Direct and indirect effects of climate on richness drive the latitudinal diversity gradient in forest trees

Chengjin Chu[1,*], James A. Lutz[2], Kamil Král[3], Tomáš Vrška[3], Xue Yin[1], Jonathan A. Myers[4], Iveren Abiem[5,6], Alfonso Alonso[7], Norm Bourg[8], David F.R.P. Burslem[9], Min Cao[10], Hazel Chapman[11], Richard Condit[12], Suqin Fang[1], Gunter A. Fischer[13], Lianming Gao[14], Zhanqin Hao[15], Billy C.H. Hau[16], Qing He[1], Andrew Hector[17], Stephen P. Hubbell[18], Mingxi Jiang[19], Guangze Jin[20], David Kenfack[21,22], Jiangshan Lai[23], Buhang Li[1], Xiankun Li[24], Yide Li[25], Juyu Lian[26], Luxiang Lin[10], Yankun Liu[27], Yu Liu[28,29], Yahuang Luo[14], Keping Ma[23], William McShea[8], Hervé Memiaghe[30], Xiangcheng Mi[23], Ming Ni[1], Michael J. O'Brien[31], Alexandre A. de Oliveira[32], David A. Orwig[33], Geoffrey G. Parker[34], Xiujuan Qiao[19], Haibao Ren[23], Glen Reynold[35], Weiguo Sang[36], Guochun Shen[29], Zhiyao Su[37], Xinghua Sui[1], I-Fang Sun[38], Songyan Tian[27], Bin Wang[24], Xihua Wang[29], Xugao Wang[15], Youshi Wang[1], George D. Weiblen[39], Shujun Wen[24], Nianxun Xi[1], Wusheng Xiang[24], Han Xu[25], Kun Xu[40], Wanhui Ye[26], Bingwei Zhang[1], Jiaxin Zhang[19], Xiaotong Zhang[1], Yingming Zhang[41], Kai Zhu[42], Jess Zimmerman[43], David Storch[44,45], Jennifer L. Baltzer[46], Kristina J. Anderson-Teixeira[8,21], Gary G. Mittelbach[47], Fangliang He[28,48]

[1] *Department of Ecology, State Key Laboratory of Biocontrol and School of Life Sciences, Sun Yat-sen University, 510275 Guangzhou*
[2] *Wildland Resources Department, Utah State University, Logan, UT, USA*
[3] *Department of Forest Ecology, Silva Tarouca Research Institute, Brno, Czech Republic*
[4] *Department of Biology and Tyson Research Center, Washington University in St. Louis, St. Louis, MO, USA*
[5] *Department of Plant Science and Technology, University of Jos, Jos, Nigeria*
[6] *A. P. Leventis Ornithological Research Institute, Jos, Nigeria*
[7] *Center for Conservation Education and Sustainability, Smithsonian Conservation Biology Institute, National Zoological Park, Washington, DC, USA*
[8] *Conservation Ecology Center, Smithsonian Conservation Biology Institute, National Zoological Park, Front Royal, VA, USA*
[9] *School of Biological Sciences, University of Aberdeen, Aberdeen, UK*
[10] *Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, 650223 Kunming*
[11] *School of Biological Sciences, University of Canterbury, Christchurch, New Zealand*
[12] *Smithsonian Tropical Research Institute, Balboa, Ancon, Republic of Panama*
[13] *Kadoorie Farm and Botanic Garden, Tai Po, Hong Kong*
[14] *Key Laboratory for Plant Diversity and Biogeography of East Asia, Kunming Institute of Botany, Chinese Academy of Sciences, 650201 Kunming*
[15] *Institute of Applied Ecology, Chinese Academy of Sciences, 110016 Shenyang*
[16] *Kadoorie Institute and School of Biological Sciences, The University of Hong Kong, Pokfulam, Hong Kong*
[17] *Department of Plant Sciences, University of Oxford, Oxford OX1 3RB, UK*

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

[19] *Key Laboratory of Aquatic Botany and Watershed Ecology, Wuhan Botanical Garden, Chinese Academy of Sciences, 430074 Wuhan*

[20] *Center for Ecological Research, Northeast Forestry University, 150040 Harbin*

[21] *Center for Tropical Forest Science-Forest Global Earth Observatory, Smithsonian Tropical Research Institute, Panama, Republic of Panama*

[22] *Department of Botany, National Museum of Natural History, Washington, DC, USA*

[23] *State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, The Chinese Academy of Sciences, 100093 Beijing*

[24] *Guangxi Institute of Botany, Chinese Academy of Sciences, 541006 Guilin*

[25] *Research Institute of Tropical Forestry, Chinese Academy of Forestry, 510000 Guangzhou*

[26] *Key Laboratory of Vegetation Restoration and Management of Degraded Ecosystems, South China Botanical Garden, Chinese Academy of Sciences, 510650 Guangzhou*

[27] *Heilongjiang Forestry Enginerring and Environment Institute, 150040 Harbin*

[28] *ECNU-Alberta Joint Lab for Biodiversity Study, Tiantong National Station for Forest Ecosystem Research, East China Normal University, 200241 Shanghai*

[29] *Tiantong National Station for Forest Ecosystem Research, School of Ecology and Environmental Sciences, East China Normal University, 200241 Shanghai*

[30] *Institut de Recherche en Ecologie Tropicale/Centre National de la Recherche Scientifique et Technologique, Libreville, Gabon*

[31] *Estación Experimental de Zonas Áridas, Consejo Superior de Investigaciones Científicas, Carretera de Sacramento s/n, E-04120 La Cañada, Almería, Spain*

[32] *Departamento Ecologia, Universidade de São Paulo, Instituto de Biociências, Cidade Universitária, São Paulo, SP, Brazil*

[33] *Harvard Forest, Harvard University, Petersham, MA, USA*

[34] *Forest Ecology Group, Smithsonian Environmental Research Center, Edgewater, MD, USA*

[35] *Southeast Asia Rainforest Research Partnership, Danum Valley Field Centre, PO Box 60282, 91112 Lahad Datu, Sabah, Malaysia*

[36] *Minzu University of China; and Institute of Botany, Chinese Academy of Sciences, 100093 Beijing*

[37] *College of Forestry, South China Agricultural University, 510642 Guangzhou*

[38] *Department of Natural Resources and Environmental Studies, National Dong Hwa University, 97401 Hualien*

[39] *Department of Plant & Microbial Biology, University of Minnesota, St. Paul, MN, USA*

[40] *Lijiang Forest Ecosystem Research Station, Kunming Instituted of Botany, Chinese Academy of Sciences, 674100 Lijiang*

[41] *Guangdong Chebaling National Nature Reserve, 512500 Shaoguan*

[42] *Department of Environmental Studies, University of California, Santa Cruz, CA 95064, USA*

[43] *Institute for Tropical Ecosystem Studies, University of Puerto Rico, San Juan, Puerto Rico 00936, USA*

[44] *Center for Theoretical Study, Charles University and the Academy of Sciences of the Czech Republic, Praha, Czech Republic*

[45] *Department of Ecology, Faculty of Science, Charles University, Praha, Czech Republic*

[46] *Biology Department, Wilfrid Laurier University, Waterloo, ON, Canada*

[47] *Kellogg Biological Station and Department of Integrative Biology, Michigan State University, Hickory Corners, Michigan 49060, USA*

[48] *Department of Renewable Resources, University of Alberta, Edmonton, Alberta, T6G 2H1, Canada*

Type of article: Letters

Running title: Climate and the latitudinal tree diversity gradient

Number of words in the abstract: 146

Number of words in the main text: 4867

Number of references: 58

Number of figures: 4

Number of tables: 2

Author contributions: CC designed research, compiled and analyzed data. CC wrote the first draft, with substantial input from K.J.A-T., K.K., J.L.B., G.G.M., J.A.L., D.S., T.V., J.A.M. and F.H. Many authors contributed to data collection of forest censuses and all authors contributed to revisions of the manuscript.

Data accessibility statement: Full census data are available upon reasonable request from the ForestGEO data portal, http://ctfs.si.edu/datarequest/.

Keywords: Climate tolerance hypothesis, CTFS-ForestGEO, latitudinal diversity gradient, more-individuals hypothesis, species-energy relationship, structural equation modeling

* **Corresponding author:** Chengjin Chu; Mailing address: Xingang Xi Road 135, Sun Yat-sen University, Guangzhou, 510275, China; Tel: (+86)2084111541; E-mail: chuchjin@mail.sysu.edu.cn.

Abstract

Climate is widely recognized as an important determinant of the latitudinal diversity gradient. However, most existing studies make no distinction between direct and indirect effects of climate, which substantially hinders our understanding of how climate constrains biodiversity globally. Using data from 35 large forest plots, we test hypothesized relationships among climate, topography, forest structural attributes (stem abundance, tree size variation and stand basal area) and tree species richness to better understand drivers of latitudinal tree diversity patterns. Climate influences tree richness both directly, with more species in warm, moist, aseasonal climates, and indirectly, with more species at higher stem abundance. These results imply direct limitation of species diversity by climatic stress and more rapid (co-)evolution and narrower niche partitioning in warm climates. They also support the idea that increased numbers of individuals associated with high primary productivity are partitioned to support a greater number of species.

INTRODUCTION

Although the latitudinal diversity gradient – i.e., the pronounced increase in species richness from the poles to the equator – has been recognized for centuries (Gaston 2000; Brown 2014; Fine 2015; Ricklefs & He 2016; Comita 2017; Kinlock *et al.* 2018), the primary factors determining this fundamental gradient in biodiversity remain unresolved. This gradient is shaped by a combination of evolutionary and ecological mechanisms (Mittelbach 2012; Brown 2014; Ricklefs & He 2016), with climate at the forefront of most hypotheses (Kreft & Jetz 2007; Mittelbach 2012; Schluter 2015). There are numerous interrelated mechanisms through which climate may influence diversity (Fig. 1). Major mechanisms shaping the latitudinal diversity gradient include the tropical origins of most clades, niche partitioning, kinetics of ecological interactions and evolution, and primary productivity (Brown 2014).

The tropics have acted as both a cradle and museum of biodiversity, with the majority of clades originating and persisting there (Jablonski *et al.* 2006; Mittelbach *et al.* 2007; Cavender-Bares *et al.* 2011; Bowen *et al.* 2013). Rates of speciation are highest in the tropics, and higher rates of speciation than extinction have led to a buildup of tropical biodiversity. Given that most clades have originated in the moist tropics, climatic conditions associated with higher latitudes (e.g., freezing temperatures, aridity, strong seasonality) are encountered as stressors, and only a portion of lineages are able to adapt to and persist in these environments, resulting in a latitudinal gradient in diversity.

Niche partitioning, driven by both abiotic and biotic mechanisms, also plays a role in shaping the latitudinal diversity gradient. Species adapted to more abiotically variable habitats can tolerate a wider range of abiotic conditions and therefore have wider niches, larger elevational ranges and the associated potential to disperse over mountain range barriers, and broader geographic ranges (Terborgh 1973; Stevens 1989; Gaston & Chown 1999). This effect is compounded by biotic interactions, leading to high niche specialization at lower latitudes (Brown 2014). Thus, niche breadth and the looseness of species "packing" within ecological communities and across local (e.g., topographic) environmental gradients increase with latitude.

The latitudinal variation in evolution rate and biotically driven niche specialization described above is probably driven by temperature (Brown 2014). In general, biological rates tend to increase with temperature through temperature effects on the kinetics of the biochemical reactions underlying metabolism (Brown *et al.* 2004; Sibly *et al.* 2012). Specifically relevant here, rates of DNA evolution, speciation, and biological interactions (e.g., competition, herbivory, predation, parasitism) all increase with temperature (Gillooly *et al.* 2005; Allen *et al.* 2006). This provides a possible mechanistic explanation for the above-described latitudinal gradients in evolution rate and Red Queen coevolution, leading to the argument of Brown (2014) that "the Red Queen runs faster when she is hot."

While the above mechanisms determine regional species pools, local plot richness is ultimately constrained by forest structure including the number and sizes of individuals that can coexist. Indeed, the species-energy hypothesis posits that climate strongly influences primary productivity, or the total energy available for partitioning within most ecological communities, thereby *indirectly* affecting species richness via its impact on the number and size of individuals that can be supported (Hutchinson 1959; Currie *et al.* 2004; Brown 2014; Chu *et al.* 2016b; Storch *et al.* 2018). Specifically, both gross and net primary productivity increase with temperature across the latitudinal gradient (Luyssaert *et al.* 2007). This greater energy availability in the tropics can be partitioned to support more individuals. In turn, more individuals could represent more species because of a statistical effect (rare species are more likely to be absent in small samples) and/or larger population sizes per unit area, the latter of which would be associated with decreased extinction rates and thereby maintenance of species richness (O'Brien 1998; Srivastava & Lawton 1998; Currie *et al.* 2004; Storch *et al.* 2018). However, evidence that this actually occurs is mixed; for example, higher tree abundance (i.e., stem abundance) does not necessarily translate to increased species richness (Hawkins *et al.* 2003; Currie *et al.* 2004; Šímová *et al.* 2011; Storch *et al.* 2018). In large part, this may be due to the fact that productivity can also be partitioned to support fewer larger, as opposed to more, individuals. If increased energy goes primarily to support a few larger individuals, it may have little impact on species richness, or may even suppress diversity through associated competition for limiting resources (Franklin *et al.* 2002). For instance, larger trees often have a disproportionally large effect on smaller ones through overtopping, resulting in size-asymmetric competition for light, water, or nutrients (Coomes *et al.* 2011; Lutz *et al.* 2014; Farrior *et al.* 2016).

The above hypotheses are neither mutually exclusive nor easily disentangled, yet they do result in specifically testable and sometimes distinct empirical predictions that can help determine the relative importance of the various mechanisms (Fig. 1). In particular, it should be possible to distinguish the direct and indirect (via the number of individuals) effects of climate on species richness, yet most previous studies have focused instead on the total or net effect of climatic variables on broad-scale variation in species diversity (Hawkins *et al.* 2003; Currie *et al.* 2004; Šímová *et al.* 2011). This has contributed to conflicting conclusions regarding the drivers of species-energy relationships (Šímová *et al.* 2011; Storch *et al.* 2018). Simultaneous consideration of direct and indirect effects will substantially improve our understanding of the mechanisms underlying climatic drivers of species richness (e.g., see Menéndez *et al.* (2007) for butterflies, Ferger *et al.* (2014) for birds, and Marshall & Baltzer (2015) for subarctic plant communities).

Similar to other taxa, tree species richness usually displays a pronounced latitudinal diversity gradient (Kreft & Jetz 2007; Šímová *et al.* 2011). Here, we attempt to tease apart the indirect role of climate mediated through forest structural attributes (species-energy hypothesis) from the more direct effects of climate on global tree species richness. This is made possible with data from 35 large (9-60 ha) stem-mapped forest plots across the globe (Anderson-Teixeira *et al.* 2015). We use a structural equation modelling approach (SEM; Grace 2006) to test hypothesized causal relationships amongst climate, topography, forest structural attributes (stem abundance, tree size variation, and stand basal area), and tree species richness. Our two major objectives were to: (1) Disentangle the direct and indirect effects of climate on tree species diversity across global forest plots, thereby evaluating the relative importance of mechanisms described above (Fig. 1), and (2) Quantify the effects of forest structural attributes on local tree species richness within each forest plot, in order to assess whether the importance of these drivers varies systematically with latitude.

METHODS

Study sites, topographic and climatic data

Thirty-five forest dynamics plots compiled from the CTFS-ForestGEO network (http://www.forestgeo.si.edu/) and other sources were used in this study (Fig. 2a, and Supplementary Information Table 1). In each plot, all freestanding woody stems with a diameter at breast height (DBH) ≥ 1 cm were identified to species, tagged, measured and mapped according to a standardized census protocol (Condit 1998). The size of the plots ranges from 9 ha (Liangshui, China) to 60 ha (Jianfengling, China) and these plots span a broad latitudinal gradient from -25.10° (Ilha do Cardoso, Brazil) to 61.30° (Scotty Creek, Canada). Data from the first census for all forest plots were used for the present analyses except Barro Colorado Island, where the seventh census was used to be temporally comparable to the other, more recently established plots.

Each forest plot was divided into non-overlapping quadrats at two spatial scales: 20 m × 20 m and 50 m × 50 m, which allowed us to account for the possible scale-dependence of forest structural patterns and processes (Chisholm *et al.* 2013) and to test the hypothesis that species richness increases more rapidly with increasing spatial scale at lower latitudes (Fig. 1). We excluded shrubs and lianas from the analyses and focused only on trees. In each quadrat, in addition to tree species richness we calculated three easily measured and ecologically important forest structural attributes: stem abundance (the total number of stems), stand basal area (the sum of stem basal area), and tree size variation measured by the coefficient of variation (CV) of tree DBH within a quadrat.

Elevation was recorded at the intersections of the 20 m × 20 m grid for each plot, which was used to estimate additional topographic variables including slope, convexity and aspect (Baldeck *et al.* 2013), and was extrapolated to estimate topographic factors at the various scales of interest. Following previous definitions (Harms *et al.* 2001; Baldeck *et al.* 2013), elevation of a quadrat was calculated as the mean elevation of four corners. Slope was derived from the average slope of the four planes formed by connecting three corners of a quadrat at a time. Convexity was defined as the elevation of a quadrat minus the mean elevation of all immediate neighbor quadrats. Aspect refers to the direction in which a slope faces; sin(aspect) and cos(aspect) were calculated in order to use aspect in the within-forest plot analyses (Legendre *et al.* 2009). To account for the potential effect of fine-scale environmental heterogeneity on species richness and forest structural attributes, we calculated the ranges of elevation, slope and convexity within each quadrat at the spatial scales of 20 m × 20 m and 50 m × 50 m, based on the topographic variables at the finer spatial scale of 10 m × 10 m. In addition, we calculated the ranges of elevation, slope and convexity within individual forest plots at the two spatial scales, resulting in a total of nine topographic variables.

We compiled climate data for the 35 forests to analyze the relationship among topography, climate, forest structure, and tree species richness (across-forest plot analyses at the two spatial scales using the same climatic information). We used standardized climate data with the 0.5-degree spatial resolution from the CRU TS4.01 database (http://catalogue.ceda.ac.uk/uuid/58a8802721c94c66ae45c3baa4d814d0; downloaded April 2018) for each forest plot. We retrieved monthly data for 1901-2016 for nine variables: cloud cover (%), diurnal temperature range (°C), frost day frequency (days), precipitation (mm), daily mean temperature (°C), monthly average daily minimum temperature (°C), monthly average daily maximum temperature (°C), vapour pressure (hectopascals), wet day frequency (days), and potential evapotranspiration (mm day^{-1}). We calculated the annual temperature range (°C) as follows: the maximum value of monthly average daily maximum temperature minus the minimum value of monthly average daily maximum temperature. Monthly data were used to calculate the annual values, which were then averaged over 1901-2016 to obtain climatic averages for individual plots. Potential evapotranspiration (mm year^{-1}) data were extracted from the Global Aridity Index (Global-Aridity) and the Global Potential Evapo-Transpiration (Global-PET) Geospatial Database (http://www.cgiar-csi.org/data/global-aridity-and-pet-database). Incoming solar radiation (kJ m^{-2} day^{-1}) data were downloaded from the WorldClim database (http://worldclim.org/version2) for the spatial resolution of 30 seconds. In total, twelve climatic variables were included in the analyses.

In the following analyses, three forest structural variables (stem abundance, tree size variation, and stand basal area) and tree species richness were log-transformed to account for the power relationship of stem abundance with species richness (Ricklefs & He 2016). Topographic and climatic variables were standardized to the 0-1 range by $(x - x_{min}) / (x_{max} - x_{min})$.

Statistical analyses

Our structural equation model was constructed using the following assumptions. We assumed that climate/topography could directly drive the variation of forest structural attributes and tree species richness, as many previous studies have shown (Vayreda *et al.* 2012; Chu *et al.* 2016a; Lechuga *et al.* 2017; Lutz *et al.* 2018). Higher stem abundance – i.e., increased number of individuals – was expected to increase tree species richness by reducing the number of species that go extinct due to demographic stochasticity (i.e., the more-individuals hypothesis (O'Brien 1998; Srivastava & Lawton 1998; Currie *et al.* 2004); but see Storch *et al.* (2018)) and increase tree size variation due to competition (Weiner *et al.* 2001). Stand basal area is jointly determined by the number and the size of trees. If an increase in stand basal area was due to increased stem abundance, stand basal area was predicted to exert a similar role as stem abundance on species richness. Conversely, if the increase in stand basal area was mainly caused by the increased size of trees, stand basal area should result in the opposite effect, i.e. decreasing species richness and increasing tree size variation as the result of competition (Canham *et al.* 2004; Franklin *et al.* 2002). The relationship between tree size variation and species richness was unpredictable. On the one hand, greater tree species richness may increase the degree of tree size variation in forests (Hakkenberg *et al.* 2016; Pretzsch & Schütze 2016). On the other hand, larger tree size variation may lead to increased species richness by creating more ecological niches (Terborgh 1985), or may decrease species richness through strong asymmetric competition for light, especially in more diverse forests with a higher proportion of rare species (Larson *et al.* 2008; Hakkenberg *et al.* 2016). As such, we defined a reciprocal interaction between tree species richness and tree size variation.

We conducted both across-forest plot analyses and within-forest plot analyses. For the across-forest plot analyses, we first calculated mean tree species richness and forest structural attributes across quadrats at the two spatial scales within each forest plot. Then we explored the hypothesized relationships among these variables as well as topographic and climatic factors through structural equation modeling (SEM; Fig. 3a). SEM offers a means to evaluate hypothesized causal relationships amongst multiple variables. For the within-forest plot analyses, we applied a similar SEM structure for quadrat-level variables of forest structural attributes and topography (Fig. 3a), but without climatic variables as macroclimate is constant within a plot and microclimatic variation will largely be determined by topographic variation.

To simplify the SEM model construction and account for potential colinearity among variables, we reduced the dimensionality of the climate (twelve predictors) and topography variables (nine predictors in across-forest plot analyses: elevation, slope, convexity and the ranges of these three variables both within each quadrat and across the entire plot; eight predictors in within-forest plot analyses: elevation, slope, convexity, and the ranges of these three variables within each quadrat, sin(aspect) and cos(aspect)) by means of principal component analysis (PCA) at the two spatial scales. We present the PCA results of topography for the across-forest plot analyses and plot-specific PCA results of topography for within-forest plot analyses in Supplementary Information Table 2. We used the '*lavaan*' package (Rosseel 2012) in the *R* software platform (R Core Team 2016) to parameterize the SEM. Bivariate relationships among all variables for SEMs in both across-forest plot and within-forest plot analyses were presented in the Supplementary Information Fig. 1. To develop the final SEMs, we started with our initial hypothesized relationships among variables (Fig. 3a). We then considered a number of alternative reduced models sharing the same causal structure with the initial model, which were constructed by eliminating non-significant variables one by one (Supplementary Information Table 3). The decision to remove a path was based on the performance of overall model fit and the P-value for the path (Grace 2006). Model evaluation was determined by the following two criteria: 1) The chi-square test ($P > 0.05$ for a satisfactory fit), and 2) The Standardized Root Mean Square Residual (SRMR < 0.05 for a satisfactory fit). The Bayesian Information Criterion (BIC) was used to select the best model from models with a satisfactory fit. In the final step, we deleted non-significant paths with $P > 0.05$ in SEMs with satisfactory model fit and reassessed model fit. Standardized SEM path coefficients from within-forest plot analyses are reported in the Supplementary Information Table 4. The total effect that one variable has on another equals the sum of its direct and indirect effects through directed (causal) paths. The standard error (SE) values and *P* values for standardized path coefficients were obtained through the function *standardizedSolution* in the *'lavaan'* package.

RESULTS

Across-forest plot analyses: Direct and indirect effects of climate on global tree species richness

The first two PCA axes of 12 climatic variables explained respectively 75% and 13% of the total variation in climate in the 35 forest plots (Table 1). The first principal component ($\mathrm{Clim}_{\mathrm{PC1}}$) mainly explained the variability of temperature-related climatic factors, including average daily minimum temperature (10.9%), average daily mean temperature (10.7%), frost day frequency (10.4%), vapor pressure (10.4%), annual temperature range (10.1%), and average daily maximum temperature (10.0%). The second principal component ($\mathrm{Clim}_{\mathrm{PC2}}$) best explained the variability of incoming solar radiation (48.1%), cloud cover (22.9%) and diurnal temperature range (13.8%).

For topography, the first PCA axis explained 62.5% of the total variation in topography at the scale of 20 m × 20 m, and 62.4% at the scale of 50 m × 50 m (Supplementary Information Table 2). The first principal component ($\mathrm{Topo}_{\mathrm{PC1}}$) at both spatial scales best explained the variability in slope and ranges of elevation, slope and convexity within quadrats and across the entire plot. The second PCA axis explained 16.6% of the total variation in topography for the 20 m scale and 12.4% for the 50 m scale, which mainly explained the variability in convexity.

Tree species richness, stem abundance and richness:stem ratios displayed pronounced latitudinal gradients (Figs. 2b-2d). In particular, in forest plots at latitudes lower than 23.5°, tree species richness increased with decreasing absolute latitude at a rate of 1.82 species per degree at the scale of 20 m × 20 m, and 4.01 species per degree at the scale of 50 m × 50 m (Fig. 2b). In contrast, in plots at latitudes greater than 23.5°, the rates were 0.90 and 1.78 species per degree for the 20 and 50m scales, respectively (Fig. 2b). This demonstrated that tree richness increases more rapidly with increasing spatial scale in lower latitudes.

At the scale of 20 m × 20 m, the selected SEM explained 74% of the global variation in tree species richness (Fig. 3a). Clim_{PC1} had a significant direct effect on tree species richness with a standardized path coefficient of 0.60. Clim_{PC1} and Clim_{PC2} also influenced tree species richness indirectly via stem abundance, with standardized path coefficients of 0.20 (0.53 × 0.37) and -0.16 ([-0.44] × 0.37). Topography had no significant effects on three forest structural attributes or tree richness (Supplementary Information Table 5) resulting in the removal of these paths from the final model. The relationship between stand basal area and tree species richness, and the reciprocal interactions between tree species richness and tree size variation were also not significant (Supplementary Information Table 5). Among the three structural attributes in question, stem abundance did not influence tree size variation. In contrast, stand basal area significantly increased tree size variation globally (Supplementary Information Table 5).

Similar results were obtained at the scale of 50 m × 50 m. The SEM explained 76% of the total variation in tree species richness across plots (Fig. 3b). Climate had both direct and indirect effects on tree species richness through three pathways (Fig. 3b): one direct from $\mathrm{Clim}_{\mathrm{PC1}}$ to richness (path coefficient 0.63), two indirectly mediated by stem abundance from $\mathrm{Clim}_{\mathrm{PC1}}$ (path coefficient 0.19, i.e. 0.54 × 0.36) and $\mathrm{Clim}_{\mathrm{PC2}}$ (-0.15, i.e. [-0.43] × 0.36) to richness, respectively.

We note that an SEM model incorporating latitude explains slightly higher proportion of the variance (R^2) in tree richness than a model with climate alone (Table 2; across-forest plot SEM models including latitude are presented in the Supplementary Information Table 6). The incorporation of latitude also makes the direct path from $\mathrm{Clim}_{\mathrm{PC1}}$ to tree species richness non-significant (Supplementary Information Table 6). $\mathrm{Clim}_{\mathrm{PC1}}$ was strongly correlated to latitude (r = -0.91; Supplementary Information Fig. 2), and it was inappropriate to include two variables as tightly correlated as these into a single SEM (Grace 2006). Since the aim of our study has been to elucidate the causes of the latitudinal gradient in tree species richness, we focus on the model with climate rather than the model with latitude. Still, we cannot exclude the possibility that the effect of latitude on tree species richness goes beyond the sole effect of climate.

Within-forest plot analyses: forest structural attributes and local tree species richness

Within individual forest plots, the direction and strength of SEM path coefficients between three forest structural attributes and tree species richness varied substantially (Fig. 4; Supplementary Information Table 4). In total, at the scale of 20 m × 20 m, stem abundance positively influenced tree richness in 34 of 35 forest plots (with the boreal forest plot, Scotty Creek, the exception). Tree size variation was positively correlated with tree richness in six plots, and stand basal area was positively correlated with species richness in 18 plots and negatively in 9 plots. At the scale of 50 m × 50 m, stem abundance positively influenced tree richness in 25 out of 35 plots; tree size variation was positively correlated with tree richness in six plots and negatively in one plot (Wanang); and stand basal area was negatively correlated with richness in 13 plots and positively in four.

The effect of stem abundance on tree species richness displayed a significant latitudinal trend (Fig. 4b; $P < 0.01$, $R^2 = 0.27$) at the scale of 20 m × 20 m, with the effect of stem abundance being more pronounced at lower latitudes. This temperate/tropical difference was less apparent at the scale of 50 m × 50 m (Fig. 4e; $P = 0.062$, $R^2 = 0.10$).

The proportion of the explained variance in tree richness within plots in relation to topography and structural traits ranged from 0.050 (Zofin) to 0.88 (Ngel Nyaki) with a mean of 0.36 at the scale of 20 m × 20 m, and from 0.042 (Zofin) to 0.89 (Ngel Nyaki) with a mean of 0.35 at the scale of 50 m × 50 m (Supplementary Information Table 4).

DISCUSSION

Climate influences global tree species richness both directly and indirectly

We found clear evidence that climate influenced tree species richness both directly and indirectly (through stem abundance) in forest plots worldwide. This lends support to all of the major mechanisms considered here (Fig. 1) and yields insights into their relative importance.

At the two spatial scales explored, there were strong, direct effects of climate on tree species richness (Fig. 3), with the first PC axis, $\mathrm{Clim}_{\mathrm{PC1}}$, explaining more than 70% of the variation. This axis mainly represented temperature-related climatic factors, with 50% reflecting the harshness and variability of environmental conditions (Table 1). Thus, regions with less variable intra-annual climate and higher average daily minimum temperature harbor more tree species, which is consistent with but does not distinguish among three mechanisms shaping the latitudinal gradient in diversity (Fig. 1): (1) difficulty for lineages of tropical origin to adapt to and establish in cold/seasonal climates, (2) higher extinction rates in cold/seasonal climates, and (3) wider niches of species adapted to variable climates. The analysis also revealed a positive effect of temperature, with positive loadings of mean, minimum, and maximum temperature plus vapor pressure totaling 60% of $\mathrm{Clim}_{\mathrm{PC1}}$. This finding supports the direct role of kinetics in shaping the latitudinal gradient through accelerated evolution, biotic interactions, and productivity under warmer temperatures (Brown 2014).

Apart from the strong direct constraints of climate on species distribution, climate influenced global tree species richness indirectly via stem abundance at both spatial scales tested (Fig. 3), supporting the species-energy hypothesis (O’Brien 1998; Hawkins *et al.* 2003; Currie *et al.* 2004). Climate influenced tree stem abundance through positive effects of temperature ($\mathrm{Clim}_{\mathrm{PC1}}$), negative effects of solar radiation, temperature variation and freezing temperatures (Clim_{PC1}, solar radiation and daily temperature range in Clim_{PC2}), and a positive effect of moisture (precipitation in Clim_{PC1}, cloud cover and wet day frequency in Clim_{PC2}). Thus, our results lend clear support for the species-energy hypothesis that climate influences tree species richness through abundance of individuals (Srivastava & Lawton 1998; Hawkins *et al.* 2003; Currie *et al.* 2004; Ricklefs & He 2016; Storch *et al.* 2018). At the same time, our analysis clearly demonstrates that the species-energy hypothesis alone is insufficient to account for latitudinal trends in diversity. In addition to the fact that our across-forest plot structural equation model showed stronger direct than indirect effects of climate, the increase in species diversity with decreasing latitude was far too steep to be explained only by the abundance of individuals (Fig. 2d) (Brown 2014). Specifically, species richness increased 17-fold from high to low latitudes for 20 m × 20 m plots and 77-fold for 50 m × 50 m plots in the present study. Given the decelerating rate at which species accumulate as more individuals are sampled, stem abundance would need to increase by ~4 orders of magnitude for every order-of-magnitude increase in species richness (Brown 2014), implying the need for a >10,000-fold increase in stem abundance to explain the observed latitudinal trend in richness. In fact, stem abundance increased by only 25-fold (Fig. 2c). Thus, our results demonstrate a small but significant role for stem abundance in shaping the latitudinal gradient in forest tree diversity.

We acknowledge that we could not rule out the possibility that other unmeasured factors which are strongly correlated with latitude influenced the observed latitudinal diversity gradient of trees, as indicated by the significant and strong effect of latitude in the SEM. Since latitude is a composite variable that incorporates many factors, both contemporary and historical (evolutionary), the strong effect of latitude on global tree species richness patterns is expectable (Table 2). In extreme, it is even possible that the observed effect of climate may reflect just another (unknown) causal factor which is correlated with latitude similarly as climate. However, it is unclear what such a factor would be, and thus we focus on the central role of climate.

Latitudinal trends in the local stem abundance effect

The within-forest plot results showed pronounced variation among forest sites in how specific forest structural attributes affected tree species richness. For example, we found no significant relationship between tree species richness and stand basal area in the across-forest plot analyses (Fig. 3; Supplementary Information Table 5). However, in the within-forest plot analyses, stand basal area was negatively correlated with local tree species richness in nine plots at the scale of 20 m × 20 m and 13 plots at the scale of 50 m × 50 m. The negative effect of stand basal area on tree richness likely implies strong competition among trees for limited resources in these forests.

Among three forest structural attributes, the effect of stem abundance on tree species richness decreased with increasing latitude at the scale of 20 m × 20 m (Fig. 4b), which means that on average a change in one standard-deviation unit in stem abundance could result in a more pronounced change in tree species richness in tropical forests than in temperate forests, probably due to the higher tree species richness in tropical forests. In hyper-diverse tropical plots, the species pool is higher than the number of individuals at the 20 m × 20 m but not at the 50 m × 50 m quadrat scale; adding any additional individuals thus has the potential to increase the species richness of a 20 × 20 m quadrat (Fig. 2d). On the contrary, in species-poor temperate plots, the highest realizable levels of diversity may be attained with far fewer individuals and above certain densities adding more individuals will not further increase species richness of a quadrat. The higher local effect of stem abundance on species richness in tropical than in temperate forests may also be amplified by significantly higher conspecific negative density dependence in the tropics (Shao *et al.* 2018).

Our findings also indicate some promising future directions of investigation. First, only three forest structural attributes were evaluated. The role of other structural metrics such as canopy height and foliar profile representing the vertical dimensions of forest structure remains a promising area for additional studies. Another important factor might be an effect of climatic seasonality and soil resources on site (plot-level) species richness (Baldeck *et al.* 2013; Jucker *et al.* 2018), and consequently on the latitudinal pattern of tree species richness. Finally, the considerable unexplained variance at some sites suggests that other unmeasured factors (e.g., the abundance of herbivores and pathogens; Janzen (1970)) may play a greater role in determining species richness in these forests.

In summary, our results demonstrate that climate simultaneously influenced global tree species richness both directly by climatic extremes and temperature, and indirectly via changes in the number of individuals. These findings show that a number of mechanisms are acting in concert to shape the latitudinal gradient in diversity, with no single mechanism being sufficient on its own. Our work also suggests that a more comprehensive framework for the effects of multiple variables including climate and historical factors on the latitudinal diversity gradient is needed (Brown 2014).

ACKNOWLEDGEMENTS

We thank Margie Mayfield, three anonymous reviewers and Jacob Weiner for constructive comments on the manuscript. This study was financially supported by the National Key R&D Program of China (2017YFC0506100), the National Natural Science Foundation of China (31622014 and 31570426), and the Fundamental Research Funds for the Central Universities (17lgzd24) to CC. XW was supported by the Strategic Priority Research Program of the Chinese Academy of Sciences (XDB3103). DS was supported by the Czech Science Foundation (grant no. 16-26369S). Yves Rosseel provided us valuable suggestions on using the *lavaan* package conducting SEM analyses. Funding and citation information for each forest plot is available in the Supplementary Information Text 1.

REFERENCES

Allen, A.P., Gillooly, J.F., Savage, V.M. & Brown, J.H. (2006). Kinetic effects of temperature on rates of genetic divergence and speciation. *Proc. Natl. Acad. Sci. USA*, 103, 9130–9135.

Anderson-Teixeira, K.J., Davies, S.J., Bennett, A.C., Gonzalez-Akre, E.B., Muller-Landau, H.C., Joseph Wright, S., *et al.* (2015). CTFS-ForestGEO: a worldwide network monitoring forests in an era of global change. *Glob. Change Biol.*, 21, 528–549.

Baldeck, C.A., Harms, K.E., Yavitt, J.B., John, R., Turner, B.L., Valencia, R., *et al.* (2013). Soil resources and topography shape local tree community structure in tropical forests. *Proc. R. Soc. B Biol. Sci.*, 280, 20122532.

Bowen, B.W., Rocha, L.A., Toonen, R.J. & Karl, S.A. (2013). The origins of tropical marine biodiversity. *Trends Ecol. Evol.*, 20, 1–8.

Brown, J.H. (2014). Why are there so many species in the tropics? *J. Biogeogr.*, 41, 8–22.

Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M. & West, G.B. (2004). Toward a metabolic theory of ecology. *Ecology*, 85, 1771–1789.

Canham, C.D., LePage, P.T. & Coates, K.D. (2004). A neighborhood analysis of canopy tree competition: Effects of shading versus crowding. *Can. J. For. Res.*, 34, 778–787.

Cavender-Bares, J., Gonzalez-Rodriguez, A., Pahlich, A., Koehler, K. & Deacon, N. (2011). Phylogeography and climatic niche evolution in live oaks (Quercus series Virentes) from the tropics to the temperate zone. *J. Biogeogr.*, 38, 962–981.

Chisholm, R.A., Muller-Landau, H.C., Abdul Rahman, K., Bebber, D.P., Bin, Y., Bohlman, S.A., *et al.* (2013). Scale-dependent relationships between tree species richness and ecosystem function in forests. *J. Ecol.*, 101, 1214–1224.

Chu, C., Bartlett, M., Wang, Y., He, F., Weiner, J., Chave, J., *et al.* (2016a). Does climate directly influence NPP globally? *Glob. Change Biol.*, 22, 12–24.

Chu, C., Kleinhesselink, A.R., Havstad, K.M., McClaran, M.P., Peters, D.P., Vermeire, L., *et al.* (2016b). Direct effects dominate responses to climate perturbations in grassland plant communities. *Nat. Commun.*, 7, 11766.

Comita, L.S. (2017). How latitude affects biotic interactions. *Science*, 356, 1328.

Condit, R.S. (1998). *Tropical Forest Census Plots - Methods and Results from Barro Colorado Island, Panama and a Comparison with Other Plots.* Springer-Verlag Berlin Heidelberg, Springer-Verlag, Berlin, and R G. Landes Company, Georgetown, TX, USA.

Coomes, D.A., Lines, E.R. & Allen, R.B. (2011). Moving on from Metabolic Scaling Theory: hierarchical models of tree growth and asymmetric competition for light. *J. Ecol.*, 99, 748–756.

Currie, D.J., Mittelbach, G.G., Cornell, H.V., Field, R., Guégan, J.-F., Hawkins, B.A., *et al.* (2004). Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecol. Lett.*, 7, 1121–1134.

Farrior, C.E., Bohlman, S.A., Hubbell, S. & Pacala, S.W. (2016). Dominance of the suppressed: Power-law size structure in tropical forests. *Science*, 351, 155–157.

Ferger, S.W., Schleuning, M., Hemp, A., Howell, K.M. & Böhning-Gaese, K. (2014). Food resources and vegetation structure mediate climatic effects on species richness of birds. *Glob. Ecol. Biogeogr.*, 23, 541–549.

Fine, P.V.A. (2015). Ecological and evolutionary drivers of geographic variation in species diversity.

Annu. Rev. Ecol. Evol. Syst., 46, 369–392.

Franklin, J.F., Spies, T.A., Pelt, R.V., Carey, A.B., Thornburgh, D.A., Berg, D.R., *et al.* (2002). Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. *For. Ecol. Manag.*, 155, 399–423.

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

Gaston, K.J. & Chown, S.L. (1999). Why Rapoport's rule does not generalise. *Oikos*, 84, 309–312.

Gillooly, J.F., Allen, A.P., West, G.B. & Brown, J.H. (2005). The rate of DNA evolution: effects of body size and temperature on the molecular clock. *Proc. Natl. Acad. Sci. USA*, 102, 140–145.

Grace, J.B. (2006). *Structural Equation Modeling and Natural Systems*. Cambridge University Press, Cambridge, U.K.

Hakkenberg, C.R., Song, C., Peet, R.K. & White, P.S. (2016). Forest structure as a predictor of tree species diversity in the North Carolina Piedmont. *J. Veg. Sci.*, 27, 1151–1163.

Harms, K.E., Condit, R., Hubbell, S.P. & Foster, R.B. (2001). Habitat associations of trees and shrubs in a 50-ha neotropical forest plot. *J. Ecol.*, 89, 947–959.

Hawkins, B.A., Field, R., Cornell, H.V., Currie, D.J., Guégan, J.-F., Kaufman, D.M., *et al.* (2003). Energy, water, and broad-scale geographic patterns of species richness. *Ecology*, 84, 3105–3117.

Hutchinson, G.E. (1959). Homage to Santa Rosalia or why are there so many kinds of animals? *Am. Nat.*, 93, 145–159.

Jablonski, D., Roy, K. & Valentine, J.W. (2006). Out of the tropics: evolutionary dynamics of the latitudinal diversity gradient. *Science*, 314, 102–106.

Janzen, D.H. (1970). Herbivores and the number of tree species in tropical forests. *Am. Nat.*, 104, 501–528.

Jucker, T., Bongalov, B., Burslem, D.F.R.P., Nilus, R., Dalponte, M., Lewis, S.L., *et al.* (2018). Topography shapes the structure, composition and function of tropical forest landscapes. *Ecol. Lett.*, 21, 989–1000.

Kinlock, N.L., Prowant, L., Herstoff, E.M., Foley, C.M., Akin-Fajiye, M., Bender, N., *et al.* (2018). Explaining global variation in the latitudinal diversity gradient: Meta-analysis confirms known patterns and uncovers new ones. *Glob. Ecol. Biogeogr.*, 27, 125–141.

Kreft, H. & Jetz, W. (2007). Global patterns and determinants of vascular plant diversity. *Proc. Natl. Acad. Sci.*, 104, 5925–5930.

Larson, A.J., Lutz, J.A., Gersonde, R.F., Franklin, J.F. & Hietpas, F.F. (2008). Potential site productivity influences the rate of forest structural development. *Ecol. Appl.*, 18, 899–910.

Lechuga, V., Carraro, V., Viñegla, B., Carreira, J.A. & Linares, J.C. (2017). Managing drought-sensitive forests under global change. Low competition enhances long-term growth and water uptake in Abies pinsapo. *For. Ecol. Manag.*, 406, 72–82.

Legendre, P., Mi, X.C., Ren, H.B., Ma, K.P., Yu, M.J., Sun, I.F., *et al.* (2009). Partitioning beta diversity in a subtropical broad-leaved forest of China. *Ecology*, 90, 663–674.

Lutz, J.A., Furniss, T.J., Johnson, D.J., Davies, S.J., Allen, D., Alonso, A., *et al.* (2018). Global importance of large-diameter trees. *Glob. Ecol. Biogeogr.*, 27, 849–864.

Lutz, J.A., Larson, A.J., Furniss, T.J., Donato, D.C., Freund, J.A., Swanson, M.E., *et al.* (2014). Spatially nonrandom tree mortality and ingrowth maintain equilibrium pattern in an old-growth Pseudotsuga–Tsuga forest. *Ecology*, 95, 2047–2054.

Luyssaert, S., Inglima, I., Jung, M., Richardson, A.D., Reichstein, M., Papale, D., *et al.* (2007). CO2 balance of boreal, temperate, and tropical forests derived from a global database. *Glob.*

Change Biol., 13, 2509–2537.

Marshall, K.E. & Baltzer, J.L. (2015). Decreased competitive interactions drive a reverse species richness latitudinal gradient in subarctic forests. *Ecology*, 96, 461–470.

Menéndez, R., González-Megías, A., Collingham, Y., Fox, R., Roy, D.B., Ohlemüller, R., *et al.* (2007). Direct and indirect effects of climate and habitat factors on butterfly diversity. *Ecology*, 88, 605–611.

Mittelbach, G.G. (2012). *Community Ecology*. Sinauer Associates.

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.

O'Brien, E.M. (1998). Water-energy dynamics, climate, and prediction of woody plant species richness: an interim general model. *J. Biogeogr.*, 25, 379–398.

Pretzsch, H. & Schütze, G. (2016). Effect of tree species mixing on the size structure, density, and yield of forest stands. *Eur. J. For. Res.*, 135, 1–22.

R Core Team. (2016). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Ricklefs, R.E. & He, F. (2016). Region effects influence local tree species diversity. *Proc. Natl. Acad. Sci.*, 113, 674–679.

Rosseel, Y. (2012). lavaan: An R Package for Structural Equation Modeling. *J. Stat. Softw.*, 48, 1–36.

Schluter, D. (2015). Speciation, ecological opportunity, and latitude. *Am. Nat.*, 187, 1–18.

Shao, X.N., Brown, C., Worthy, S.J., Liu, L., Cao, M., Li, Q.M., *et al.* (2018). Intra-specific relatedness, spatial clustering and reduced demographic performance in tropical rainforest trees. *Ecol. Lett.*, 21, 1174–1181.

Sibly, R.M., Brown, J.H. & Kodric-Brown, A. (2012). *Metabolic Ecology: A Scaling Approach*. Wiley-Blackwell.

Šímová, I., Storch, D., Keil, P., Boyle, B., Phillips, O.L. & Enquist, B.J. (2011). Global species–energy relationship in forest plots: role of abundance, temperature and species climatic tolerances. *Glob. Ecol. Biogeogr.*, 20, 842–856.

Srivastava, D.S. & Lawton, J.H. (1998). Why more productive sites have more species: An experimental test of theory using tree-hole communities. *Am. Nat.*, 152, 510–529.

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

Storch, D., Bohdalková, E. & Okie, J. (2018). The more-individuals hypothesis revisited: the role of community abundance in species richness regulation and the productivity–diversity relationship. *Ecol. Lett.*, 21, 920–937.

Terborgh, J. (1973). On the notion of favorableness in plant ecology. *Am. Nat.*, 107, 481–501.

Terborgh, J. (1985). The vertical component of plant species diversity in temperate and tropical forests. *Am. Nat.*, 126, 760–776.

Vayreda, J., Martinez-Vilalta, J., Gracia, M. & Retana, J. (2012). Recent climate changes interact with stand structure and management to determine changes in tree carbon stocks in Spanish forests. *Glob. Change Biol.*, 18, 1028–1041.

Weiner, J., Stoll, P., Muller-Landau, H. & Jasentuliyana, A. (2001). The effects of density, spatial pattern, and competitive symmetry on size variation in simulated plant populations. *Am. Nat.*, 158, 438–450.

SUPPORTING INFORMATION

Supplementary Information includes:

1. **Figure 1** Bivariate relationships among all variables for SEM
2. **Table 1** Plot characteristics
3. **Table 2** PCA results for topographic variables
4. **Table 3** Alternative SEMs for across-forest plot analyses at both spatial scales
5. **Table 4** SEM results from within-forest plot analyses at both spatial scales
6. **Table 5** SEM results from across-forest plot analyses at both spatial scales
7. **Table 6** SEM results from across-forest plot analyses with latitude
8. **Text 1** Plot funding and citation information

Competing financial interests: The authors declare no competing financial interests.

Table 1 Percentage contributions (%) and loadings of the twelve individual climatic variables to the first two principal components ($Clim_{PC1}$ and $Clim_{PC2}$). The two principal components explained 88% of the variation in climate (75% by $Clim_{PC1}$ and 13% by $Clim_{PC2}$).

		atr	*cld*	*dtr*	*frs*	*pet*	*pre*	*rad*	*tmn*	*tmp*	*tmx*	*vap*	*wet*
$Clim_{PC1}$	Percent	10.1	5.3	6.8	10.4	8.4	9.0	1.8	10.9	10.7	10.0	10.4	6.1
	Loading	-0.32	0.23	-0.26	-0.32	0.29	0.30	0.14	0.33	0.33	0.32	0.32	0.25
$Clim_{PC2}$	Percent	0.23	22.9	13.8	0.2	4.2	0.05	48.1	0.12	1.02	3.34	0.03	6.03
	Loading	0	-0.49	0.37	0	0.21	0	0.69	0	0.10	0.18	0	-0.25

atr, annual temperature range; *cld*, cloud cover; *dtr*, diurnal temperature range; *frs*, frost day frequency; *pet*, potential evapotranspiration; *pre*, precipitation; *rad*, solar radiation; *tmn*, average daily minimum temperature; *tmp*, average daily mean temperature; *tmx*, average daily maximum temperature; *vap*, vapour pressure; *wet*, wet day frequency.

Table 2 Proportion of the explained variance (R^2) in global tree species richness in models with the predictor of climate or latitude at the plot scales of 20 m × 20 m and 50 m × 50 m. On the top of the hypothesized relationships (Supplementary Information Fig. 1), latitude was assumed to have both a direct effect (i.e. an arrow from latitude to tree species richness) and an indirect effect (i.e. an indirect latitudinal effect via temperature, especially the first PCA axis of 12 climatic variables) on global tree species richness. The results of SEM models with latitude were presented in the Supplementary Information Table 6.

SEM	**20 m × 20 m**	**50 m × 50 m**
Climate	0.74	0.76
Latitude	0.80	0.82

Figure legends

Figure 1 Schematic diagram illustrating major hypotheses/mechanisms shaping the latitudinal diversity gradient, including the tropical origins of most clades, niche partitioning, kinetics of ecological interactions and evolution, and primary productivity. Different hypotheses have overlap in mechanisms and lead to different empirical patterns, among which our analyses were designated to distinguish. In particular, the finding that regions with less variable intra-annual climate and higher average daily minimum temperature harbor more tree species is consistent with but does not distinguish among three mechanisms with the explained variation of more than 70%: (1) difficulty for lineages of tropical origin to adapt to and establish in cold/ seasonal climates, (2) higher extinction rates in cold/seasonal climates, and (3) wider niches of species adapted to variable climates. Meanwhile, our results demonstrate a small but significant role of stem abundance in explaining the latitudinal tree diversity gradient (~5%). Hypotheses and mechanisms are primarily as reviewed in Brown (2014). Italics indicate empirical pattern that would be expected if the associated mechanism were the only one causing the latitudinal gradient in diversity.

Figure 2 Global distribution of 35 forest dynamics plots used in this study (**a**), and the latitudinal gradients of tree species richness (**b**), stem abundance (**c**), and species richness/ stand stem ratios (**d**). Richness and stem abundance measured at plot scales of 20 m × 20 m and 50 m × 50 m. Descriptions of each site can be found in the Supplementary Information Table 1. Colors indicate increasing absolute latitude from pink to turquoise.

Figure 3 (a) The conceptual structural equation model (SEM), which was used to examine the linkages among climate, topography, forest structural attributes, and tree species richness. The variables Topo and Clim represent topographic and climatic factors, respectively. Besides the linkages represented by directed arrows, a correlation between stem abundance and stand basal area was set. This full model including both Topo and Clim was used for the across-forest plot analyses, and the one without the Clim variable (i.e. removing gray paths) was designated for the within-forest plot analyses. Panels (**b**) and (**c**) for the across-forest plot SEM analyses at the scales of 20 m × 20 m and 50 m × 50 m, respectively. Paths from topography, tree size variation, and stand basal area to tree species richness were not significant. The results of the final SEM models including other significant paths (ones from climate and stand basal area to tree size variation) and the uncertainty (SE) of each path coefficient were presented in the Supplementary Information Table 5. $\mathrm{Clim}_{\mathrm{PC1}}$ and $\mathrm{Clim}_{\mathrm{PC2}}$ represented the first two principal components (PC) of the 12 climatic variables. Statistical significance was indicated by asterisks (*** $P < 0.001$).

Figure 4 The effects of forest structural attributes on tree diversity derived from the within-forest plot SEM analyses. Panels **a**, **b**, and **c** at the scale of 20 m × 20 m, and panels **d**, **e**, and **f** at the scale of 50 m × 50 m. The effect of stem abundance on tree species richness showed a significant latitudinal trend at the scale of 20 m × 20 m (panel **b**; $P < 0.01$, $R^2 = 0.27$). Standardized path coefficients ± 1 SE are shown; SE's are smaller than the size of the symbol for some forest plots. Colors indicate increasing absolute latitude from pink to turquoise.

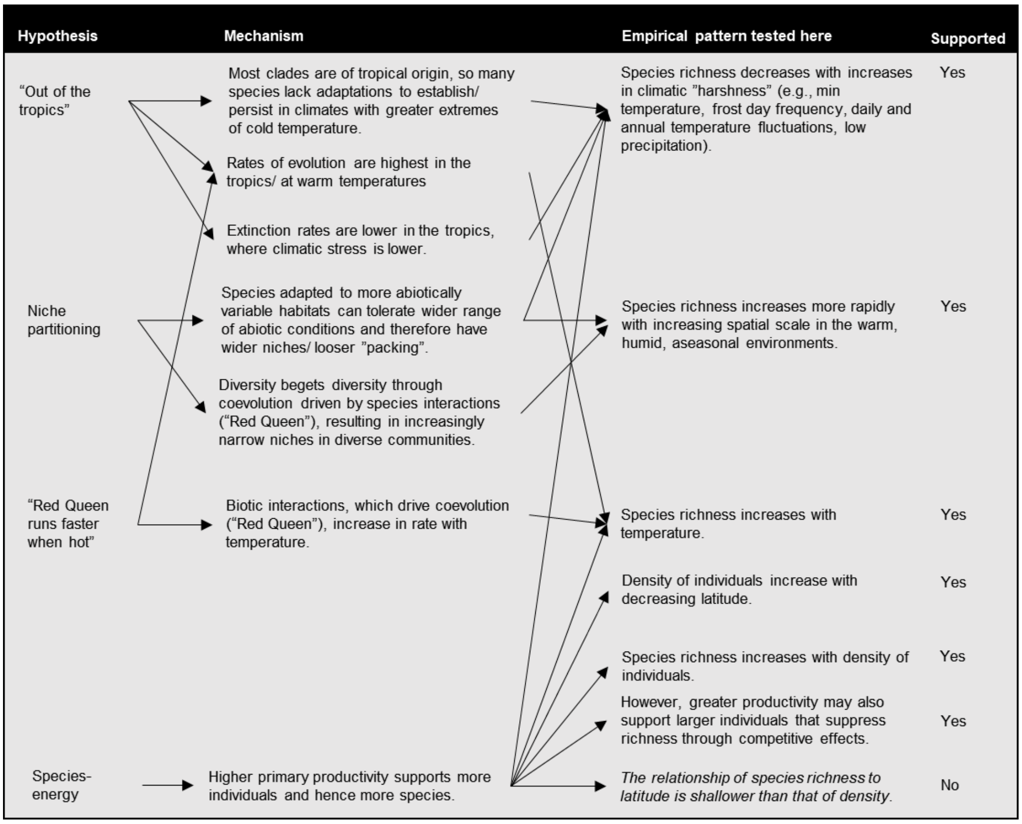

Figure 1 Schematic diagram illustrating major hypotheses/mechanisms shaping the latitudinal diversity gradient, including the tropical origins of most clades, niche partitioning, kinetics of ecological interactions and evolution, and primary productivity. Different hypotheses have overlap in mechanisms and lead to different empirical patterns, among which our analyses were designated to distinguish. In particular, the finding that regions with less variable intra-annual climate and higher average daily minimum temperature harbor more tree species is consistent with but does not distinguish among three mechanisms with the explained variation of more than 70%: (1) difficulty for lineages of tropical origin to adapt to and establish in cold/ seasonal climates, (2) higher extinction rates in cold/seasonal climates, and (3) wider niches of species adapted to variable climates. Meanwhile, our results demonstrate a small but significant role of stem abundance in explaining the latitudinal tree diversity gradient (~5%). Hypotheses and mechanisms are primarily as reviewed in Brown (2014). Italics indicate empirical pattern that would be expected if the associated mechanism were the only one causing the latitudinal gradient in diversity.

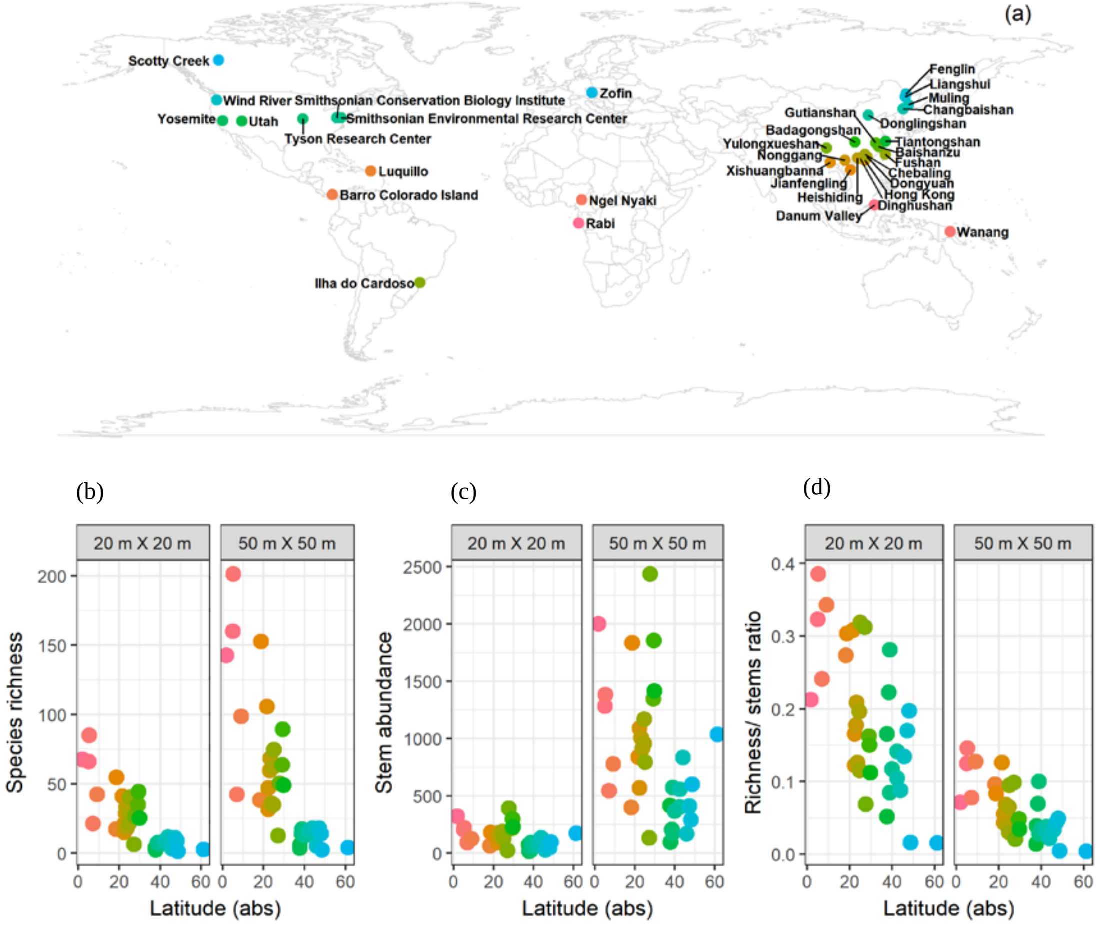

Figure 2 Global distribution of 35 forest dynamics plots used in this study (**a**), and the latitudinal gradients of tree species richness (**b**), stem abundance (**c**), and species richness/ stand stem ratios (**d**). Richness and stem abundance measured at plot scales of 20 m × 20 m and 50 m × 50 m. Descriptions of each site can be found in the Supplementary Information Table 1. Colors indicate increasing absolute latitude from pink to turquoise.

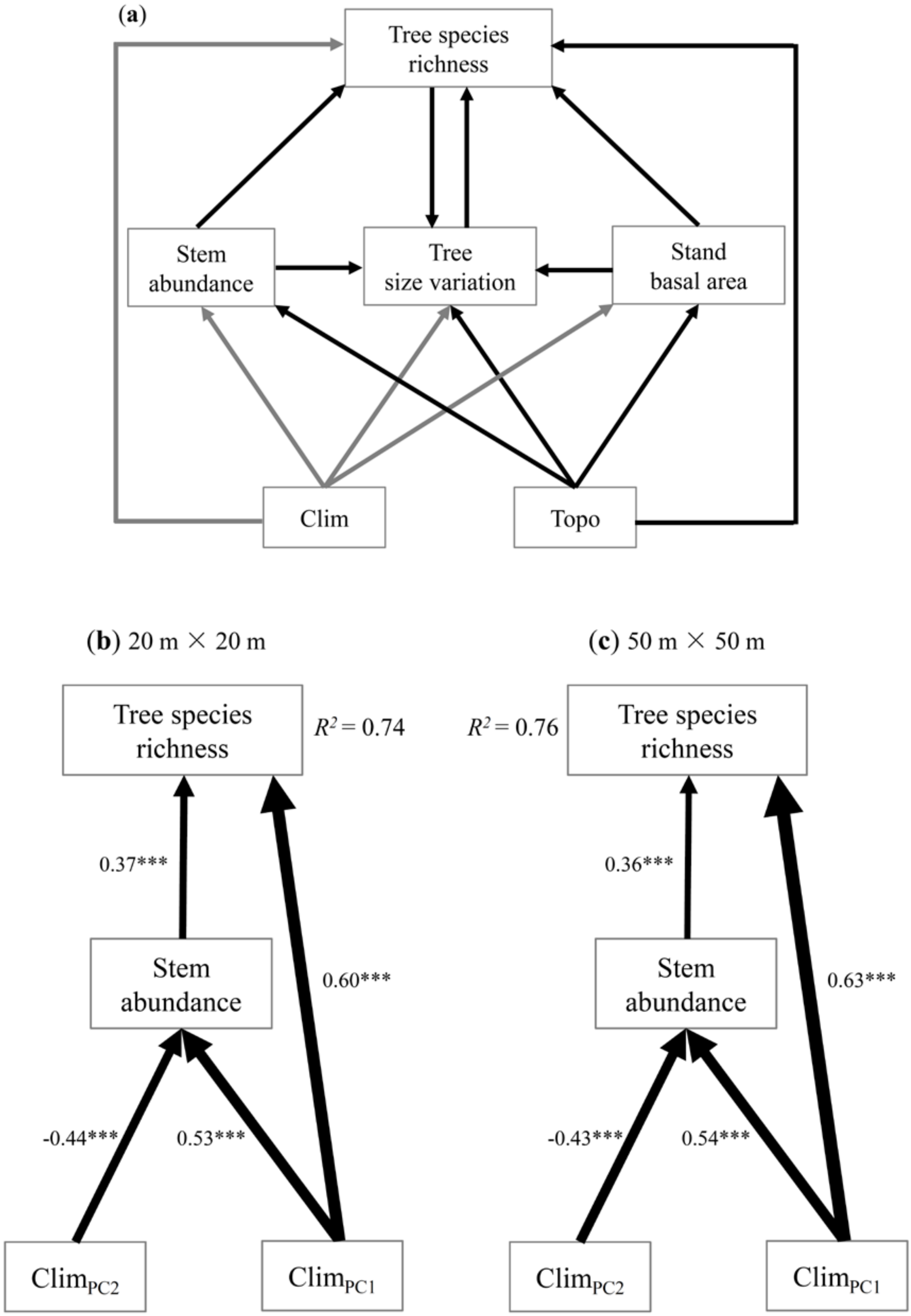

Figure 3 (a) The conceptual structural equation model (SEM), which was used to examine the linkages among climate, topography, forest structural attributes, and tree species richness. The variables Topo and Clim represent topographic and climatic factors, respectively. Besides the linkages represented by directed arrows, a correlation between stem abundance and stand basal area was set. This full model including both Topo and Clim was used for the across-forest plot analyses, and the one without the Clim variable (i.e. removing gray paths) was designated for the within-forest plot analyses. Panels (**b**) and (**c**) for the across-forest plot SEM analyses at the scales of 20 m × 20 m and 50 m × 50 m, respectively. Paths from topography, tree size variation, and stand basal area to tree species richness were not significant. The results of the final SEM models including other significant paths (ones from climate and stand basal area to tree size variation) and the uncertainty (SE) of each path coefficient were presented in the Supplementary Information Table 5. $\mathrm{Clim}_{\mathrm{PC1}}$ and $\mathrm{Clim}_{\mathrm{PC2}}$ represented the first two principal components (PC) of the 12 climatic variables. Statistical significance was indicated by asterisks (*** $P < 0.001$).

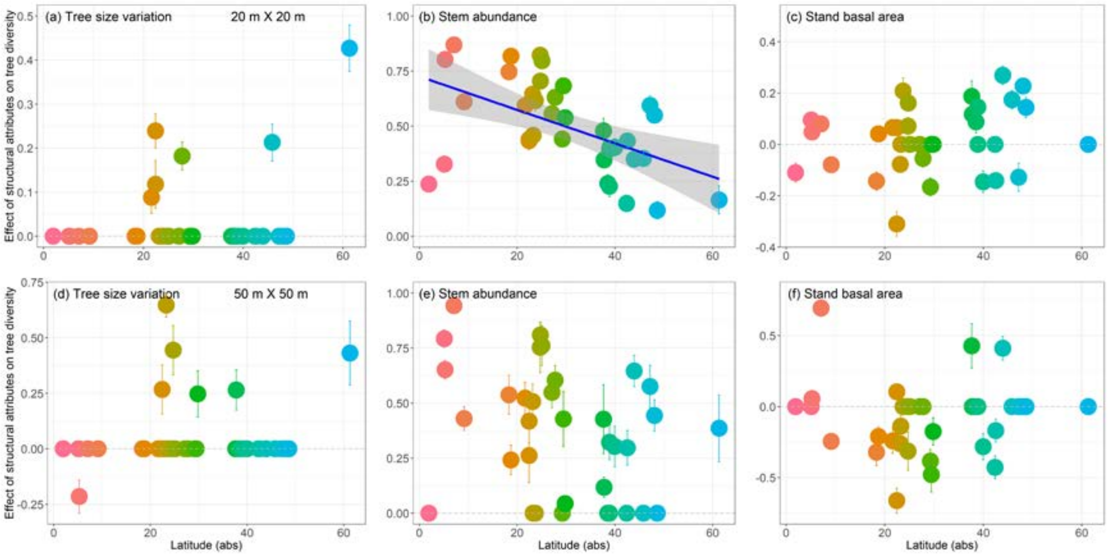

Figure 4 The effects of forest structural attributes on tree diversity derived from the within-forest plot SEM analyses. Panels **a**, **b**, and **c** at the scale of 20 m × 20 m, and panels **d**, **e**, and **f** at the scale of 50 m × 50 m. The effect of stem abundance on tree species richness showed a significant latitudinal trend at the scale of 20 m × 20 m (panel **b**; $P < 0.01$, $R^2 = 0.27$). Standardized path coefficients ± 1 SE are shown; SE's are smaller than the size of the symbol for some forest plots. Colors indicate increasing absolute latitude from pink to turquoise.