

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

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92 **Type of article:** Letters

93 **Running title:** Climate and the latitudinal tree diversity gradient

94 **Number of words in the abstract:** 146

95 **Number of words in the main text:** 4867

96 **Number of references:** 58

97 **Number of figures:** 4

98 **Number of tables:** 2

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

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

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

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111 **Abstract**

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

125 INTRODUCTION

126 Although the latitudinal diversity gradient – i.e., the pronounced increase in species
127 richness from the poles to the equator – has been recognized for centuries (Gaston
128 2000; Brown 2014; Fine 2015; Ricklefs & He 2016; Comita 2017; Kinlock *et al.*
129 2018), the primary factors determining this fundamental gradient in biodiversity
130 remain unresolved. This gradient is shaped by a combination of evolutionary and
131 ecological mechanisms (Mittelbach 2012; Brown 2014; Ricklefs & He 2016), with
132 climate at the forefront of most hypotheses (Kreft & Jetz 2007; Mittelbach 2012;
133 Schluter 2015). There are numerous interrelated mechanisms through which climate
134 may influence diversity (Fig. 1). Major mechanisms shaping the latitudinal diversity
135 gradient include the tropical origins of most clades, niche partitioning, kinetics of
136 ecological interactions and evolution, and primary productivity (Brown 2014).

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

146 Niche partitioning, driven by both abiotic and biotic mechanisms, also plays a

147 role in shaping the latitudinal diversity gradient. Species adapted to more abiotically
148 variable habitats can tolerate a wider range of abiotic conditions and therefore have
149 wider niches, larger elevational ranges and the associated potential to disperse over
150 mountain range barriers, and broader geographic ranges (Terborgh 1973; Stevens
151 1989; Gaston & Chown 1999). This effect is compounded by biotic interactions,
152 leading to high niche specialization at lower latitudes (Brown 2014). Thus, niche
153 breadth and the looseness of species “packing” within ecological communities and
154 across local (e.g., topographic) environmental gradients increase with latitude.

155 The latitudinal variation in evolution rate and biotically driven niche
156 specialization described above is probably driven by temperature (Brown 2014). In
157 general, biological rates tend to increase with temperature through temperature effects
158 on the kinetics of the biochemical reactions underlying metabolism (Brown *et al.*
159 2004; Sibly *et al.* 2012). Specifically relevant here, rates of DNA evolution,
160 speciation, and biological interactions (e.g., competition, herbivory, predation,
161 parasitism) all increase with temperature (Gillooly *et al.* 2005; Allen *et al.* 2006). This
162 provides a possible mechanistic explanation for the above-described latitudinal
163 gradients in evolution rate and Red Queen coevolution, leading to the argument of
164 Brown (2014) that “the Red Queen runs faster when she is hot.”

165 While the above mechanisms determine regional species pools, local plot richness
166 is ultimately constrained by forest structure including the number and sizes of
167 individuals that can coexist. Indeed, the species-energy hypothesis posits that climate
168 strongly influences primary productivity, or the total energy available for partitioning

169 within most ecological communities, thereby *indirectly* affecting species richness via
170 its impact on the number and size of individuals that can be supported (Hutchinson
171 1959; Currie *et al.* 2004; Brown 2014; Chu *et al.* 2016b; Storch *et al.* 2018).
172 Specifically, both gross and net primary productivity increase with temperature across
173 the latitudinal gradient (Luyssaert *et al.* 2007). This greater energy availability in the
174 tropics can be partitioned to support more individuals. In turn, more individuals could
175 represent more species because of a statistical effect (rare species are more likely to
176 be absent in small samples) and/or larger population sizes per unit area, the latter of
177 which would be associated with decreased extinction rates and thereby maintenance
178 of species richness (O'Brien 1998; Srivastava & Lawton 1998; Currie *et al.* 2004;
179 Storch *et al.* 2018). However, evidence that this actually occurs is mixed; for example,
180 higher tree abundance (i.e., stem abundance) does not necessarily translate to
181 increased species richness (Hawkins *et al.* 2003; Currie *et al.* 2004; Šímová *et al.*
182 2011; Storch *et al.* 2018). In large part, this may be due to the fact that productivity
183 can also be partitioned to support fewer larger, as opposed to more, individuals. If
184 increased energy goes primarily to support a few larger individuals, it may have little
185 impact on species richness, or may even suppress diversity through associated
186 competition for limiting resources (Franklin *et al.* 2002). For instance, larger trees
187 often have a disproportionately large effect on smaller ones through overtopping,
188 resulting in size-asymmetric competition for light, water, or nutrients (Coomes *et al.*
189 2011; Lutz *et al.* 2014; Farrior *et al.* 2016).

190 The above hypotheses are neither mutually exclusive nor easily disentangled,

191 yet they do result in specifically testable and sometimes distinct empirical predictions
192 that can help determine the relative importance of the various mechanisms (Fig. 1). In
193 particular, it should be possible to distinguish the direct and indirect (via the number
194 of individuals) effects of climate on species richness, yet most previous studies have
195 focused instead on the total or net effect of climatic variables on broad-scale variation
196 in species diversity (Hawkins *et al.* 2003; Currie *et al.* 2004; Šímová *et al.* 2011). This
197 has contributed to conflicting conclusions regarding the drivers of species-energy
198 relationships (Šímová *et al.* 2011; Storch *et al.* 2018). Simultaneous consideration of
199 direct and indirect effects will substantially improve our understanding of the
200 mechanisms underlying climatic drivers of species richness (e.g., see Menéndez *et al.*
201 (2007) for butterflies, Ferger *et al.* (2014) for birds, and Marshall & Baltzer (2015) for
202 subarctic plant communities).

203 Similar to other taxa, tree species richness usually displays a pronounced
204 latitudinal diversity gradient (Kreft & Jetz 2007; Šímová *et al.* 2011). Here, we
205 attempt to tease apart the indirect role of climate mediated through forest structural
206 attributes (species-energy hypothesis) from the more direct effects of climate on
207 global tree species richness. This is made possible with data from 35 large (9-60 ha)
208 stem-mapped forest plots across the globe (Anderson-Teixeira *et al.* 2015). We use a
209 structural equation modelling approach (SEM; Grace 2006) to test hypothesized
210 causal relationships amongst climate, topography, forest structural attributes (stem
211 abundance, tree size variation, and stand basal area), and tree species richness. Our
212 two major objectives were to: (1) Disentangle the direct and indirect effects of climate

213 on tree species diversity across global forest plots, thereby evaluating the relative
214 importance of mechanisms described above (Fig. 1), and (2) Quantify the effects of
215 forest structural attributes on local tree species richness within each forest plot, in
216 order to assess whether the importance of these drivers varies systematically with
217 latitude.

218

219 **METHODS**

220 **Study sites, topographic and climatic data**

221 Thirty-five forest dynamics plots compiled from the CTFS-ForestGEO network
222 (<http://www.forestgeo.si.edu/>) and other sources were used in this study (Fig. 2a, and
223 Supplementary Information Table 1). In each plot, all freestanding woody stems with
224 a diameter at breast height (DBH) ≥ 1 cm were identified to species, tagged, measured
225 and mapped according to a standardized census protocol (Condit 1998). The size of
226 the plots ranges from 9 ha (Liangshui, China) to 60 ha (Jianfengling, China) and these
227 plots span a broad latitudinal gradient from -25.10° (Ilha do Cardoso, Brazil) to
228 61.30° (Scotty Creek, Canada). Data from the first census for all forest plots were
229 used for the present analyses except Barro Colorado Island, where the seventh census
230 was used to be temporally comparable to the other, more recently established plots.

231 Each forest plot was divided into non-overlapping quadrats at two spatial
232 scales: $20\text{ m} \times 20\text{ m}$ and $50\text{ m} \times 50\text{ m}$, which allowed us to account for the possible
233 scale-dependence of forest structural patterns and processes (Chisholm *et al.* 2013)
234 and to test the hypothesis that species richness increases more rapidly with increasing

235 spatial scale at lower latitudes (Fig. 1). We excluded shrubs and lianas from the
236 analyses and focused only on trees. In each quadrat, in addition to tree species
237 richness we calculated three easily measured and ecologically important forest
238 structural attributes: stem abundance (the total number of stems), stand basal area (the
239 sum of stem basal area), and tree size variation measured by the coefficient of
240 variation (CV) of tree DBH within a quadrat.

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

257 resulting in a total of nine topographic variables.

258 We compiled climate data for the 35 forests to analyze the relationship among
259 topography, climate, forest structure, and tree species richness (across-forest plot
260 analyses at the two spatial scales using the same climatic information). We used
261 standardized climate data with the 0.5-degree spatial resolution from the CRU TS4.01
262 database (<http://catalogue.ceda.ac.uk/uuid/58a8802721c94c66ae45c3baa4d814d0>; downloaded
263 April 2018) for each forest plot. We retrieved monthly data for 1901-2016 for nine
264 variables: cloud cover (%), diurnal temperature range (°C), frost day frequency
265 (days), precipitation (mm), daily mean temperature (°C), monthly average daily
266 minimum temperature (°C), monthly average daily maximum temperature (°C),
267 vapour pressure (hectopascals), wet day frequency (days), and potential
268 evapotranspiration (mm day^{-1}). We calculated the annual temperature range (°C) as
269 follows: the maximum value of monthly average daily maximum temperature minus
270 the minimum value of monthly average daily maximum temperature. Monthly data
271 were used to calculate the annual values, which were then averaged over 1901-2016
272 to obtain climatic averages for individual plots. Potential evapotranspiration (mm
273 year^{-1}) data were extracted from the Global Aridity Index (Global-Aridity) and the
274 Global Potential Evapo-Transpiration (Global-PET) Geospatial Database
275 (<http://www.cgiar-csi.org/data/global-aridity-and-pet-database>). Incoming solar radiation (kJ
276 $\text{m}^{-2} \text{day}^{-1}$) data were downloaded from the WorldClim database
277 (<http://worldclim.org/version2>) for the spatial resolution of 30 seconds. In total, twelve
278 climatic variables were included in the analyses.

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

284 **Statistical analyses**

285 Our structural equation model was constructed using the following assumptions. We
286 assumed that climate/topography could directly drive the variation of forest structural
287 attributes and tree species richness, as many previous studies have shown (Vayreda *et*
288 *al.* 2012; Chu *et al.* 2016a; Lechuga *et al.* 2017; Lutz *et al.* 2018). Higher stem
289 abundance – i.e., increased number of individuals – was expected to increase tree
290 species richness by reducing the number of species that go extinct due to demographic
291 stochasticity (i.e., the more-individuals hypothesis (O’Brien 1998; Srivastava &
292 Lawton 1998; Currie *et al.* 2004); but see Storch *et al.* (2018)) and increase tree size
293 variation due to competition (Weiner *et al.* 2001). Stand basal area is jointly
294 determined by the number and the size of trees. If an increase in stand basal area was
295 due to increased stem abundance, stand basal area was predicted to exert a similar role
296 as stem abundance on species richness. Conversely, if the increase in stand basal area
297 was mainly caused by the increased size of trees, stand basal area should result in the
298 opposite effect, i.e. decreasing species richness and increasing tree size variation as
299 the result of competition (Canham *et al.* 2004; Franklin *et al.* 2002). The relationship
300 between tree size variation and species richness was unpredictable. On the one hand,

301 greater tree species richness may increase the degree of tree size variation in forests
302 (Hakkenberg *et al.* 2016; Pretzsch & Schütze 2016). On the other hand, larger tree
303 size variation may lead to increased species richness by creating more ecological
304 niches (Terborgh 1985), or may decrease species richness through strong asymmetric
305 competition for light, especially in more diverse forests with a higher proportion of
306 rare species (Larson *et al.* 2008; Hakkenberg *et al.* 2016). As such, we defined a
307 reciprocal interaction between tree species richness and tree size variation.

308 We conducted both across-forest plot analyses and within-forest plot analyses.
309 For the across-forest plot analyses, we first calculated mean tree species richness and
310 forest structural attributes across quadrats at the two spatial scales within each forest
311 plot. Then we explored the hypothesized relationships among these variables as well
312 as topographic and climatic factors through structural equation modeling (SEM; Fig.
313 3a). SEM offers a means to evaluate hypothesized causal relationships amongst
314 multiple variables. For the within-forest plot analyses, we applied a similar SEM
315 structure for quadrat-level variables of forest structural attributes and topography (Fig.
316 3a), but without climatic variables as macroclimate is constant within a plot and
317 microclimatic variation will largely be determined by topographic variation.

318 To simplify the SEM model construction and account for potential colinearity
319 among variables, we reduced the dimensionality of the climate (twelve predictors) and
320 topography variables (nine predictors in across-forest plot analyses: elevation, slope,
321 convexity and the ranges of these three variables both within each quadrat and across
322 the entire plot; eight predictors in within-forest plot analyses: elevation, slope,

323 convexity, and the ranges of these three variables within each quadrat, $\sin(\text{aspect})$ and
324 $\cos(\text{aspect})$) by means of principal component analysis (PCA) at the two spatial
325 scales. We present the PCA results of topography for the across-forest plot analyses
326 and plot-specific PCA results of topography for within-forest plot analyses in
327 Supplementary Information Table 2. We used the '*lavaan*' package (Rosseel 2012) in
328 the *R* software platform (R Core Team 2016) to parameterize the SEM. Bivariate
329 relationships among all variables for SEMs in both across-forest plot and within-
330 forest plot analyses were presented in the Supplementary Information Fig. 1. To
331 develop the final SEMs, we started with our initial hypothesized relationships among
332 variables (Fig. 3a). We then considered a number of alternative reduced models
333 sharing the same causal structure with the initial model, which were constructed by
334 eliminating non-significant variables one by one (Supplementary Information Table
335 3). The decision to remove a path was based on the performance of overall model fit
336 and the *P*-value for the path (Grace 2006). Model evaluation was determined by the
337 following two criteria: 1) The chi-square test ($P > 0.05$ for a satisfactory fit), and 2)
338 The Standardized Root Mean Square Residual (SRMR < 0.05 for a satisfactory fit).
339 The Bayesian Information Criterion (BIC) was used to select the best model from
340 models with a satisfactory fit. In the final step, we deleted non-significant paths with
341 $P > 0.05$ in SEMs with satisfactory model fit and reassessed model fit. Standardized
342 SEM path coefficients from within-forest plot analyses are reported in the
343 Supplementary Information Table 4. The total effect that one variable has on another
344 equals the sum of its direct and indirect effects through directed (causal) paths. The

345 standard error (SE) values and *P* values for standardized path coefficients were
346 obtained through the function *standardizedSolution* in the 'lavaan' package.

347

348 **RESULTS**

349 **Across-forest plot analyses: Direct and indirect effects of climate on global tree** 350 **species richness**

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

359 For topography, the first PCA axis explained 62.5% of the total variation in
360 topography at the scale of 20 m × 20 m, and 62.4% at the scale of 50 m × 50 m
361 (Supplementary Information Table 2). The first principal component (Top_{PC1}) at both
362 spatial scales best explained the variability in slope and ranges of elevation, slope and
363 convexity within quadrats and across the entire plot. The second PCA axis explained
364 16.6% of the total variation in topography for the 20 m scale and 12.4% for the 50 m
365 scale, which mainly explained the variability in convexity.

366 Tree species richness, stem abundance and richness:stem ratios displayed

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

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

387 Similar results were obtained at the scale of 50 m × 50 m. The SEM explained
388 76% of the total variation in tree species richness across plots (Fig. 3b). Climate had

389 both direct and indirect effects on tree species richness through three pathways (Fig.
390 3b): one direct from Clim_{PC1} to richness (path coefficient 0.63), two indirectly
391 mediated by stem abundance from Clim_{PC1} (path coefficient 0.19, i.e. 0.54×0.36) and
392 Clim_{PC2} (-0.15, i.e. $[-0.43] \times 0.36$) to richness, respectively.

393 We note that an SEM model incorporating latitude explains slightly higher
394 proportion of the variance (R^2) in tree richness than a model with climate alone (Table
395 2; across-forest plot SEM models including latitude are presented in the
396 Supplementary Information Table 6). The incorporation of latitude also makes the
397 direct path from Clim_{PC1} to tree species richness non-significant (Supplementary
398 Information Table 6). Clim_{PC1} was strongly correlated to latitude ($r = -0.91$;
399 Supplementary Information Fig. 2), and it was inappropriate to include two variables
400 as tightly correlated as these into a single SEM (Grace 2006). Since the aim of our
401 study has been to elucidate the causes of the latitudinal gradient in tree species
402 richness, we focus on the model with climate rather than the model with latitude. Still,
403 we cannot exclude the possibility that the effect of latitude on tree species richness
404 goes beyond the sole effect of climate.

405 **Within-forest plot analyses: forest structural attributes and local tree species** 406 **richness**

407 Within individual forest plots, the direction and strength of SEM path coefficients
408 between three forest structural attributes and tree species richness varied substantially
409 (Fig. 4; Supplementary Information Table 4). In total, at the scale of $20 \text{ m} \times 20 \text{ m}$,
410 stem abundance positively influenced tree richness in 34 of 35 forest plots (with the

411 boreal forest plot, Scotty Creek, the exception). Tree size variation was positively
412 correlated with tree richness in six plots, and stand basal area was positively
413 correlated with species richness in 18 plots and negatively in 9 plots. At the scale of
414 50 m × 50 m, stem abundance positively influenced tree richness in 25 out of 35 plots;
415 tree size variation was positively correlated with tree richness in six plots and
416 negatively in one plot (Wanang); and stand basal area was negatively correlated with
417 richness in 13 plots and positively in four.

418 The effect of stem abundance on tree species richness displayed a significant
419 latitudinal trend (Fig. 4b; $P < 0.01$, $R^2 = 0.27$) at the scale of 20 m × 20 m, with the
420 effect of stem abundance being more pronounced at lower latitudes. This
421 temperate/tropical difference was less apparent at the scale of 50 m × 50 m (Fig. 4e; P
422 = 0.062, $R^2 = 0.10$).

423 The proportion of the explained variance in tree richness within plots in
424 relation to topography and structural traits ranged from 0.050 (Zofin) to 0.88 (Ngel
425 Nyaki) with a mean of 0.36 at the scale of 20 m × 20 m, and from 0.042 (Zofin) to
426 0.89 (Ngel Nyaki) with a mean of 0.35 at the scale of 50 m × 50 m (Supplementary
427 Information Table 4).

428

429 **DISCUSSION**

430 **Climate influences global tree species richness both directly and indirectly**

431 We found clear evidence that climate influenced tree species richness both directly
432 and indirectly (through stem abundance) in forest plots worldwide. This lends support

433 to all of the major mechanisms considered here (Fig. 1) and yields insights into their
434 relative importance.

435 At the two spatial scales explored, there were strong, direct effects of climate
436 on tree species richness (Fig. 3), with the first PC axis, Clim_{PC1} , explaining more than
437 70% of the variation. This axis mainly represented temperature-related climatic
438 factors, with 50% reflecting the harshness and variability of environmental conditions
439 (Table 1). Thus, regions with less variable intra-annual climate and higher average
440 daily minimum temperature harbor more tree species, which is consistent with but
441 does not distinguish among three mechanisms shaping the latitudinal gradient in
442 diversity (Fig. 1): (1) difficulty for lineages of tropical origin to adapt to and establish
443 in cold/seasonal climates, (2) higher extinction rates in cold/seasonal climates, and (3)
444 wider niches of species adapted to variable climates. The analysis also revealed a
445 positive effect of temperature, with positive loadings of mean, minimum, and
446 maximum temperature plus vapor pressure totaling 60% of Clim_{PC1} . This finding
447 supports the direct role of kinetics in shaping the latitudinal gradient through
448 accelerated evolution, biotic interactions, and productivity under warmer temperatures
449 (Brown 2014).

450 Apart from the strong direct constraints of climate on species distribution,
451 climate influenced global tree species richness indirectly via stem abundance at both
452 spatial scales tested (Fig. 3), supporting the species-energy hypothesis (O'Brien 1998;
453 Hawkins *et al.* 2003; Currie *et al.* 2004). Climate influenced tree stem abundance
454 through positive effects of temperature (Clim_{PC1}), negative effects of solar radiation,

455 temperature variation and freezing temperatures (Clim_{PC1}, solar radiation and daily
456 temperature range in Clim_{PC2}), and a positive effect of moisture (precipitation in
457 Clim_{PC1}, cloud cover and wet day frequency in Clim_{PC2}). Thus, our results lend clear
458 support for the species-energy hypothesis that climate influences tree species richness
459 through abundance of individuals (Srivastava & Lawton 1998; Hawkins *et al.* 2003;
460 Currie *et al.* 2004; Ricklefs & He 2016; Storch *et al.* 2018). At the same time, our
461 analysis clearly demonstrates that the species-energy hypothesis alone is insufficient
462 to account for latitudinal trends in diversity. In addition to the fact that our across-
463 forest plot structural equation model showed stronger direct than indirect effects of
464 climate, the increase in species diversity with decreasing latitude was far too steep to
465 be explained only by the abundance of individuals (Fig. 2d) (Brown 2014).
466 Specifically, species richness increased 17-fold from high to low latitudes for 20 m ×
467 20 m plots and 77-fold for 50 m × 50 m plots in the present study. Given the
468 decelerating rate at which species accumulate as more individuals are sampled, stem
469 abundance would need to increase by ~4 orders of magnitude for every order-of-
470 magnitude increase in species richness (Brown 2014), implying the need for
471 a >10,000-fold increase in stem abundance to explain the observed latitudinal trend in
472 richness. In fact, stem abundance increased by only 25-fold (Fig. 2c). Thus, our
473 results demonstrate a small but significant role for stem abundance in shaping the
474 latitudinal gradient in forest tree diversity.

475 We acknowledge that we could not rule out the possibility that other
476 unmeasured factors which are strongly correlated with latitude influenced the

477 observed latitudinal diversity gradient of trees, as indicated by the significant and
478 strong effect of latitude in the SEM. Since latitude is a composite variable that
479 incorporates many factors, both contemporary and historical (evolutionary), the strong
480 effect of latitude on global tree species richness patterns is expectable (Table 2). In
481 extreme, it is even possible that the observed effect of climate may reflect just another
482 (unknown) causal factor which is correlated with latitude similarly as climate.
483 However, it is unclear what such a factor would be, and thus we focus on the central
484 role of climate.

485 **Latitudinal trends in the local stem abundance effect**

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

494 Among three forest structural attributes, the effect of stem abundance on tree
495 species richness decreased with increasing latitude at the scale of 20 m × 20 m (Fig.
496 4b), which means that on average a change in one standard-deviation unit in stem
497 abundance could result in a more pronounced change in tree species richness in
498 tropical forests than in temperate forests, probably due to the higher tree species

499 richness in tropical forests. In hyper-diverse tropical plots, the species pool is higher
500 than the number of individuals at the 20 m × 20 m but not at the 50 m × 50 m quadrat
501 scale; adding any additional individuals thus has the potential to increase the species
502 richness of a 20 × 20 m quadrat (Fig. 2d). On the contrary, in species-poor temperate
503 plots, the highest realizable levels of diversity may be attained with far fewer
504 individuals and above certain densities adding more individuals will not further
505 increase species richness of a quadrat. The higher local effect of stem abundance on
506 species richness in tropical than in temperate forests may also be amplified by
507 significantly higher conspecific negative density dependence in the tropics (Shao *et*
508 *al.* 2018).

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

519 In summary, our results demonstrate that climate simultaneously influenced
520 global tree species richness both directly by climatic extremes and temperature, and

521 indirectly via changes in the number of individuals. These findings show that a
522 number of mechanisms are acting in concert to shape the latitudinal gradient in
523 diversity, with no single mechanism being sufficient on its own. Our work also
524 suggests that a more comprehensive framework for the effects of multiple variables
525 including climate and historical factors on the latitudinal diversity gradient is needed
526 (Brown 2014).

527

528 **ACKNOWLEDGEMENTS**

529 We thank Margie Mayfield, three anonymous reviewers and Jacob Weiner for
530 constructive comments on the manuscript. This study was financially supported by the
531 National Key R&D Program of China (2017YFC0506100), the National Natural
532 Science Foundation of China (31622014 and 31570426), and the Fundamental
533 Research Funds for the Central Universities (17lgzd24) to CC. XW was supported by
534 the Strategic Priority Research Program of the Chinese Academy of Sciences
535 (XDB3103). DS was supported by the Czech Science Foundation (grant no. 16-
536 26369S). Yves Rosseel provided us valuable suggestions on using the *lavaan* package
537 conducting SEM analyses. Funding and citation information for each forest plot is
538 available in the Supplementary Information Text 1.

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SUPPORTING INFORMATION

670

671 **Supplementary Information** includes:

672 (1) **Figure 1** Bivariate relationships among all variables for SEM

673 (2) **Table 1** Plot characteristics

674 (3) **Table 2** PCA results for topographic variables

675 (4) **Table 3** Alternative SEMs for across-forest plot analyses at both spatial scales

676 (5) **Table 4** SEM results from within-forest plot analyses at both spatial scales

677 (6) **Table 5** SEM results from across-forest plot analyses at both spatial scales

678 (7) **Table 6** SEM results from across-forest plot analyses with latitude

679 (8) **Text 1** Plot funding and citation information

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

681 **Table 1** Percentage contributions (%) and loadings of the twelve individual climatic
682 variables to the first two principal components (Clim_{PC1} and Clim_{PC2}). The two
683 principal components explained 88% of the variation in climate (75% by Clim_{PC1} and
684 13% by Clim_{PC2}).

		<i>atr</i>	<i>cld</i>	<i>dtr</i>	<i>frs</i>	<i>pet</i>	<i>pre</i>	<i>rad</i>	<i>tmn</i>	<i>tmp</i>	<i>tmx</i>	<i>vap</i>	<i>wet</i>
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

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

689

690 **Table 2** Proportion of the explained variance (R^2) in global tree species richness in
691 models with the predictor of climate or latitude at the plot scales of 20 m × 20 m and
692 50 m × 50 m. On the top of the hypothesized relationships (Supplementary
693 Information Fig. 1), latitude was assumed to have both a direct effect (i.e. an arrow
694 from latitude to tree species richness) and an indirect effect (i.e. an indirect latitudinal
695 effect via temperature, especially the first PCA axis of 12 climatic variables) on global
696 tree species richness. The results of SEM models with latitude were presented in the
697 Supplementary Information Table 6.

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

698

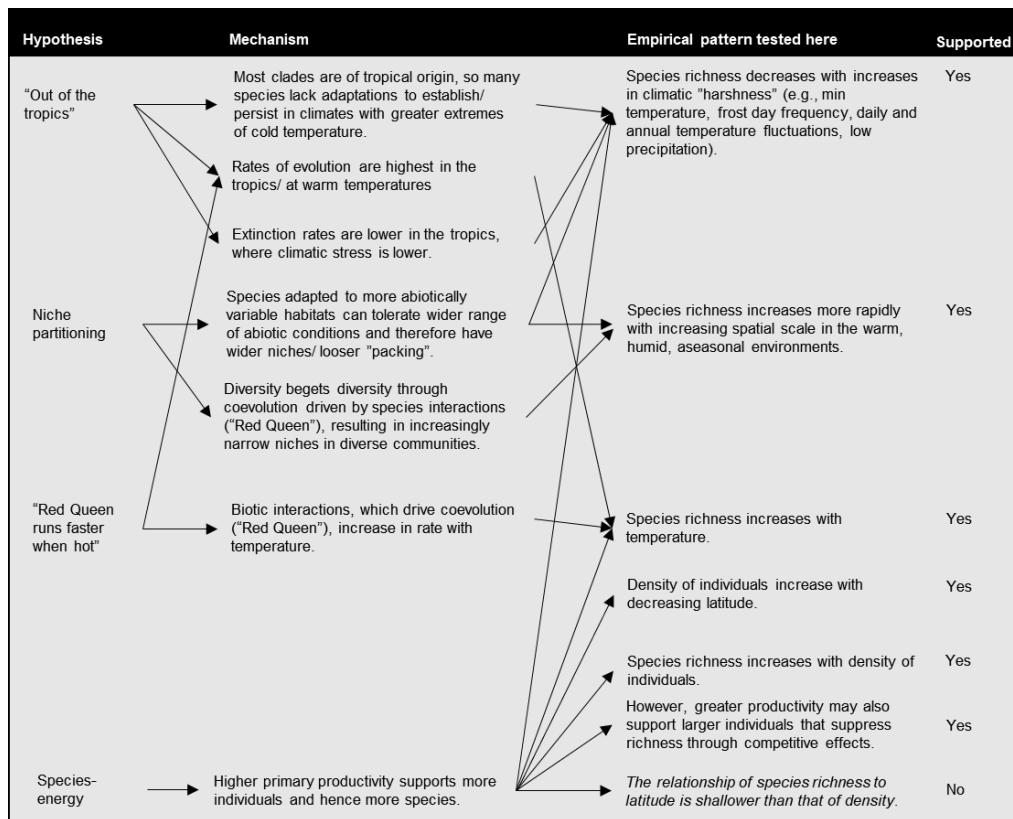
699 **Figure legends**

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

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

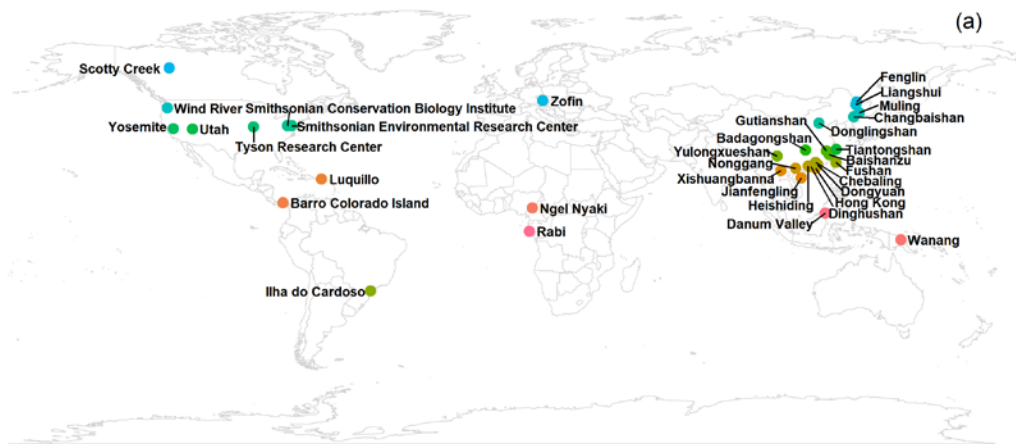
722 **Figure 3 (a)** The conceptual structural equation model (SEM), which was used to
723 examine the linkages among climate, topography, forest structural attributes, and tree
724 species richness. The variables Topo and Clim represent topographic and climatic
725 factors, respectively. Besides the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

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

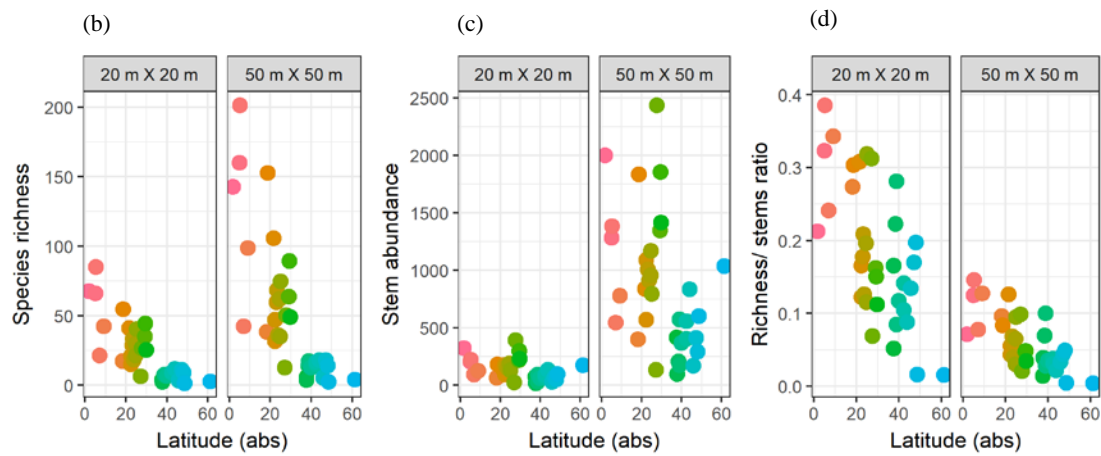


744

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



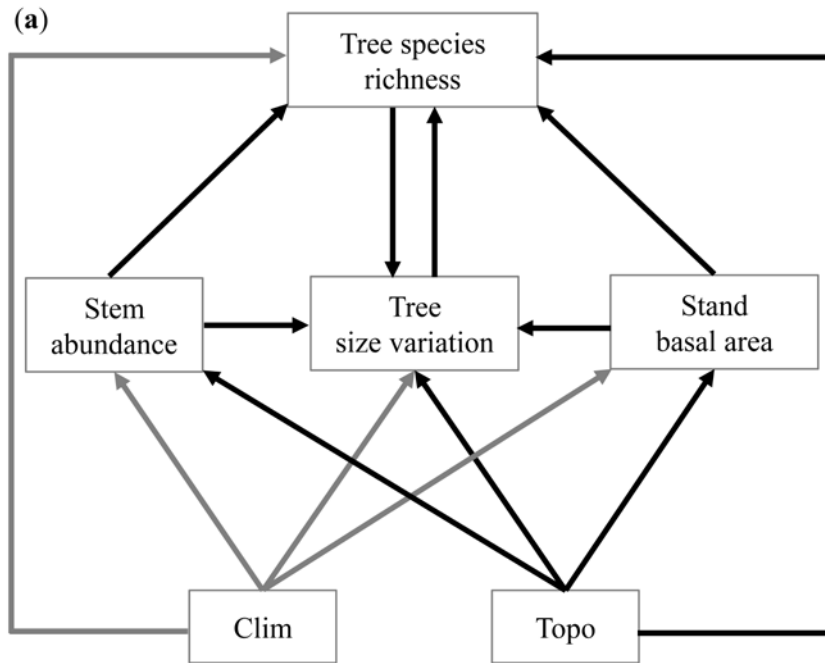
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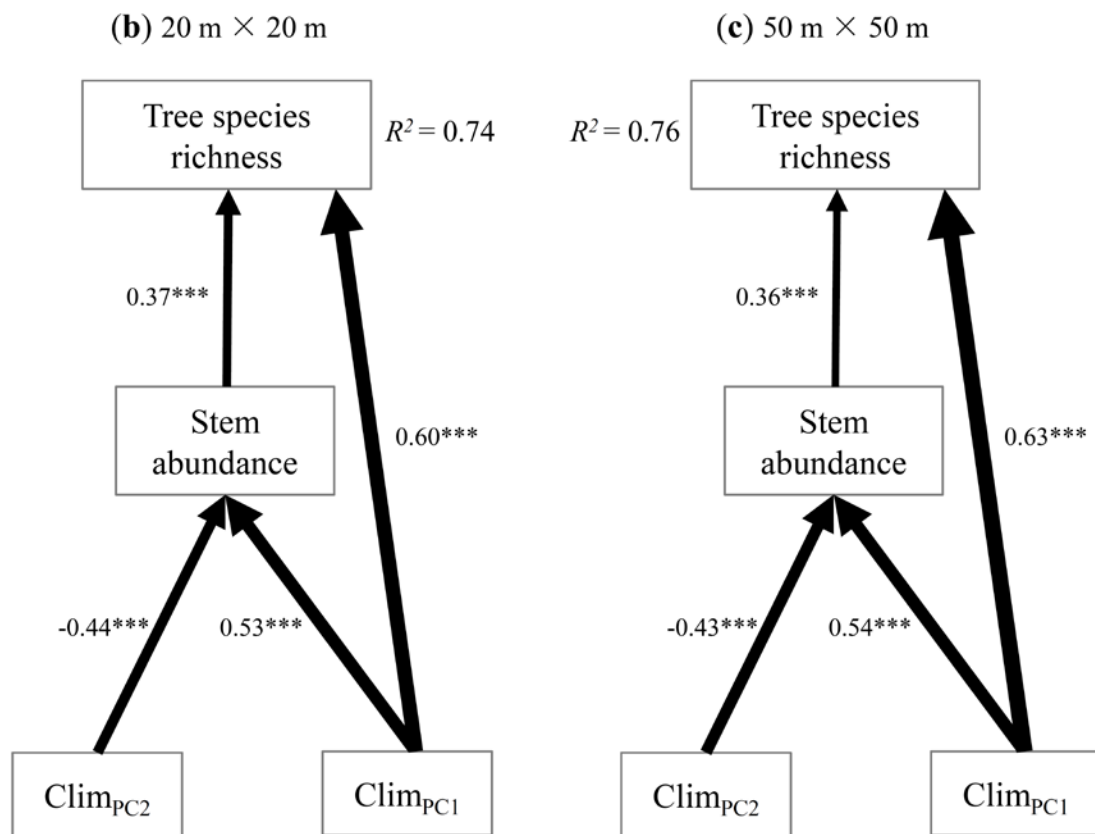
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763 **Figure 2** Global distribution of 35 forest dynamics plots used in this study (a), and the
 764 latitudinal gradients of tree species richness (b), stem abundance (c), and species
 765 richness/ stand stem ratios (d). Richness and stem abundance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

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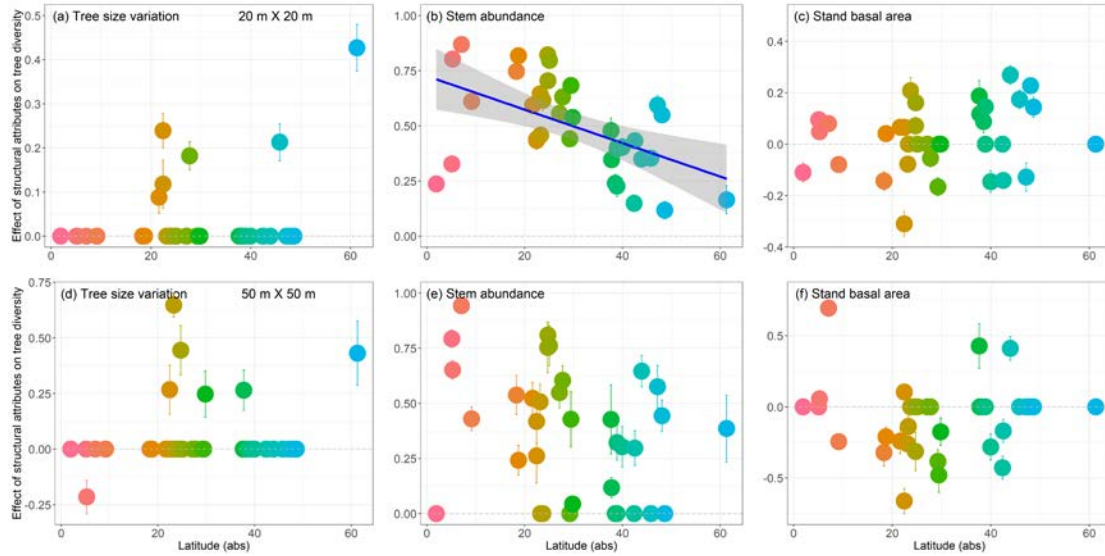
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773 **Figure 3** (a) The conceptual structural equation model (SEM), which was used to
 774 examine the linkages among climate, topography, forest structural attributes, and tree
 775 species richness. The variables Topo and Clim represent topographic and climatic
 776 factors, respectively. Besides the linkages represented by directed arrows, a

777 correlation between stem abundance and stand basal area was set. This full model
778 including both Topo and Clim was used for the across-forest plot analyses, and the
779 one without the Clim variable (i.e. removing gray paths) was designated for the
780 within-forest plot analyses. Panels (b) and (c) for the across-forest plot SEM analyses
781 at the scales of 20 m × 20 m and 50 m × 50 m, respectively. Paths from topography,
782 tree size variation, and stand basal area to tree species richness were not significant.
783 The results of the final SEM models including other significant paths (ones from
784 climate and stand basal area to tree size variation) and the uncertainty (SE) of each
785 path coefficient were presented in the Supplementary Information Table 5. Clim_{PC1}
786 and Clim_{PC2} represented the first two principal components (PC) of the 12 climatic
787 variables. Statistical significance was indicated by asterisks (***) $P < 0.001$).



788

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