship between the natural logarithm of phylogenetic similarity (i.e. PhyloSor) and geographical distance within each of four latitudinal zones (a through d). Lines and slopes result from least squares linear fits to the data.
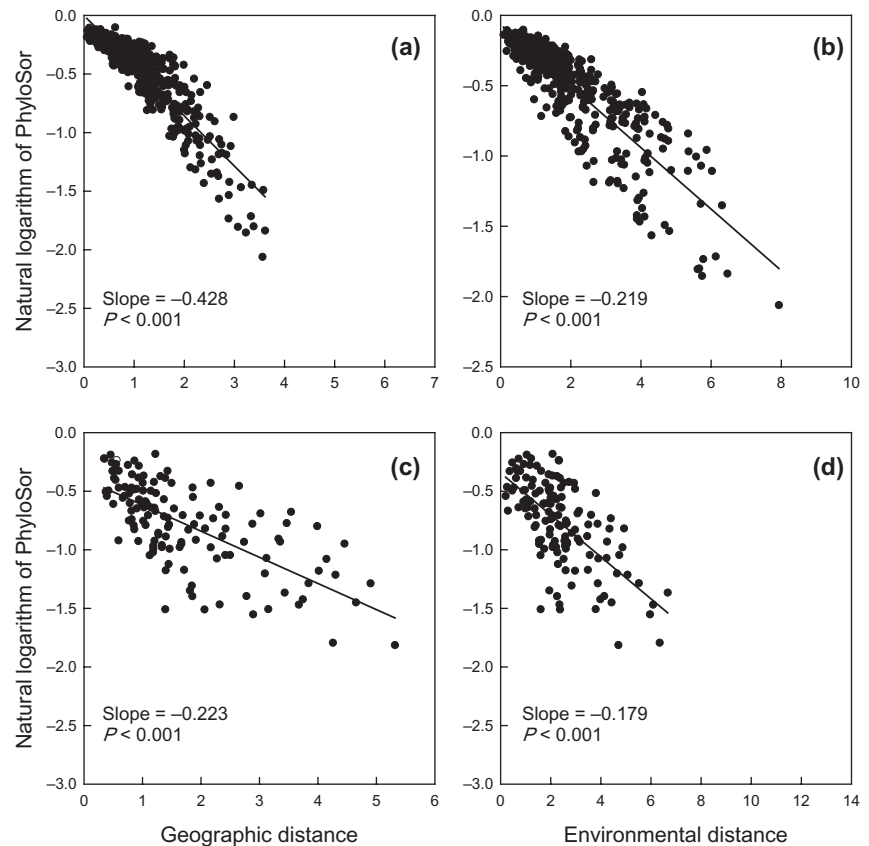

Figure 4 Relationships of the natural logarithm of phylogenetic similarity (i.e. PhyloSor) with geographical distance (1000 km) (a, c) and environmental distance (b, d) for eastern North America (a, b) and western North America (c, d). Lines and slopes result from least squares linear fits to the data.
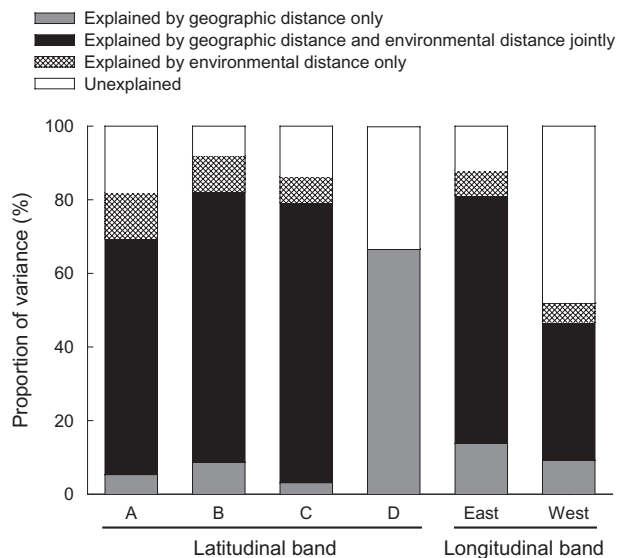
Figure 5 Partition of the variance in the natural logarithm of phylogenetic similarity (i.e. PhyloSor) explained by geographical distance and environmental distance for four latitudinal zones and two longitudinal bands (see Figs S1 and S2).

between the two types of distances, given the present study design, except for latitudinal band D (Fig. 5). However, on average, about 25% of the variation in phylogenetic similarity was explained independently by either geographical or environmental distance across the six latitudinal or longitudinal bands. Environmental distances explained more variation in phylogenetic similarity than geographical distances in three of the four latitudinal bands, but the pattern was reversed for latitudinal band D and for the two longitudinal bands (Fig. 5).

DISCUSSION

We used a comprehensive database, which includes all angiosperm species in North America north of Mexico, to examine patterns of species compositional similarity among major clades across the phylogenetic tree of angiosperms and patterns of phylogenetic beta diversity between floras across North America (Fig. S1). We have found several patterns, which we discuss below.

Our study shows that compositional similarity between floras varies greatly among major clades of angiosperms, with the lowest similarity in the magnoliid (plus Chloranthales) clade and the highest similarity in the two clades of monocots. Biological traits that are relevant to dispersal may have played a role in the observed pattern. Magnoliids may include the highest proportion of trees and other woody plants among all major clades examined. In contrast, monocots are largely composed of herbaceous plants. This difference in growth-form between clades (particularly magnoliids vs. monocots) may influence the compositional structure of a flora and compositional relationships between floras in several ways. Firstly, woody plants in general and trees in particular have on average larger fruits and

seeds than herbaceous plants (e.g. Moles *et al.*, 2005). Plants with larger propagules are expected to have greater dispersal limitation, and thus to have smaller distribution ranges and occupy fewer localities within distribution ranges than plants with smaller propagules. Thus, a lower compositional similarity between localities would be expected for plants with larger propagules. Previous studies have shown this pattern. For example, Ricklefs *et al.* (2008) showed that distribution ranges of woody plants are substantially smaller than herbaceous plants; Qian & Guo (2010) showed that species beta diversity is higher for woody plants than for herbaceous plants; Qian (2009) showed that beta diversity is lower for pteridophytes, which have a higher dispersal ability, than for spermatophytes, which have a lower dispersal ability, suggesting that beta diversity is negatively related to dispersal ability. Secondly, the number of seeds per species are on average likely greater for herbaceous plants than for trees; species with more propagules are expected to be distributed in more localities across their ecological ranges. Thirdly, large woody plants have climate-dominated niches, whereas herbaceous plants have edaphic and microhabitat-dominated niches (Ricklefs & Latham, 1992), as a result, herbs may have more chances to track suitable habitats than woody plants, particularly at the edges of distribution ranges. Fourthly, the geographical ranges of larger woody plants may not have regained ecological equilibria following glaciations, particularly in North America (Wright, 1964; Davis, 1986), compared with smaller herbs; thus, the present distributions of woody plants may reflect the influence of Pleistocene refugia and subsequent migration following rapid climate change (Ricklefs & Latham, 1992).

Our study shows that taxonomic beta diversity is higher than phylogenetic beta diversity. This finding is consistent with that of Graham *et al.* (2009), which also used Sørensen and PhyloSor indices. Lower phylogenetic beta diversity relative to taxonomic beta diversity is consistent with closely related species turning over in space particularly. Thus the results indicate that the species turnover between two floras is largely the turnover of species from similar clades and each flora is largely composed of the same phylogenetic components (i.e. the same genera and families).

When considering the differences in phylogenetic beta diversity across latitudinal bands, we found that phylogenetic turnover was generally lower at higher latitudes. This finding is consistent with species turnover, though the magnitude of the phylogenetic turnover is lower for reasons explained in the preceding paragraphs. In latitudinal bands A, B and C environmental distance explained more variation in PhyloSor than geographical distance, but in latitudinal band D this pattern is reversed. There are two possible reasons for this pattern. The first possibility is that environmental gradients in latitude bands A through C are driven by patterns of coastal to interior to coastal climates, rather than monotonic gradients like those found in latitudinal band D. In this scenario of environmental gradients, it is logical to expect that environmental distance would be a better predictor for phylogenetic beta diversity than geographical distance. A second possibility, that is not mutually

exclusive, is that there is a greater magnitude of environmental heterogeneity along spatial gradients in latitudinal bands A through C, compared to latitudinal band D. This change in the relative degree of gradient steepness across latitude could produce the observed result.

In addition to analyzing phylogenetic beta diversity in latitudinal bands, we examined the phylogenetic beta diversity in longitudinal bands and determined how much of the variation in that diversity could be explained by geographical and environmental distances. We found that geographical distance explained more variation in phylogenetic beta diversity than environmental distance in both longitudinal bands, but the geographical and environmental distances together explained much more variation in phylogenetic beta diversity in the eastern band than in the western band. This is likely because floras in the west are in post-glaciation non-equilibrium at a greater degree, compared with floras in the east. This inference is supported by the steeper slope in phylogenetic similarity with geographical distance in eastern North America than western North America. Specifically, we believe that the gradient in floristic compositional changes from the south to the north in eastern North America is nearly fully, if not fully, driven by the gradient of re-colonization after glaciation through the processes of habitat filtering and species sorting. In contrast, because Alaska was a biological refugium during the Last Glacial Maximum (Brubaker *et al.*, 2005), the gradient of floristic changes in western North America is not fully driven by re-colonization of species from the south to the north. Furthermore, the western band features a gradient from dry temperate (or Mediterranean) up to boreal, while the gradient in the eastern band is from wet (subtropical) to boreal. Taken together, geographical and environmental distances would have less power to predict the gradient of phylogenetic similarity (or beta diversity) in western North America, compared with eastern North America.

Here, we have investigated the phylogenetic beta diversity of floristic assemblages across North America north of Mexico and have highlighted where it deviates from species beta diversity in space and within particular clades. Specifically, we have shown that taxonomic beta diversity differs among major phylogenetic lineages and that this result can be potentially related to major differences in dispersal mode among these lineages. We have also demonstrated that phylogenetic beta diversity is generally lower than taxonomic beta diversity, which suggests that phylogenetic beta diversity in the study system is governed, at least partially, by the turn over of closely related species along environmental gradients. This points to the influence of evolutionary divergence along environmental axes within clades governing their distributions and ultimately the patterns of biodiversity we presently observe.

ACKNOWLEDGEMENTS

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Figure S1 A map showing the division of North America into five latitudinal zones.
Figure S2 A map showing localities in eastern and western longitudinal bands in North America.
Table S1 The first three principal components of a principal component analysis.

BIOSKETCHES

Hong Qian's research is multidisciplinary and particularly lies at the interface of ecology and biogeography. His research involves a wide range of spatial scales (from local to global) and a variety of taxa (e.g. bryophytes, vascular plants, vertebrates and invertebrates). In particular, he is interested in understanding the relative roles of historical and contemporary factors in determining the patterns in biodiversity.

Nathan Swenson is interested in the evolution of functional diversity and how it is distributed in plant assemblages through space and time.

Jinlong Zhang is interested in evolutionary ecology, biodiversity and biogeography, with special regards to community phylogenetics, patterns of phylogenetic diversity and niche evolution. His work has focused on understanding the influence of ecological and historical factors on plant distribution and assembly over various scales.

Editor: Arndt Hampe