LETTER

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

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Abstract

Climate is widely recognised 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 hypothesised relationships amongst 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.

Keywords

Climate tolerance hypothesis, CTFS-ForestGEO, latitudinal diversity gradient, more-individuals hypothesis, species-energy relationship, structural equation modelling.

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INTRODUCTION

Although the latitudinal diversity gradient – i.e. the pronounced increase in species richness from the poles to the equator – has been recognised 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 specialisation 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 specialisation described above is probably driven by temperature (Brown 2014). In general, biological rates tend to increase with temperature through temperature effects on the

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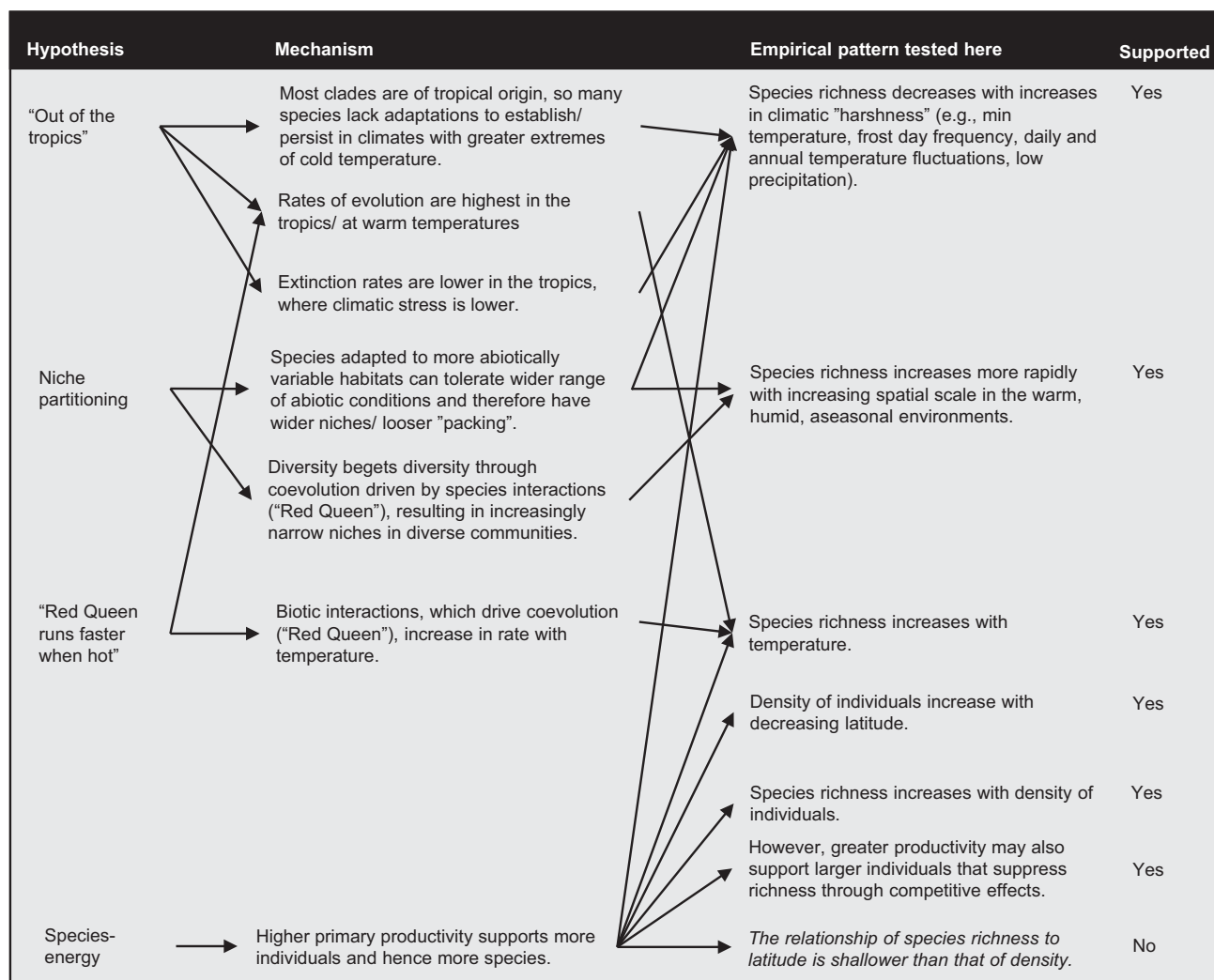
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Hypothesis	Mechanism	Empirical pattern tested here	Supported
"Out of the tropics"	Most clades are of tropical origin, so many species lack adaptations to establish/persist in climates with greater extremes of cold temperature.	Species richness decreases with increases in climatic "harshness" (e.g., min temperature, frost day frequency, daily and annual temperature fluctuations, low precipitation).	Yes
	Rates of evolution are highest in the tropics/ at warm temperatures		
	Extinction rates are lower in the tropics, where climatic stress is lower.		
Niche partitioning	Species adapted to more abiotically variable habitats can tolerate wider range of abiotic conditions and therefore have wider niches/ looser "packing".	Species richness increases more rapidly with increasing spatial scale in the warm, humid, aseasonal environments.	Yes
	Diversity begets diversity through coevolution driven by species interactions ("Red Queen"), resulting in increasingly narrow niches in diverse communities.		
"Red Queen runs faster when hot"	Biotic interactions, which drive coevolution ("Red Queen"), increase in rate with temperature.	Species richness increases with temperature.	Yes
		Density of individuals increase with decreasing latitude.	Yes
		Species richness increases with density of individuals.	Yes
		However, greater productivity may also support larger individuals that suppress richness through competitive effects.	Yes
Species-energy	Higher primary productivity supports more individuals and hence more species.	*The relationship of species richness to latitude is shallower than that of density.*	No

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, amongst which our analyses were designated to distinguish. In particular, the finding that regions with less variable intraannual climate and higher average daily minimum temperature harbour more tree species is consistent with but does not distinguish amongst 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 (*c.* 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.

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 co-evolution, 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 disproportionly 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 (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 (SEM) approach (Grace 2006) to test hypothesised 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 Table S1). 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 standardised census protocol (Condit 1998). The size of the plots ranges from 9 ha (Liangshui) to 60 ha (Jianfengling) 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 $\times$ 20 m and 50 m $\times$ 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 of tree DBH within a quadrat.

Elevation was recorded at the intersections of the 20 m $\times$ 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 neighbour 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 $\times$ 20 m and 50 m $\times$ 50 m, based on the topographic variables at the finer spatial scale of 10 m $\times$ 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 analyse the relationship amongst topography, climate, forest structure and tree species richness (across-forest plot analyses at the two spatial scales using the same climatic information). We used standardised climate data with the 0.5° 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),
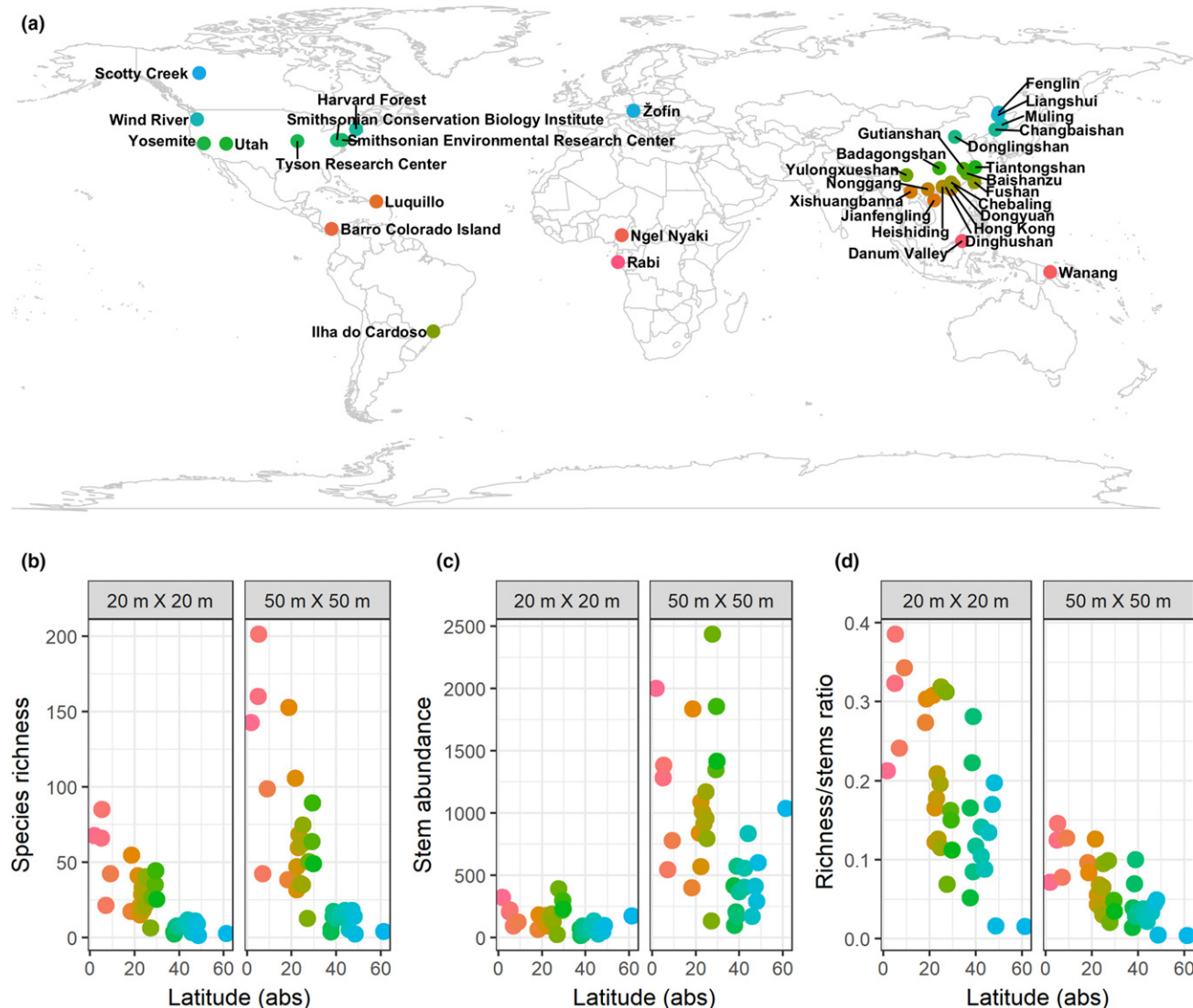
Figure 2 Global distribution of 35 forest dynamics plots used in this study (a), and the latitudinal gradients of tree species richness (b), stem abundance (c) and species richness/stand stem ratios (d). Richness and stem abundance measured at plot scales of 20 m × 20 m and 50 m × 50 m. Descriptions of each site can be found in Table S1. Colours indicate increasing absolute latitude from pink to turquoise.

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 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 s. In total, 12 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 standardised 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 (Franklin *et al.* 2002; Canham *et al.* 2004). 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 hypothesised relationships amongst these variables as well as topographic and climatic factors through SEM (Fig. 3a). SEM offers a means to evaluate hypothesised 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 amongst variables, we reduced the dimensionality of the climate (12 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 Table S2. We used the '*lavaan*' package (Rosseel 2012) in the *R* software platform (R Core Team 2016) to parameterise the SEM. Bivariate relationships amongst all variables for SEMs in both across-forest plot and within-forest plot analyses were presented in Fig. S1. To develop the final SEMs, we started with our initial hypothesised relationships amongst 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 (Table S3). 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 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. Standardised SEM path coefficients from within-forest plot analyses are reported in Table S4. The total effect that one variable has on another equals the sum of its direct and indirect effects through directed (causal) paths. The SE values and *P* values for standardised path coefficients were obtained through the function *standardisedSolution* 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 PC ($Clim_{PC1}$) 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%), vapour pressure (10.4%), annual temperature range (10.1%) and average daily maximum temperature (10.0%). The second PC ($Clim_{PC2}$) 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 (Table S2). The first PC ($Topo_{PC1}$) 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–d). 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 50 m 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. 3b). $Clim_{PC1}$ had a significant direct effect on tree species richness with a standardised path coefficient of 0.60. $Clim_{PC1}$ and $Clim_{PC2}$ also influenced tree species richness
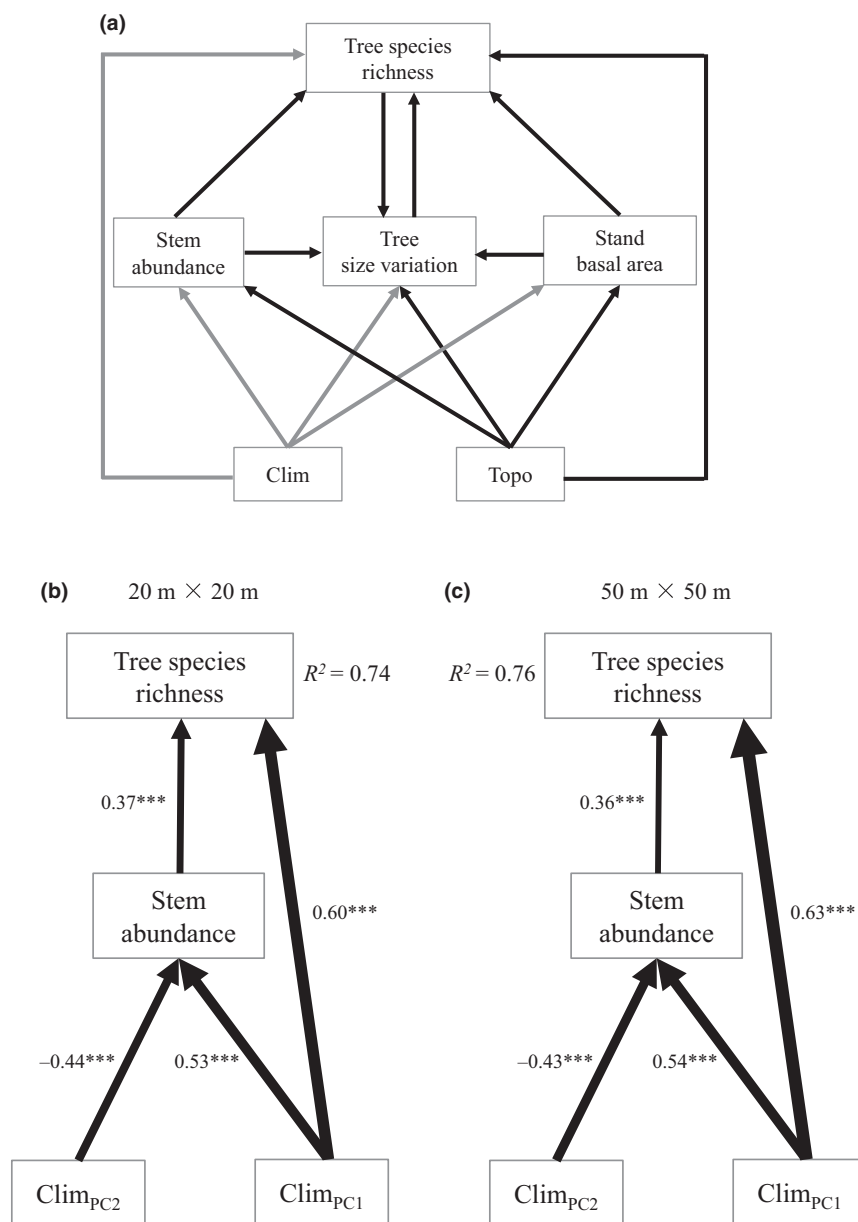
Figure 3 (a) The conceptual structural equation modelling (SEM), which was used to examine the linkages amongst climate, topography, forest structural attributes and tree species richness. The variables Topo and Clim represent topographic and climatic factors, respectively. Besides the linkages represented 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 Table S5. $Clim_{PC1}$ and $Clim_{PC2}$ represented the first two principal components (PC) of the 12 climatic variables. Statistical significance was indicated by asterisks (***$P < 0.001$).

indirectly via stem abundance, with standardised 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 (Table S5) 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 (Table S5). Amongst 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 (Table S5).

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. 3c). Climate had both direct and indirect effects on tree species richness through three pathways (Fig. 3c): one direct from $Clim_{PC1}$ to richness (path coefficient 0.63), two indirectly mediated by stem abundance from

Table 1 Percentage contributions (%) and loadings of the 12 individual climatic variables to the first two principal components (Clim$_{PC1}$ and 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

The two principal components explained 88% of the variation in climate (75% by Clim$_{PC1}$ and 13% by Clim$_{PC2}$).

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.

Clim$_{PC1}$ (path coefficient 0.19, i.e. 0.54 × 0.36) and Clim$_{PC2}$ (−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 Table S6). The incorporation of latitude also makes the direct path from Clim$_{PC1}$ to tree species richness non-significant (Table S6). Clim$_{PC1}$ was strongly correlated to latitude ($r = -0.91$; Fig. S1), 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 and Table S4). 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 nine plots. At the scale of 50 m × 50 m, stem abundance

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

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

On the top of the hypothesised relationships (Fig. 3a), 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 principal component analysis axis of 12 climatic variables) on global tree species richness. The results of structural equation modelling (SEM) models with latitude were presented in Table S6.

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 (Žofín) to 0.88 (Ngel Nyaki) with a mean of 0.36 at the scale of 20 m × 20 m, and from 0.042 (Žofín) to 0.89 (Ngel Nyaki) with a mean of 0.35 at the scale of 50 m × 50 m (Table S4).

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, Clim$_{PC1}$, 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 intraannual climate and higher average daily minimum temperature harbour more tree species, which is consistent with but does not distinguish amongst 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 vapour pressure totaling 60% of Clim$_{PC1}$. This finding
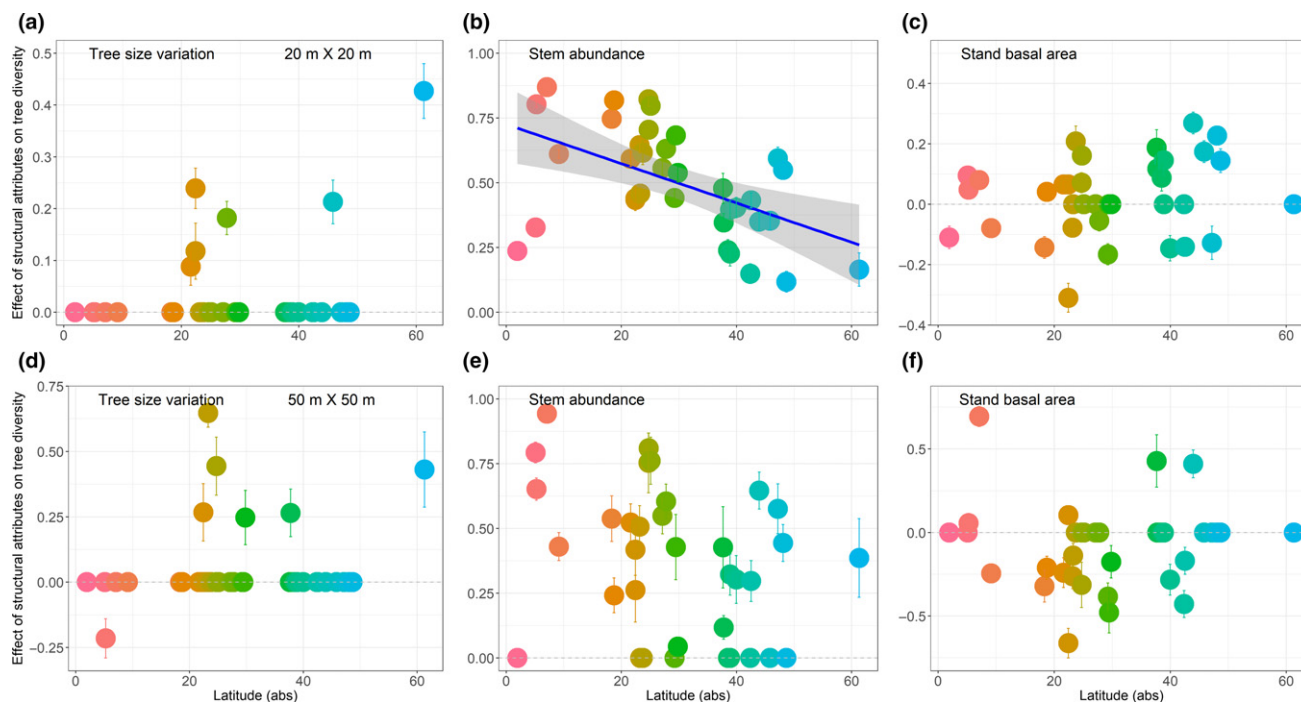
Figure 4 The effects of forest structural attributes on tree diversity derived from the within-forest plot structural equation modelling analyses. Panels a, b and c at the scale of 20 m × 20 m, and panels d, e and f at the scale of 50 m × 50 m. The effect of stem abundance on tree species richness showed a significant latitudinal trend at the scale of 20 m × 20 m (panel b; $P < 0.01$, $R^2 = 0.27$). Standardised path coefficients ± 1 SE are shown; SE's are smaller than the size of the symbol for some forest plots. Colours indicate increasing absolute latitude from pink to turquoise.

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 (Clim$_{PC1}$), 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 *c.* 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 amongst 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 and Table S5). 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 amongst trees for limited resources in these forests.

Amongst 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 realisable 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).

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