LETTER

Temperature shapes opposing latitudinal gradients of plant taxonomic and phylogenetic β diversity

Ian R. McFadden,[1]* (iD)
Brody Sandel,[2]
Constantinos Tsirogiannis,[3]
Naia Morueta-Holme,[4]
Jens-Christian Svenning,[5,6]
Brian J. Enquist[7,8] and
Nathan J.B. Kraft[1]

Abstract

Latitudinal and elevational richness gradients have received much attention from ecologists but there is little consensus on underlying causes. One possible proximate cause is increased levels of species turnover, or β diversity, in the tropics compared to temperate regions. Here, we leverage a large botanical dataset to map taxonomic and phylogenetic β diversity, as mean turnover between neighboring 100 × 100 km cells, across the Americas and determine key climatic drivers. We find taxonomic and tip-weighted phylogenetic β diversity is higher in the tropics, but that basal-weighted phylogenetic β diversity is highest in temperate regions. Supporting Janzen's 'mountain passes' hypothesis, tropical mountainous regions had higher β diversity than temperate regions for taxonomic and tip-weighted metrics. The strongest climatic predictors of turnover were average temperature and temperature seasonality. Taken together, these results suggest β diversity is coupled to latitudinal richness gradients and that temperature is a major driver of plant community composition and change.

Keywords

Americas, biome assembly, elevation, Jaccard dissimilarity, New World, UniFrac.

Ecology Letters (2019) **22**: 1126–1135

INTRODUCTION

The global distribution of biodiversity is highly heterogeneous. A core aim of both community ecology and biogeography is to determine how this variation is created and maintained (MacArthur 1972; Gaston 2000). Gradients in α diversity across latitude and elevation in particular are a common pattern in many taxonomic groups, but there is still much debate about which processes have acted to create them (Hillebrand 2004; Schluter 2016). One potential way to infer how richness gradients are formed is to examine the patterns of species turnover across localities, or β diversity (Harrison *et al.* 1992; Anderson *et al.* 2011), as high rates of turnover within a region will tend to increase species richness compared to areas with lower turnover (Koleff *et al.* 2003). For example it has been hypothesised that the high diversity of the tropics may be caused by increased endemism and smaller range sizes due to favourable climatic conditions, which could lead to higher species turnover compared to temperate regions (Stevens 1989). Causality has also been ascribed in the opposite direction, with higher regional or γ diversity leading to higher β diversity (Kraft *et al.* 2011). Therefore, the degree to which turnover is related to latitude, γ diversity or climatic variation can suggest which mechanism or combination of mechanisms may be driving richness

gradients (McKnight *et al.* 2007; Qian & Ricklefs 2007; Kraft *et al.* 2011).

While classical measures of β diversity focus solely on the turnover of species, further insights may come from a consideration of turnover in additional dimensions of diversity (Graham & Fine 2008; Swenson 2011). Phylogenetic β diversity, for example can quantify turnover in the evolutionary relatedness of assemblages across space at both deep and shallow nodes (Graham & Fine 2008). Contrasting patterns of phylogenetic β diversity, via metrics that either more heavily weight turnover at the tips or basal nodes of phylogenies, can suggest whether community composition is most influenced by ancient or more recent speciation events (e.g. Duarte *et al.* 2014). In addition, phylogenetic β diversity metrics can detect community similarity when two focal communities share few or no species, which is particularly useful in highly diverse regions where this is often the case (e.g. Fine & Kembel 2011). Finally, examining taxonomic and phylogenetic β diversity together can provide insights into both contemporary ecological and historical evolutionary factors shaping variation in local assemblages (Hardy & Senterre 2007; Graham & Fine 2008).

One key process thought to influence species turnover is variation in climate, either alone or via its interaction with elevation and topographic complexity (Hardy & Senterre

[1]*Department of Ecology and Evolutionary Biology, University of California, Los Angeles, CA 90095, USA*

[2]*Department of Biology, Santa Clara University, 500 El Camino Real, Santa Clara, CA 95053, USA*

[3]*Center for Massive Data Algorithmics, Department of Computer Science, Aarhus University, Aarhus, Denmark*

[4]*Center for Macroecology, Evolution and Climate, Department of Biology, University of Copenhagen, Copenhagen, Denmark*

[5]*Center for Biodiversity Dynamics in a Changing World (BIOCHANGE), Department of Bioscience, Aarhus University, 8000 Aarhus C, Denmark*

[6]*Section for Ecoinformatics and Biodiversity, Department of Bioscience, Aarhus University, 8000 Aarhus C, Denmark*

[7]*Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ 85721, USA*

[8]*The Santa Fe Institute, Santa Fe, NM 8750, USA*

Correspondence: E-mail: imcfadden@ucla.edu

2007; Melo *et al.* 2009; Anacker & Harrison 2012). For example Janzen's 'mountain passes' hypothesis states that the greater intra-annual temperature stability of tropical mountains compared with temperate mountains should lead to narrower thermal tolerances for tropical species (Janzen 1967). The increased temperature stability of tropical regions, including longer term stability at geological timescales (Dynesius & Jansson 2000), may lead to higher rates of allopatric speciation and species turnover (Janzen 1967; Ghalambor *et al.* 2006). More recently, climate-change velocity (Loarie *et al.* 2009; Sandel *et al.* 2011) has been used to understand how historical climates shape present-day species distributions, which may not be captured by current climate conditions (Svenning & Skov 2004).

To date, many studies of β diversity have been focused at or below regional scales (e.g. Harrison *et al.* 1992; Novotny *et al.* 2007; Soininen *et al.* 2007; Morlon *et al.* 2011), with some exceptions (McKnight *et al.* 2007; Kraft *et al.* 2011). It is therefore unclear whether the drivers of turnover at small scales are the same at regional or continental scales. Here we map taxonomic and phylogenetic β diversity across the Americas at the 100×100 km scale and determine the major climatic correlates of turnover across the region using the Botanical Information and Ecology Network (BIEN, Enquist *et al.* 2016), a database that includes occurrence records and evolutionary relationships for over 81,000 plant species. Our study has two main aims: to determine if taxonomic and phylogenetic β diversity vary systematically with latitude and elevation across the Americas, using metrics that largely control for the influence of regional or γ diversity, and to assess the climatic and topographic correlates of turnover across the region. We hypothesise that (i) the tropics will have overall higher β diversity than temperate regions, (ii) tropical mountains will have higher β diversity than temperate mountains as predicted by theory (Janzen 1967) and (iii) favourable climates (e.g. high temperature and precipitation, low short- and long-term temporal variation) will tend to increase β diversity. We find β diversity is higher in the tropics than the temperate zone for both taxonomic and tip-weighted phylogenetic measures, but that a reverse latitudinal gradient exists in the turnover of deeper phylogenetic structure. In addition, temperature was the strongest predictor of turnover, suggesting ongoing climate change may reshape patterns of biodiversity across the Americas.

METHODS

Quantifying latitudinal and elevational β diversity gradients

To test our hypotheses about latitudinal trends and climatic correlates of β diversity we compiled ranges and phylogenetic data for more than 81 000 vascular land plants found in the Americas using the BIEN2 database (Enquist *et al.* 2016), which includes both collection records and plot-based observations. Species ranges were estimated via three different methods based on the total number of observations. For species with five or more observations ranges were modelled via MaxEnt (Phillips & Dudík 2008) using climatic data for 1960-1990 from World Clim 1.4 (Hijmans *et al.* 2005) and several

spatial filters to incorporate non-climatic factors such as dispersal limitation. For species with three to four observations we used convex hulls and for species with fewer than three observations ranges were defined as a 75 000 km² bounding box around occurrences. More details on range size estimation can be found in Goldsmith *et al.* (2016). The land area of the Americas was then divided into 100×100 km grid cells and the species assemblage of each grid cell was defined as all species with ranges falling within the cell.

To examine β diversity patterns in space we included as focal cells only those with seven or eight occupied neighboring cells, causing some cells at continental margins and on islands to be removed. We defined the tropics as the land area between 23.5 and −23.5 degrees latitude and areas to the north and south of this band as the temperate zone. Mountainous areas were delineated following the United Nations Environment Programme (UNEP) definition based on elevation, slope and several other criteria (Blyth *et al.* 2002). Our $\sim 0.01^2$ degree latitude resolution map of mountainous areas was upscaled and re-projected to 100×100 km cells and areas with fewer than three mountainous cells were excluded to focus solely on mountain ranges. Afterwards, we were left with a total of 4113 and 861 focal cells for analyses of the entire Americas region and only mountainous regions respectively. To find a single β diversity value for each focal cell, we then calculated the pairwise β diversity of the focal cell and all of its neighboring cells and then averaged them. This value represents the mean turnover across an area of 90 000 km² in the case of a focal cell with eight neighbors and 80 000 km² for cells with seven neighbors.

We quantified β diversity using one taxonomic and two phylogenetic metrics. We calculated phylogenetic metrics with a phylogeny of 81 274 terrestrial vascular plants found in the BIEN2 database (Enquist *et al.* 2016). To assemble this phylogeny a species-level multi-gene tree for $\sim 65 000$ species was made from the *atpB-rbcL*, *ndhF*, *psbA*, *psbA-psbH*, *rbcL* and *trnT-trnL-trnF* regions via the software program PHLAWD (Smith *et al.* 2009), which automatically queries GenBank sequence records. Then, the tree was estimated using RAxML 7.3.0 (Stamatakis 2006) with the unconstrained maximum likelihood search method and treePL[2] (Smith & O'meara 2012) was used to estimate divergence times. Remaining taxa from the 88,824 in the BIEN2 database without genetic data were randomly placed within their genus or removed if generic affinities were not known.

To minimise the influence of regional diversity we chose multivariate pairwise metrics in which γ is not included in calculations of β (Bennett & Gilbert 2016). Specifically, we used multivariate pairwise metrics that quantify the fraction of species or branch length unique to a single community in a pair of focal communities, as well as the average pairwise phylogenetic distance between members of two communities. We measured taxonomic β diversity with Jaccard dissimilarity, the fraction of species unique to a single community and tip-weighted phylogenetic β diversity via the unique fraction of branch length (UniFrac, Lozupone & Knight 2005), a phylogenetic analogue of Jaccard dissimilarity. Both Jaccard and UniFrac metrics are most sensitive to turnover near the tips of phylogenies, either in the form of species turnover or the

turnover of more recently diverged clades. We estimated basal-weighted β diversity via the community distance phylogenetic β diversity metric, also called D_{pw} (Webb *et al.* 2008; Swenson 2011), which more heavily weights turnover of deeper divergences at the root of the phylogeny. D_{pw} measures the mean pairwise phylogenetic distance between all species pairs in two communities and is therefore the multi-community equivalent of mean pairwise distance (MPD) at the level of a single community. D_{pw} more heavily weights deeper divergences because measuring the pairwise distance between distantly related species necessitates traversing to deeper nodes of the shared phylogeny.

Combined, tip-weighted and basal-weighted metrics can be used to assess the relative contribution of contemporary ecological sorting, and recent and deeper-time diversification to latitudinal and elevational diversity gradients. Finally, to determine whether β diversity patterns show latitudinal trends, we regressed the mean β diversity of each focal cell with absolute latitude and compared the magnitude of turnover in tropical and temperate regions with two-sided *t*-tests. BIC was used to select the best regression model from among linear, exponential, 2nd and 3rd degree polynomial fits. To compare β diversity between tropical and temperate mountainous regions we subsetted the data to only mountains regions and reanalysed the data in the same way.

Climatic and topographic drivers of β diversity

To determine the climatic and topographic drivers of β diversity for the Americas we examined the spatial association between β diversity and several topoclimatic variables. We used elevational range (m) within a cell to capture fine-scale topography, as this contributes to the diversity of environmental variation in a given area (i.e. 'topoclimate' effects, Slavich *et al.* 2014). Annual precipitation (mm) and mean annual temperature (°C) were also included because both are important drivers of plant productivity and biome distribution (Whittaker 1970). Finally, we used temperature seasonality (°C) to capture annual variability in temperature and late quaternary climate-change velocity (m year^{-1}, Sandel *et al.* 2011) for longer term variation in temperature. Climate-change velocity is a measure of how fast a species would need to move to track a given change in climate (Loarie *et al.* 2009), and in this case incorporates climatic changes in mean annual temperature since the Last Glacial Maximum (LGM) ~ 21k years ago. For example northeastern North America was covered by the Laurentide Ice Sheet during the LGM, but has since warmed considerably – this region therefore has high late-Quaternary climate-change velocity (see Fig. S1d in Supporting Information). We obtained climate-change velocity data from Sandel *et al.* (2011) and all other topoclimatic variables from the World Clim database (V1.4, 1960-1990 conditions, Hijmans *et al.* 2005). To match the scale of β diversity observations, topoclimatic values for each cell were calculated as the combined average of the focal cell and all of its neighbors.

To perform our analyses we used both bivariate linear regressions and multivariate linear and simultaneous autoregressive (SAR_{err}) models following Kissling & Carl (2008) and

Morueta-Holme *et al.* (2013). We first regressed each β diversity metric against all variables using bivariate linear OLS regressions. Topoclimatic variables were log-transformed and scaled and β diversity values were log-transformed. To understand the influence of climate in general and to test the climatic stability predictions of Janzen's 'mountain passes' hypothesis (Janzen 1967), these calculations were performed for all areas and for mountainous regions only. We then used multiple linear regression to determine the most important topoclimatic predictors of each form of β diversity, again using log-transformed and scaled variables. To avoid collinearity we excluded temperature seasonality from our multivariate analyses because of its strong correlation with mean annual temperature ($r = -0.93$, Table S1). We found all model residuals exhibited significant spatial autocorrelation, which can affect parameter estimates and significance tests (Dormann *et al.* 2007). To correct for this autocorrelation we then fit SAR_{err} models, which include a spatial weights matrix as an additional error term to account for the effect of neighboring values on parameter estimates (Kissling & Carl 2008).

As the degree and structure of spatial autocorrelation varies by dataset, we produced candidate sets of SAR_{err} models with a range of neighbor distances (100, 200, 300, 400, 500, 1000, 3000 and 5000 km) and two ways of coding the spatial weights matrix. Coding was either binary, where locations are either neighbors or not, or row-standardised, which takes into account the number of neighbor surrounding each cell. Models were then selected using minimum residual spatial autocorrelation (minRSA) criteria (Kissling & Carl 2008). minRSA is a measure of the autocorrelation of model residuals in space and is the sum of the absolute value of Moran's I at the first 20 distance classes, which should be minimised to ensure accurate parameter estimates. We then reduced the best models to significant predictor sets for each β diversity metric using AIC. All analyses were performed in R version 3.3.1 (R Core Team 2016), SAR_{err} models were implemented using the *spdep* and *ncf* R packages.

RESULTS

β diversity gradients

We found strong spatial variation in β diversity across the Americas with significant latitudinal trends, but major differences between metrics. There were several hotspots of taxonomic β diversity with turnover of ~ 30–40% (Fig. 1a), including The Andes, much of Central America and Mexico, the Caribbean and large portions of the United States. Though most turnover was less than 40% (95th quantile = 0.37%), a small subset of cells had turnover between 80 and 100% (Fig. 1a). These cells often contained small islands adjacent to more species-rich neighboring cells on a mainland, which may have caused elevated turnover. Despite measuring different dimensions of diversity, taxonomic and tip-weighted phylogenetic β diversity were highly correlated ($r = 0.92$). Tip-weighted β diversity values were in general lower, which is expected as phylogenetic metrics capture deeper evolutionary similarity in community composition. In contrast, basal-weighted β diversity was highest in the north- and south-
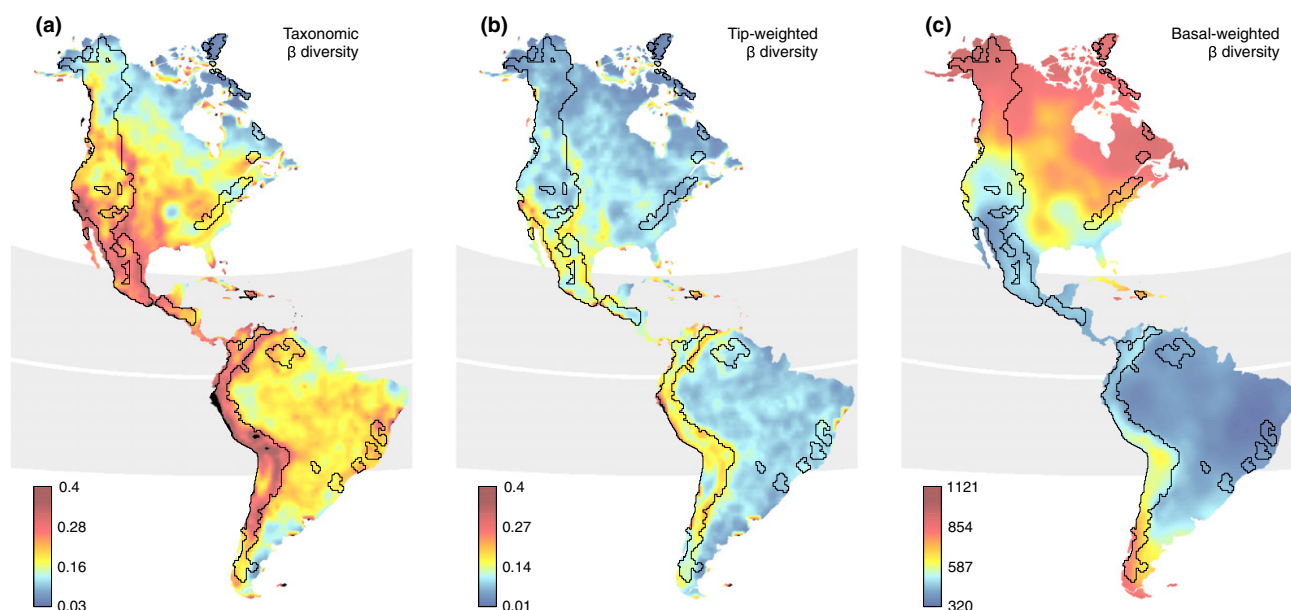
Figure 1 Botanical β diversity of the Americas. Colors represent the average of all pairwise comparisons between a cell and each of its adjoining neighbors, with warmer colors indicating higher turnover. As ~ 99% of values in A & B were below 0.4, values above 0.4 are shown in black. Grey polygons represent the inter-tropical zone and the central white line denotes the Equator. Cells classified as containing mountains per the UNEP definition and that are part of a group of three or more such cells are outlined in black and represent mountain ranges. To better display land edges and mountainous area contours the resolution of the 100×100 km grid cells used in the analyses was increased by a factor of five using local interpolation. See Fig. S2 for un-interpolated maps.
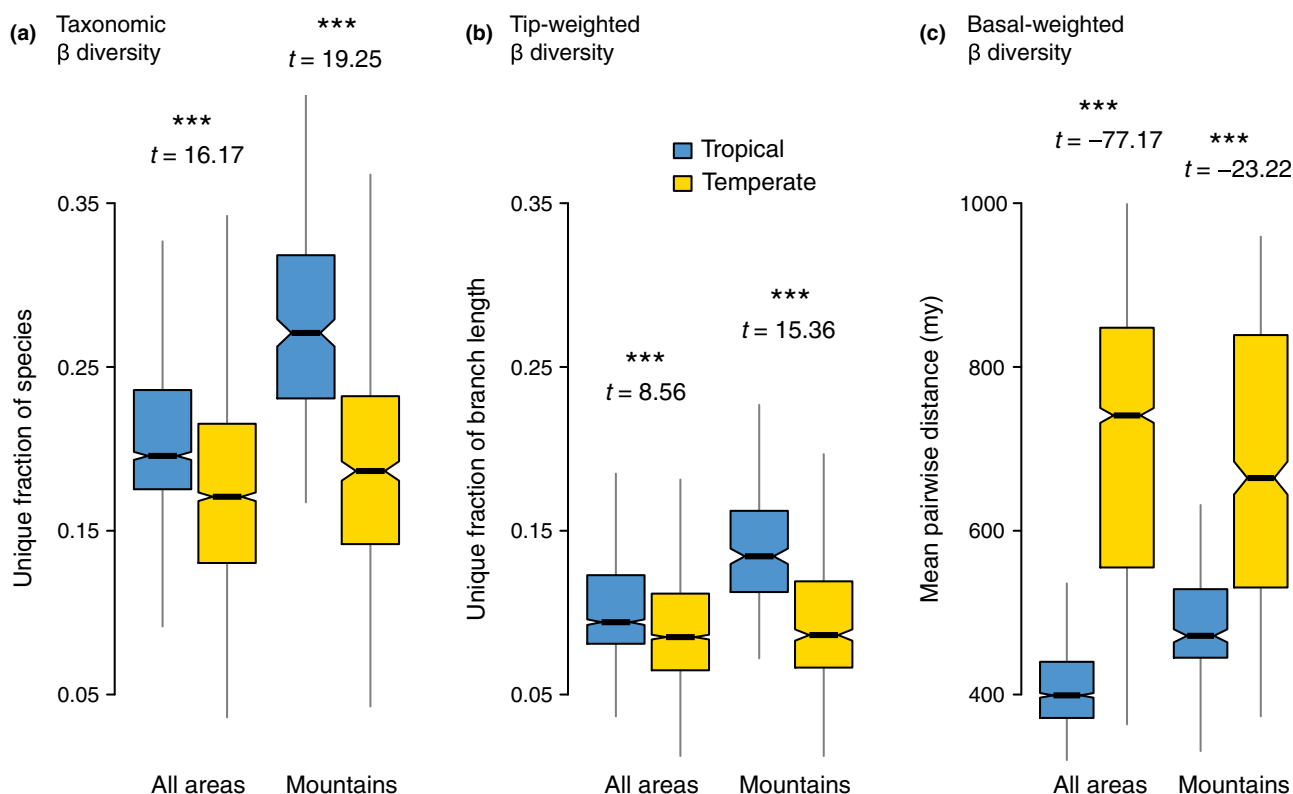
Figure 2 Tropical-temperate comparisons of β diversity for all areas and only mountainous regions. Regions north of the Tropic of Cancer (23.5° latitude) and south of the Tropic of Capricorn (−23.5° latitude) are classified as temperate and those in between as tropical, *** symbols indicate $P < 0.001$.

temperate zones. In addition, this metric exhibited less spatial variation and was weakly and negatively correlated with other metrics (Fig. 1c, $r = -0.15$ and $= -0.32$ respectively). Interestingly, the Andes displayed elevated levels of basal-weighted β diversity despite the fact that most other areas of the tropics had low levels of turnover.

Supporting our first hypothesis, taxonomic and tip-weighted β diversity were significantly higher in the tropics overall (Fig. 2a,b). Supporting our second hypothesis, results were similar when only mountainous regions were compared and the effect was stronger (Fig. 2a,b). Contrary to our hypotheses, basal-weighted β diversity displayed opposite patterns – with significantly higher levels of turnover in temperate regions and temperate mountainous regions (Fig. 2c). β diversity increased towards the equator when regressed against absolute latitude for both taxonomic and tip-weighted metrics (Fig. 3a,b, $R^2 = 0.25$ and 0.09 respectively) and peaked near the boundary of the tropics at $\sim \pm 20$ degrees latitude. This relationship strengthened when only mountainous regions were included (Fig. 3d,e, $R^2 = 0.61$ and 0.48 respectively). Basal-weighted β diversity again showed an opposite and stronger relationship with absolute latitude for both all regions and montane subsets ($R^2 = 0.82$ and 0.7, respectively, Fig. 3c,f).

Climatic drivers of β diversity

Multivariate SAR$_{err}$ models significantly reduced the autocorrelation of residuals compared to multivariate OLS regressions.

Both mean annual temperature and climate-change velocity were retained in all SAR$_{err}$ model subsets and were related positively to taxonomic and tip-weighted β and negatively to basal-weighted β (Table 1). Elevational range was retained in all taxonomic and tip-weighted subsets and annual precipitation was retained in tip-weighted β subsets as well as for basal-weighted β of all cells. In bivariate regressions mean annual temperature was the strongest predictor of all types of β diversity (Fig. 4), and temperature seasonality was the second most important in all comparisons (Table 2), supporting our third hypothesis. Taxonomic and tip-weighted β were related positively to mean annual temperature and negatively to temperature seasonality, whereas basal-weighted β showed the opposite pattern. Elevational range, annual precipitation and climate-change velocity had low predictive power for most β diversity metrics (Table 2).

DISCUSSION

Here we have leveraged a large dataset of species distributions and evolutionary relationships to map taxonomic and phylogenetic turnover in species assemblages across the Americas. We find β diversity is higher in the tropics for both taxonomic and tip-weighted phylogenetic measures, but that a reverse and stronger latitudinal gradient exists in basal-weighted β diversity. The finding of higher turnover in the temperate zone for basal-weighted β diversity is unexpected given the large number of studies reporting the opposite trend with latitude (Soininen *et al.* 2007, 2018). The higher turnover of deep phylogenetic structure found here is counter to the prevailing
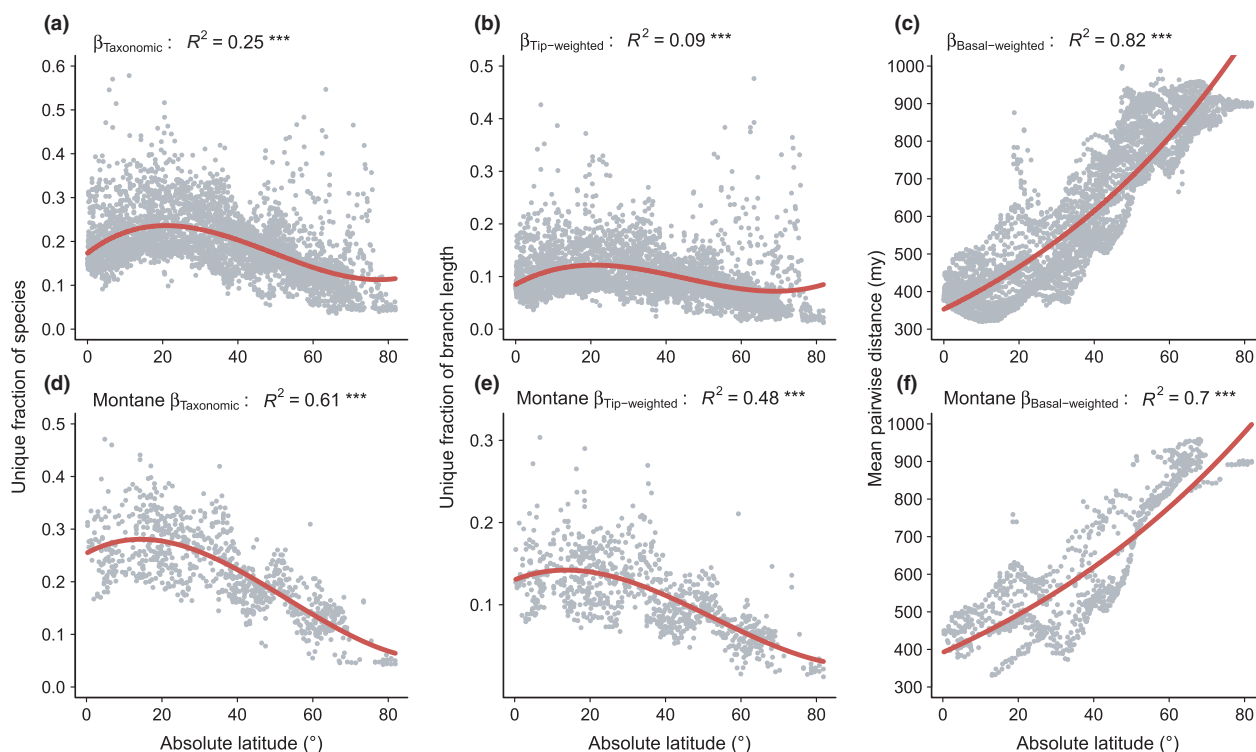
Figure 3 β diversity as a function of absolute latitude for the Americas. (a–c) Taxonomic, tip-weighted and basal-weighted β diversity patterns, respectively, (d–f) β diversity patterns of mountainous regions only. For clarity in panels a, b and c five, five and one cells, respectively, with high β values were excluded. Taxonomic and tip-weighted diversity values (a, b, d and e) were fit with a third-degree polynomial and basal-weighted β diversity (c, f) with an exponential. *** indicates P < 0.001. Fig. S3 shows β diversity as a function of non-absolute latitude.

hypothesis suggesting higher speciation and origination rates in tropics drive the latitudinal diversity gradient (Mittelbach *et al.* 2007), but is in line with several studies of vertebrate taxa showing higher diversification rates in the temperate zone (Weir & Schluter 2007; Rabosky *et al.* 2018). However, if faster and more recent speciation creates shorter branch lengths, the pattern of smaller pairwise distances between species in the tropics may also be consistent with the increased tropical speciation hypothesis. Future work should look beyond patterns of turnover alone and examine diversification rates of assemblages in each region to better understand these patterns.

Counter to our expectations, basal-weighted β diversity was related positively to temperature seasonality and negatively to mean annual temperature and precipitation. One explanation for this could be these conditions favour lineages common to temperate regions such as gymnosperms and mosses, which are less diverse in the tropics (Mateo *et al.* 2016). To test whether this pattern is driven by the inclusion of non-angiosperm lineages we reanalysed the data using only angiosperm taxa, which comprise ~98% of species in the dataset (79591 spp.) and only gymnosperm taxa, which account for < 1% of the species (289 spp.). For the angiosperm subset, though pairwise distances between communities were lower than when all taxa were included, temperate regions still had higher basal-weighted β diversity compared to the tropics (Fig. S4). This may be because temperate regions contain a mix of both tropical- and temperate-derived angiosperm lineages that contribute to higher basal-weighted β diversity. Indeed, basal-weighted β was highest at ± 40 degrees latitude, which is a transition zone between the subtropical and temperate regions. In contrast, basal-weighted gymnosperm β diversity was higher in the tropics (Fig. S5). This may be due to the fact that the tropics harbor both north and south-temperate gymnosperm clades, especially in mountainous regions (Graham 2010).

The increase in taxonomic and tip-weighted β diversity towards lower latitudes is in line with our hypotheses and other studies of taxonomic and phylogenetic β diversity of North American vascular plants (Qian *et al.* 2013), and suggests greater rates of turnover in the tropics may be one proximate cause of the latitudinal diversity gradient. In addition, peak turnover for taxonomic and tip-weighted β was near ± 20 degrees latitude, which suggests the transition from tropical to sub-tropical biomes may be an important driver of this pattern. Our results differ from recent studies reporting no latitudinal trends in the β deviation, an effect size measure which uses a null model to control for γ diversity when estimating β diversity (Kraft *et al.* 2011; Myers *et al.* 2013). This could be because our study did not calculate β deviation, though the pairwise metrics used in this study do not incorporate γ diversity and may therefore be invariant to it (Bennett & Gilbert 2016). Another possibility for this discrepancy is the larger grain size used in our study compared to previous studies.

As mentioned previously, a related property of species distributions predicted to influence richness gradients is latitudinal variation in species range size (Stevens 1989). Supporting this hypothesis, Morueta-Holme *et al.* (2013) found that mean

range size for vascular plants increases northwards in North America, but found the opposite trend south of the equator. The higher β diversity in the tropics we find may therefore be a consequence of larger range sizes in northern temperate regions. Supporting our climatic stability hypothesis, taxonomic and tip-weighted β diversity was inversely related to temperature seasonality and correlated positively with annual temperature, precipitation and local elevational range – all conditions which may favour local specialisation, smaller ranges and higher species turnover.

Although β diversity is higher in the tropics overall for taxonomic and tip-weighted β diversity, some areas with high α diversity such as the Amazon Basin had low β diversity. This may be because many plant species collected in this region have large ranges (Morueta-Holme *et al.* 2013; ter Steege *et al.* 2013), which should decrease rates of turnover. However, there may also be an issue of botanical under-collection in the Amazon Basin (Feeley 2015), which could result in the underestimation of β diversity for this region due to undiscovered small-ranged species (Hubbell *et al.* 2008).

The β diversity of montane areas peaked in the tropical Andes and increased more rapidly towards the equator than total β diversity for taxonomic and tip-weighted metrics. This may be due to the decrease in seasonality and increase in temperature towards the equator creating stable climatic zones

Table 1 Best fit SARerr models predicting log-transformed taxonomic and phylogenetic β diversity, including all cells and mountain-only subsets

β metric	Subset	Distance	minRSA	Max I	R^2	Final topoclimatic predictor set
β_T	All cells	200	1.20	0.28	0.90	MAT (+), CCV (+), ER (+)
β_T	Mountains	200	0.79	0.25	0.89	MAT (+), CCV (+), ER (+)
β_{T-W}	All cells	100	0.76	0.25	0.90	MAT (+), CCV (+), ER (+), AP (−)
β_{T-W}	Mountains	100	0.66	0.10	0.90	MAT (+), CCV (+), ER (+), AP (−)
β_{B-W}	All cells	100	1.42	0.71	0.99	MAT (−), CCV (−), AP (+)
β_{B-W}	Mountains	200	0.99	0.32	0.99	MAT (−), CCV (−)

β_T: Taxonomic β diversity; β_{T-W}: Tip-weighted β diversity, β_{B-W}: Basal-weighted β diversity. Distance: neighborhood matrix radius (km). AIC: Akaike's information criterion; minRSA: minimum residual spatial autocorrelation (sum of absolute values of Moran's I over first 20 distance classes); Max I: highest Moran's I value in first 20 distance classes; R^2: pseudo-R^2, squared Pearson correlation of predicted and observed values. MAT: Mean annual temperature, CCV: Climate-change velocity, ER: Elevational range, AP: Annual precipitation. The spatial weights matrix for all best fit model subsets had row-standardized ('W') coding. Predictor units are given in Table 2 and *Methods*. Topoclimatic variables were log-transformed and standardized before analysis, see Table S1 for correlations among variables
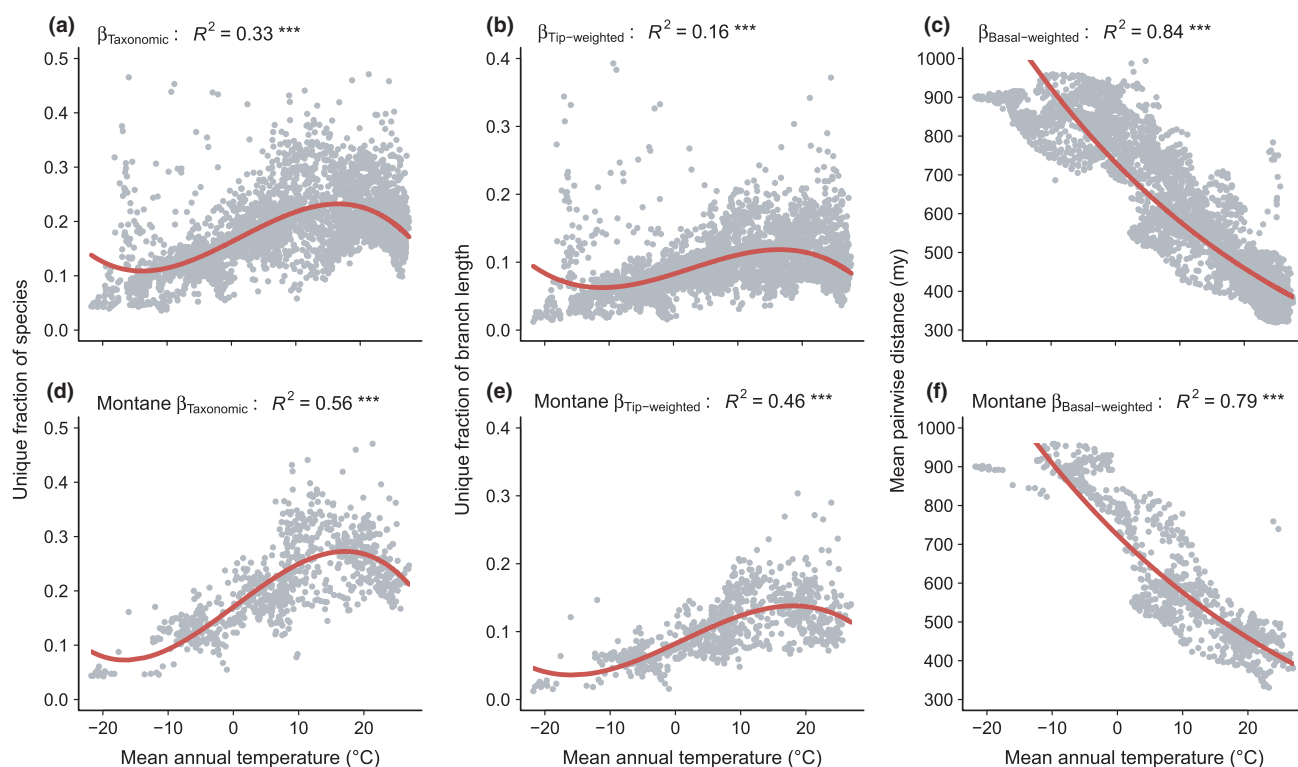
Figure 4 β diversity as a function of mean annual temperature, the strongest predictor for all metrics and subsets. Patterns for all regions (a–c) and mountainous regions only (d–e) are shown. For clarity in panels a and b one cell with a high β value was excluded. Taxonomic and tip-weighted β diversity (a, b, d and e) was fit with a third-degree polynomial model and basal-weighted β diversity (c, f) with an exponential model. *** indicates P < 0.001.

Table 2 Single-predictor R^2 relationships of log-transformed and standardised topoclimatic predictors with log-transformed taxonomic and phylogenetic β diversity for the Americas

β metric	Subset	Elevational range (m)	Annual precipitation (mm)	Mean annual Temperature (C)	Temperature seasonality (C)	Climate-change velocity (m/yr)
$\beta_{Taxonomic}$	All areas	0.05 (+)	0.06 (+)	0.30 (+)	0.14 (−)	0.06 (−)
$\beta_{Taxonomic}$	Mountains	0.22 (+)	0.04 (+)	0.58 (+)	0.39 (−)	0.09 (−)
$\beta_{Tip-weighted}$	All areas	0.03 (+)	0.02 (+)	0.18 (+)	0.08 (−)	0.03 (−)
$\beta_{Tip-weighted}$	Mountains	0.19 (+)	0.03 (+)	0.53 (+)	0.36 (−)	0.07 (−)
$\beta_{Basal-weighted}$	All areas	< 0.01 (+)	0.31 (−)	0.75 (−)	0.72 (+)	0.17 (+)
$\beta_{Basal-weighted}$	Mountains	0.03 (−)	0.08 (−)	0.74 (−)	0.49 (+)	0.01 (+)

Values in parentheses indicate the slope of the relationship. Subsets are β diversity values for all cells or cells of mountainous regions only. All relationships are significant at P < 0.01.

and narrower thermal tolerances (Janzen 1967), which may reduce range size and increase turnover (Ghalambor *et al.* 2006; McCain 2009). Temperature seasonality was strongly and negatively related to montane taxonomic and tip-weighted β diversity, which also supports Janzen's (1967) proposed mechanism of climatic stability driving higher β diversity in tropical mountains. One explanation for this pattern may be that average range sizes of plant in tropical mountains are smaller than in temperate mountains (Morueta-Holme *et al.* 2013), as has been found in several vertebrate taxa (McCain 2009). However, an ideal test would involve replicated montane transects measuring β diversity and thermal tolerances across sites spanning a range of latitudes. Temperature seasonality also influenced β diversity in the same way across all regions of the Americas including lowlands, though the effect

was somewhat weaker than for montane subsets, possibly because climatic gradients tend to be less steep outside of mountainous regions. This indicates that seasonality in temperature is an important driver of β diversity across all of the Americas.

Although we found strong and opposing latitudinal trends in β diversity, the degree of turnover is likely not shaped by gradients in latitude per se but by (a)biotic factors that change with latitude (Rohde 1992). To examine whether latitude is necessary to explain turnover in addition to climate and topography, we modelled β diversity as a function of latitude, climate and topography together in a multivariate framework. We found that latitude was retained after model reduction in four of the six model subsets (all areas or mountain cells, for all three metrics), though its effects were weak and its relative

importance was less than temperature (Tables S2 and S3). Although the explanatory power of latitude is low, these results suggest gradients of β diversity cannot be sufficiently explained by topography and climate alone and are likely also shaped by other factors such as dispersal limitation and the strength of species interactions (Hillebrand & Azovsky 2001; Mittelbach *et al.* 2007; Schemske *et al.* 2009; Roslin *et al.* 2017).

Limitations of the data
When working with datasets of this size and complexity there are several possible limitations to consider. First, β diversity maps were made with ranges estimated via MAXENT for many species. MAXENT range models made with few observations may have difficulty capturing the true range a species inhabits (Pearson *et al.* 2007, but see Elith *et al.* 2006). However, though this is also the case when ranges are estimated using raw occurrences only, which may be more influenced by under-sampled regions. Second, the incomplete detection of rare species and issues synonymising names across locations could affect β diversity estimates (Hubbell *et al.* 2008), which ideally include complete inventories of focal communities. We attempt to address these issues by including plot-based inventories which record all stems above a certain diameter cut-off, by standardising names with the Taxonomic Name Resolution Service (Boyle *et al.* 2013) to address synonymy issues and performing geographic name processing to reduce erroneous locality information. Finally, even with equal sampling effort, range sizes in the tropics may be underestimated due simply to the higher richness and corresponding lower sampling effort per species in these regions (Colwell & Hurt 1994).

CONCLUSIONS

In our study of land plant diversity patterns across the Americas we find taxonomic and tip-weighted β diversity is higher in the tropics, but discovered the opposite trend in turnover of deeper-diverging clades. The pattern of more recent divergences in the tropics suggests that faster tropical speciation rates may be an important driver of the latitudinal diversity gradient (Rohde 1992; Mittelbach *et al.* 2007). However, our finding that basal-weighted turnover was higher in the temperate zone calls for further studies of diversification rates across latitude in plants. In addition, our results provide further evidence that the uplift of the Andean Cordillera has had an outsized influence on patterns of Neotropical plant diversity and diversity of the Americas as a whole (Hoorn *et al.* 2010, but see Antonelli *et al.* 2018). Annual temperature and temperature seasonality emerged as strong drivers of β diversity, both of which are currently being altered through anthropogenic climate change (Xu *et al.* 2013) with potentially large effects on plant distribution and diversity. Finally, understanding how climate influences β diversity can assist conservation efforts that seek to identify high diversity areas without knowledge of the species in an area using abiotic variables alone (e.g. Raxworthy *et al.* 2003). Taken together, our results suggest β diversity is coupled to the latitudinal diversity gradient and that temperature shapes multiple facets

of diversity through its effect on range sizes and speciation rates.

AUTHORSHIP

IM designed the study with BS and NK. CT wrote the phylogenetic computation algorithms and BE, NM-H, J-CS and NK helped develop the BIEN database. IM conducted the analyses with BS and NK and IM led writing of the manuscript with substantial input from all authors.

DATA ACCESSIBILITY STATEMENT

Species distribution and phylogenetic information supporting the results are from version 2 of the BIEN database (http://bien.nceas.ucsb.edu/bien/biendata/bien-2). Data supporting the results can be found in the following Dryad repository: https://doi.org/10.5061/dryad.n42g840.

REFERENCES

Anacker, B.L. & Harrison, S.P. (2012). Historical and ecological controls on phylogenetic diversity in Californian plant communities. *Am. Nat.*, 180, 257–269.

Anderson, M.J., Crist, T.O., Chase, J.M., Vellend, M., Inouye, B.D., Freestone, A.L. *et al.* (2011). Navigating the multiple meanings of beta diversity: a roadmap for the practicing ecologist. *Ecol. Lett.*, 14, 19–28.

Antonelli, A., Zizka, A., Carvalho, F.A., Scharn, R., Bacon, C.D., Silvestro, D. *et al.* (2018). Amazonia is the primary source of Neotropical biodiversity. *Proc. Natl Acad. Sci.*, 115(23), 6034–6039.

Bennett, J.R. & Gilbert, B. (2016). Contrasting beta diversity among regions: how do classical and multivariate approaches compare? *Glob. Ecol. Biogeogr.*, 25, 368–377.

Blyth, S., Groombridge, B., Lysenko, I., Miles, L. & Newton, A. (2002). *Mountain Watch: Environmental Change and Sustainable Development in Mountains*. UNEP-WCMC, Cambridge, UK.

Boyle, B., Hopkins, N., Lu, Z., Raygoza Garay, J.A., Mozzherin, D., Rees, T. et al. (2013). The taxonomic name resolution service: an online tool for automated standardization of plant names. *BMC Bioinformatics*, 14, 16.

Colwell, R. & Hurt, G. (1994). Nonbiological gradients in species richness and a spurious Rapoport effect. *Am. Nat.*, 144, 570–595.

Dormann, C.F., McPherson, J.M., Araujo, M.B., Bivand, R., Bolliger, J., Carl, G. et al. (2007). Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography*, 30, 609–628.

Duarte, L.D.S., Bergamin, R.S., Marcilio-Silva, V., Dos Santos Seger, G.D. & Mendes Marques, M.C. (2014). Phylobetadiversity among forest types in the Brazilian Atlantic Forest complex. *PLoS ONE*, 9, e105043.

Dynesius, M. & Jansson, R. (2000). Evolutionary consequences of changes in species' geographical distributions driven by Milankovitch climate oscillations. *Proc. Natl Acad. Sci.*, 97, 9115–9120.

Elith, J., Graham, C.H., Anderson, R.P., Dudík, M., Ferrier, S., Guisan, A. et al. (2006). Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, 29, 129–151.

Enquist, B.J., Condit, R., Peet, R.K., Schildhauer, M. & Thiers, B.M. (2016). Cyberinfrastructure for an integrated botanical information network to investigate the ecological impacts of global climate change on plant biodiversity. *PeerJ Preprints*, e2615v1.

Feeley, K. (2015). Are we filling the data void? An assessment of the amount and extent of plant collection records and census data available for tropical South America. *PLoS ONE*, 10, e0125629.

Fine, P.V. & Kembel, S.W. (2011). Phylogenetic community structure and phylogenetic turnover across space and edaphic gradients in western Amazonian tree communities. *Ecography*, 34, 552–565.

Gaston, K.J. (2000). Global patterns in biodiversity. *Nature*, 405, 220–227.

Ghalambor, C.K., Huey, R.B., Martin, P.R., Tewksbury, J.J. & Wang, G. (2006). Are mountain passes higher in the tropics? Janzen's hypothesis revisited. *Integr. Comp. Biol.*, 46, 5–17.

Goldsmith, G.R., Morueta-Holme, N., Sandel, B., Fitz, E.D., Fitz, S.D., Boyle, B. et al. (2016). Plant-O-Matic: a dynamic and mobile guide to all plants of the Americas. *Methods Ecol. Evol.*, 7, 960–965.

Graham, A. (2010). *A Natural History of the New World*. University of Chicago Press, Chicago, IL.

Graham, C.H. & Fine, P.V.A. (2008). Phylogenetic beta diversity: linking ecological and evolutionary processes across space in time. *Ecol. Lett.*, 11, 1265–1277.

Hardy, O.J. & Senterre, B. (2007). Characterizing the phylogenetic structure of communities by an additive partitioning of phylogenetic diversity. *J. Ecol.*, 95, 493–506.

Harrison, S., Ross, S.J. & Lawton, J.H. (1992). Beta-Diversity on Geographic Gradients in Britain. *J. Anim. Ecol.*, 61, 151–158.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.*, 25, 1965–1978.

Hillebrand, H. (2004). On the generality of the latitudinal diversity gradient. *Am. Nat.*, 163, 192–211.

Hillebrand, H. & Azovsky, A.I. (2001). Body size determines the strength of the latitudinal diversity gradient. *Ecography*, 24, 251–256.

Hoorn, C., Wesselingh, F., Ter Steege, H., Bermudez, M., Mora, A., Sevink, J. et al. (2010). Amazonia through time: andean uplift, climate change, landscape evolution, and biodiversity. *Science*, 330, 927–931.

Hubbell, S.P., He, F., Condit, R., Borda-de-Água, L., Kellner, J. & ter Steege, H. (2008). How many tree species are there in the Amazon and how many of them will go extinct? *Proc. Natl Acad. Sci.*, 105, 11498–11504.

Janzen, D.H. (1967). Why mountain passes are higher in the tropics. *Am. Nat.*, 101, 233–249.

Kissling, W.D. & Carl, G. (2008). Spatial autocorrelation and the selection of simultaneous autoregressive models. *Glob. Ecol. Biogeogr.*, 17, 59–71.

Koleff, P., Lennon, J.J. & Gaston, K.J. (2003). Are there latitudinal gradients in species turnover? *Glob. Ecol. Biogeogr.*, 12, 483–498.

Kraft, N.J.B., Comita, L.S., Chase, J.M., Sanders, N.J., Swenson, N.G., Crist, T.O. et al. (2011). Disentangling the drivers of beta diversity along latitudinal and elevational gradients. *Science*, 333, 1755–1758.

Loarie, S.R., Duffy, P.B., Hamilton, H., Asner, G.P., Field, C.B. & Ackerly, D.D. (2009). The velocity of climate change. *Nature*, 462, 1052.

Lozupone, C. & Knight, R. (2005). UniFrac: a new phylogenetic method for comparing microbial communities. *Appl. Environ. Microbiol.*, 71, 8228–8235.

MacArthur, R.H. (1972). *Geographical Ecology*. Princeton University Press, Princeton, NJ.

Mateo, R.G., Broennimann, O., Normand, S., Petitpierre, B., Araújo, M.B., Svenning, J.-C. et al. (2016). The mossy north: an inverse latitudinal diversity gradient in European bryophytes. *Sci. Rep.*, 6, 25546.

McCain, C.M. (2009). Vertebrate range sizes indicate that mountains may be 'higher' in the tropics. *Ecol. Lett.*, 12, 550–560.

McKnight, M.W., White, P.S., McDonald, R.I., Lamoreux, J.F., Sechrest, W., Ridgely, R.S. et al. (2007). Putting beta-diversity on the map: broad-scale congruence and coincidence in the extremes. *PLoS Biol.*, 5, 2424–2432.

Melo, A.S., Rangel, T.F.L. & Diniz-Filho, J.A.F. (2009). Environmental drivers of beta-diversity patterns in New-World birds and mammals. *Ecography*, 32, 226–236.

Mittelbach, G.G., Schemske, D.W., Cornell, H.V., Allen, A.P., Brown, J.M., Bush, M.B. et al. (2007). Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. *Ecol. Lett.*, 10, 315–331.

Morlon, H., Schwilk, D.W., Bryant, J.A., Marquet, P.A., Rebelo, A.G., Tauss, C. et al. (2011). Spatial patterns of phylogenetic diversity. *Ecol. Lett.*, 14, 141–149.

Morueta-Holme, N., Enquist, B.J., McGill, B.J., Boyle, B., Jorgensen, P.M., Ott, J.E. et al. (2013). Habitat area and climate stability determine geographical variation in plant species range sizes. *Ecol. Lett.*, 16, 1446–1454.

Myers, J.A., Chase, J.M., Jimenez, I., Jorgensen, P.M., Araujo-Murakami, A., Paniagua-Zambrana, N. et al. (2013). Beta-diversity in temperate and tropical forests reflects dissimilar mechanisms of community assembly. *Ecol. Lett.*, 16, 151–157.

Novotny, V., Miller, S.E., Hulcr, J., Drew, R.A.I., Basset, Y., Janda, M. et al. (2007). Low beta diversity of herbivorous insects in tropical forests. *Nature*, 448, 692–695.

Pearson, R.G., Raxworthy, C.J., Nakamura, M. & Townsend Peterson, A. (2007). Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. *J. Biogeogr.*, 34, 102–117.

Phillips, S.J. & Dudík, M. (2008). Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography*, 31, 161–175.

Qian, H. & Ricklefs, R.E. (2007). A latitudinal gradient in large-scale beta diversity for vascular plants in North America. *Ecol. Lett.*, 10, 737–744.

Qian, H., Swenson, N.G. & Zhang, J. (2013). Phylogenetic beta diversity of angiosperms in North America. *Glob. Ecol. Biogeogr.*, 22, 1152–1161.

R Core Team (2016). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Rabosky, D.L., Chang, J., Title, P.O., Cowman, P.F., Sallan, L., Friedman, M. et al. (2018). An inverse latitudinal gradient in speciation rate for marine fishes. *Nature*, 559, 392.

Raxworthy, C.J., Martinez-Meyer, E., Horning, N., Nussbaum, R.A., Schneider, G.E., Ortega-Huerta, M.A. et al. (2003). Predicting distributions of known and unknown reptile species in Madagascar. *Nature*, 426, 837.

Rohde, K. (1992). Latitudinal gradients in species diversity: the search for the primary cause. *Oikos*, 65, 514.

Roslin, T., Hardwick, B., Novotny, V., Petry, W.K., Andrew, N.R., Asmus, A. *et al.* (2017). Higher predation risk for insect prey at low latitudes and elevations. *Science*, 356, 742–744.

Sandel, B., Arge, L., Dalsgaard, B., Davies, R.G., Gaston, K.J., Sutherland, W.J. *et al.* (2011). The influence of Late Quaternary climate-change velocity on species endemism. *Science*, 334, 660–664.

Schemske, D.W., Mittelbach, G.G., Cornell, H.V., Sobel, J.M. & Roy, K. (2009). Is there a latitudinal gradient in the importance of biotic interactions? *Annu. Rev. Ecol. Evol. Syst.*, 40, 245–269.

Schluter, D. (2016). Speciation, ecological opportunity, and latitude. *Am. Nat.*, 187, 1–18.

Slavich, E., Warton, D.I., Ashcroft, M.B., Gollan, J.R. & Ramp, D. (2014). Topoclimate versus macroclimate: how does climate mapping methodology affect species distribution models and climate change projections? *Divers. Distrib.*, 20, 952–963.

Smith, S.A. & O'meara, B.C. (2012). treePL: divergence time estimation using penalized likelihood for large phylogenies. *Bioinformatics*, 28, 2689–2690.

Smith, S.A., Beaulieu, J.M. & Donoghue, M.J. (2009). Mega-phylogeny approach for comparative biology: an alternative to supertree and supermatrix approaches. *BMC Evol. Biol.*, 9, 37.

Soininen, J., Lennon, J.J. & Hillebrand, H. (2007). A multivariate analysis of beta diversity across organisms and environments. *Ecology*, 88, 2830–2838.

Soininen, J., Heino, J. & Wang, J. (2018). A meta-analysis of nestedness and turnover components of beta diversity across organisms and ecosystems. *Glob. Ecol. Biogeogr.*, 27, 96–109.

Stamatakis, A. (2006). RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics*, 22, 2688–2690.

ter Steege, H., Pitman, N.C.A., Sabatier, D., Baraloto, C., Salomão, R.P., Guevara, J.E. *et al.* (2013). Hyperdominance in the Amazonian tree flora. *Science*, 342, 1243092.

Stevens, G.C. (1989). The latitudinal gradient in geographical range: how so many species coexist in the tropics. *Am. Nat.*, 133, 240–256.

Svenning, J.C. & Skov, F. (2004). Limited filling of the potential range in European tree species. *Ecol. Lett.*, 7, 565–573.

Swenson, N.G. (2011). Phylogenetic beta diversity metrics, trait evolution and inferring the functional beta diversity of communities. *PLoS ONE*, 6, e21264.

Webb, C.O., Ackerly, D.D. & Kembel, S.W. (2008). Phylocom: software for the analysis of phylogenetic community structure and trait evolution. *Bioinformatics*, 24, 2098–2100.

Weir, J.T. & Schluter, D. (2007). The latitudinal gradient in recent speciation and extinction rates of birds and mammals. *Science*, 315, 1574–1576.

Whittaker, R.H. (1970). *Communities and Ecosystems*. Macmillan, London.

Xu, L., Myneni, R.B., Chapin, F.S. III, Callaghan, T.V., Pinzon, J.E., Tucker, C.J. *et al.* (2013). Temperature and vegetation seasonality diminishment over northern lands. *Nat. Clim. Chang.*, 3, 581–586.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.