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1 **Strapline: Original Article**

2
3 **Phylogenetic structure and ecological and evolutionary determinants of species richness for**
4 **angiosperm trees in forest communities in China**

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22
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25

26 **ABSTRACT**

27 **Aim** Site-level species richness is thought to result from both local conditions and species'
28 evolutionary history, but the nature of the evolutionary effect, and how much it underlies the
29 correlation with current environment, are debated. Although tropical conservatism is a widely
30 used explanatory framework along temperature gradients, it is unclear whether cold tolerance
31 is primarily a threshold effect (e.g. freezing tolerance) or represents a more continuous
32 constraint. Nor is it clear whether cold tolerance is the only major axis of conservatism or
33 whether others, such as water-stress tolerance, are additionally important or trade-off against
34 cold tolerance. We address these questions by testing associated predictions for forest plots
35 distributed across 35° latitude.

36 **Location** China.

37 **Methods** We recorded all trees within 57 0.1-ha plots, generated a phylogeny for the 462
38 angiosperm species found, and calculated phylogenetic diversity (standardized PD), net
39 relatedness index (NRI) and phylogenetic species variability (PSV) for each plot. We tested the
40 predictions using regression, variance partitioning and structural equation modelling to
41 disentangle potential influences of key climate variables on NRI and PSV, and of all variables on
42 species richness.

43 **Results** Species richness correlated very strongly with minimum temperature, non-linearly
44 overall but linearly where freezing is absent. The phylogenetic variables also correlated strongly
45 with minimum temperature. While NRI and PSV explained little additional variance in species
46 richness, they accounted for part of the species richness–current climate correlation. Water
47 stress added minimal explanatory power. All these variables showed strong latitudinal gradients.

48 **Main conclusions** Minimum temperature appeared to primarily control tree species richness, via
49 both a threshold-like freezing effect and a linear relationship in climates without freezing. We
50 found no clear signal of water-stress effects. The modelled contribution of evolutionary history
51 is consistent with cold-tolerance conservatism, but could not account for all the species
52 richness–climate relationship.

53

54 **Keywords**

55 Climate, latitudinal diversity gradient, niche conservatism, phylogenetic community ecology,
56 phylogenetic structure, tropical conservatism hypothesis

57

58 **Introduction**

59 The assemblage of species in any given location results from local gain and loss of species
60 through time. Some of this results from relatively rapid responses to local conditions and some
61 from the deeper-time evolutionary history of the region, affecting the pool of species able to
62 reach the site ('regional pool'; we favour this site-specific theoretical definition of the regional
63 pool). Over very large extents, the identities of the species found locally must depend in large
64 part on evolutionary history (Ricklefs, 1987; Algar *et al.*, 2009). In particular, the species in the
65 regional pool that can exist in a given set of environmental conditions may be strongly
66 determined by the climatic regimes under which they evolved, constrained by a tendency for
67 niches to be conserved (Diamond, 1975; Chase & Leibold, 2003; Wiens & Donoghue, 2004).
68 Because taxa differ in their niches, it is a truism that niches must be conserved on phylogenies, at
69 least to some extent. Niche conservatism as a principle is therefore commonly used for
70 understanding and explaining the effects of evolutionary history on the composition of species
71 assemblages (e.g. Chase & Leibold, 2003).

72 However, given that evolution happens, it is also a truism that niches are labile, at least to
73 some extent. Much less clear are which aspects of the climatic niche are more strongly conserved,
74 which less so, and whether key niche axes are correlated or subject to trade-offs with respect to
75 niche conservatism; here we aim to make progress towards answering these questions. To date,
76 the focus has been primarily on cold tolerance. Most lineages have evolved under warmer
77 conditions than today and temperature tolerance is thought to be strongly conserved
78 phylogenetically (tropical conservatism hypothesis, 'TCH'). Specifically, it is hypothesized that
79 cold tolerance in angiosperms has mostly evolved since the cooling that started in the early

80 Eocene (~50 mya; Graham, 2011; Condamine *et al.*, 2012), and only in relatively few lineages that
81 have since diversified to some extent (e.g. Latham & Ricklefs, 1993; Wiens & Donoghue, 2004).
82 Thus, fewer species are expected to be found today in colder climates, and these should on
83 average be more closely related to each other (more phylogenetically clustered) than in warmer
84 climates—producing predictions 1a–1c in Table 1.

85 Different versions of the TCH exist, some implying that cold tolerance is a relatively
86 continuous phenomenon, with difficult-to-evolve adaptations required for a broad range of the
87 temperatures that characterize today’s gradient from tropical to temperate to high-latitude
88 climates (e.g. Qian, 2014). For convenience, we label this the ‘continuous TCH’. Various lines of
89 evidence are consistent with such a non-threshold view of cold tolerance (e.g. Qian, 2014). From
90 this hypothesis, we expect continuous relationships between a range of temperature variables
91 and both species richness and phylogenetic relatedness (Table 1, prediction 2a).

92 In contrast, tolerance to freezing, specifically, is often stressed as key to tropical
93 conservatism (e.g. Wiens & Donoghue, 2004). In this ‘threshold TCH’, freezing represents a step-
94 change in an organism’s environmental conditions, requiring specific adaptations that may not
95 readily evolve. Under this hypothesis, the minimum temperatures experienced by organisms
96 become the main focus. For gradients that include sites experiencing freezing, species richness
97 and phylogenetic relatedness should be more strongly correlated with minimum temperature
98 than with other temperature variables (Table 1, prediction 3a; see, for example, Hawkins *et al.*,
99 2014). From this hypothesis we also expect the relationships between minimum temperature
100 and both species richness and phylogenetic relatedness to be more threshold-like (predictions 3b
101 and 3c).

102 However, it is not realistic to expect very clear thresholds because freezing tolerance is
103 complex. For trees, it may be manifest in at least three different ways, with the timing of the
104 cooling being a key distinction. First, there are winter frosts. Most trees with at least some
105 freezing tolerance have an acclimation period, in which they become more resistant to colder
106 temperatures (e.g. by increasing the concentration of solutes in their tissues, lowering the
107 freezing point of the water within them). There is wide variation between frost-hardy species in
108 just how low a temperature they can experience and still survive, once they have acclimated, but
109 this can be as low as -80°C (Sakai & Weiser, 1973). However, if acclimation has not happened, the
110 same trees may be killed or badly damaged by much milder temperatures, so the timing of the
111 coldest temperatures is also critical. Second, late-spring frosts can damage newly growing plant
112 tissue. Third, in trees in particular, early-spring warming may cause freezing-related desiccation—
113 for example when the sun warms tree crowns while the trunks remain frozen, meaning no supply
114 of water and solutes to the metabolizing crowns. Because these varying causes of damage occur
115 at different temperatures and depend on antecedent conditions and timing, a clear-cut threshold
116 is not expected in the relationship between minimum temperature and response variables that
117 aggregate across species and sites. Even so, threshold-like relationships between minimum
118 temperature and species richness or phylogenetic relatedness may emerge if freezing tolerance
119 is important.

120 Some aspects of the climatic niche may be more conserved than others under changing
121 climates, depending largely on the combination of the selection pressure and the difficulty of
122 adapting to change experienced. Freezing is both a strong selective force, because it is often
123 lethal, and difficult for many lineages to adapt to because the nature of freezing damage (e.g.

124 physical damage caused by the expansion of water as it freezes, and the desiccation of tissues)
125 often requires complex adaptations. It is not surprising, then, that freezing tolerance has received
126 considerable attention in relation to niche conservatism. Not so clear is why cold tolerance
127 should be an important structuring force in places not experiencing frost, though chilling injury is
128 known in some tropical plants at temperatures as high as 12°C (Lyons, 1973). Further, the
129 continuous (non-linear) response of the rate of chemical reactions to temperature may play a
130 role in linking non-freezing temperatures to species richness (e.g. Brown *et al.*, 2004). The
131 reasonable amount of evidence consistent with a continuous TCH probably results from a
132 research focus on cold tolerance generally, typically without explicit consideration of the exact
133 mechanism of cold tolerance involved.

134 While cold tolerance has received the most attention, it may not be the only major axis of
135 niche conservatism. In theory, any aspect of tolerance to ambient environmental conditions that
136 is both phylogenetically conserved and difficult to evolve may be important in determining
137 patterns of relatedness and, potentially, species richness. Any aspect of the environment
138 experienced by organisms that is now 'harsh' (relative to the conditions prevailing over their
139 evolutionary history) has potential for (partly) explaining composition and richness of current
140 species assemblages via a niche conservatism mechanism (Wiens & Graham, 2005). For example,
141 it is thought that the world has become drier over approximately the same time-period as it has
142 become colder (e.g. Wolfe, 1975). Tolerance of low water availability therefore represents a
143 strong candidate for attention (Wiens & Graham, 2005), yet so far it has been largely ignored.
144 From this 'water-stress conservatism' hypothesis we expect phylogenetic relatedness and species

145 richness to relate to water stress in similar ways as to cold temperatures (Table 1, predictions 4a
146 and 4b).

147 A fundamental concept underlying niche conservatism is a trade-off between niche axes,
148 but they may also be correlated; Kraft *et al.* (2007) called for research exploring correlations and
149 trade-offs between traits in the context of community assembly. Many adaptations to freezing
150 may also represent adaptations to drought because (as mentioned above) a key part of freezing
151 stress is lack of liquid water. We may therefore expect some of the same variation in species
152 richness and phylogenetic relatedness to be accounted for by both temperature and water-stress
153 variables (prediction 4c).

154 Given a large span of latitude, we expect species richness to correlate strongly with both
155 latitude and climate (Table 1, prediction 1c). This prediction is far from unique to the TCH, and
156 there is debate (e.g. Wiens & Graham, 2005; Algar *et al.*, 2009; Brown, 2014) about whether
157 species richness is determined mainly by current climate or mainly by niche conservatism, or
158 whether both contribute strongly. While it is possible that neither is a major determinant of
159 species richness, we consider this very unlikely (e.g. see Field *et al.*, 2009). Saliently, the
160 characters thought to be conserved under the TCH are directly related to climatic tolerances.
161 Therefore, with respect to species richness, it is appropriate to consider the TCH not as an
162 alternative to current climate but as a hypothesis for why current climate is correlated with
163 species richness. Given that tropical conservatism is not the only hypothetical mechanism for
164 species richness–current climate correlations (e.g. see Lavers & Field, 2006; Algar *et al.*, 2009;
165 Jocque *et al.*, 2010; Boucher-Lalonde *et al.*, 2014; Brown, 2014), it is informative to ask how

166 much of the correlation can be accounted for by phylogenetic relatedness (Table 1, predictions
167 5a–5c).

168 Here we test the predictions outlined in Table 1 by analyzing data from forest plots in
169 China, spanning 35° latitude. First, we test whether the patterns of phylogenetic relatedness in
170 our data are consistent with the TCH, and if so, which version of the TCH receives the most
171 support. For this, we focus on which of the (inter-correlated) temperature variables best account
172 for relatedness, whether the relationships are threshold-like, and whether water-stress variables
173 account for additional variation or overlap. Second, using path analysis and variance partitioning
174 (similarly to Algar *et al.*, 2009 and Qian *et al.*, 2015), we assess how much of the spatial variation
175 in species richness is accounted for by direct statistical effects of climate versus direct effects of
176 evolutionary history, the degree of overlap between the two, and the indirect effects of climate
177 routed through evolutionary history (Table 1).

178

179 **Materials and Methods**

180 *Species data*

181 Forest plots were sampled in 15 areas (Appendix S1), 14 of which are nature reserves, spanning
182 35° latitude from tropical rain forests to boreal forests. In each area, four 20 x 50 m (0.1 ha)
183 forest plots were sampled and latitude, longitude and elevation of each were recorded. Woody
184 individuals with diameter at breast height at least 3 cm were identified to species, all of which
185 are native. Species-level botanical nomenclature was standardized using the Flora of China (Wu
186 *et al.*, 1994–2013). Three forest plots with fewer than two angiosperm tree species were

187 excluded because some phylogenetic metrics used (see below) require at least two species. The
188 remaining 57 plots contained 462 angiosperm tree species in 187 genera and 64 families.

189

190 *Phylogeny*

191 We generated a phylogeny for the 462 species, based on the species-level phylogeny of Zanne *et*
192 *al.* (2014), which includes 30,535 angiosperm species and was time-calibrated using seven gene
193 regions and fossil data. Orders and families in the phylogeny were constrained according to APG
194 III (2009). All the families and 97% of the genera in our dataset were included in Zanne *et al.*'s
195 phylogeny. Of the six missing genera, *Ellipanthus* is the only genus of its family in our data and
196 thus was represented by its family branch in our phylogeny; the remaining five genera were
197 randomly distributed among tips within their respective families. Zanne *et al.*'s phylogeny
198 includes 294 (64%) of our 462 species. Of the other 168, 37 belong to genera with only one
199 species in our data and were represented by branches of their respective genera. Thus 331 (72%)
200 of the 462 species were completely resolved in our phylogeny. The remaining 131 species were
201 randomly distributed among tips within their genera, following recent literature (e.g., Brunbjerg
202 *et al.*, 2014). We checked sensitivity of results to the method used for placing unresolved species
203 in the phylogeny; see Appendix S2

204

205 *Metrics of phylogenetic diversity and phylogenetic structure*

206 We used Faith's (1992) phylogenetic diversity (PD) metric to quantify each plot's phylogenetic
207 diversity as the total phylogenetic branch length joining the basal node (here the angiosperm) to
208 the tips of all the species in the plot. Because PD correlates strongly with species richness,

209 following previous studies (e.g. Slik *et al.*, 2009) we calculated standardized PD, independent of
210 species richness. Specifically, we randomly selected 10 species from each plot and calculated PD
211 (for the 36 plots with 10 or more species). We repeated this 1000 times per plot and calculated
212 the mean of the 1000 randomized PD values.

213 We used two indices, net relatedness index (NRI; Webb, 2000) and phylogenetic species
214 variability (PSV; Helmus *et al.*, 2007), to quantify phylogenetic structure (evolutionary inertia) per
215 plot (also see Qian *et al.*, 2015). NRI is commonly used to measure the standardized effect size of
216 mean phylogenetic distance (MPD), which estimates the average phylogenetic relatedness
217 between all pairs of taxa in an assemblage. Webb (2000) defined NRI as: $NRI = -1 \times (MPD_{\text{observed}}$
218 $- MPD_{\text{randomized}}) / (sdMPD_{\text{randomized}})$, where MPD_{observed} is observed MPD, $MPD_{\text{randomized}}$ is the
219 expected MPD of randomly generated assemblages ($n = 1000$) generated by drawing a number of
220 species randomly from across the phylogeny equal to the observed number of species in the
221 assemblage, and $sdMPD_{\text{randomized}}$ is the standard deviation of the MPD for the randomized
222 assemblages. To generate randomized (null) assemblages, species in each forest plot were
223 randomly drawn from the pool of all species in the phylogeny (i.e. model 2 of Phylocom;
224 <http://phylodiversity.net/phylocom>). Positive NRI indicates lower MPD than expected by chance
225 (species more closely related than expected): phylogenetic clustering of species. Conversely,
226 negative NRI (species more distantly related than expected by chance) indicates phylogenetic
227 evenness or overdispersion. NRI was calculated using Phylocom (Webb *et al.*, 2008).

228 Helmus *et al.* (2007) defined PSV as: $PSV = (ntrC - \Sigma C) / (n(n - 1))$, where n is the species
229 richness, C is a covariance matrix summarizing the correlation structure of the community
230 phylogeny, trC is the trace (sum of the diagonal elements) of C , ΣC is the sum of all elements in C .

231 PSV is standardized to vary from zero (maximum relatedness or clustering) to one (minimal
232 relatedness or maximal evenness: all species from disparate parts of the phylogenetic tree) (Algar
233 *et al.*, 2009). It is independent of species richness (Helmus *et al.*, 2007; Savage & Cavender-Bares,
234 2012) and was calculated using Picante (Kembel *et al.*, 2010).

235

236 *Environmental variables*

237 Temperature and precipitation are typically the environmental variables most strongly correlated
238 with species richness for terrestrial plants and animals (Hawkins *et al.*, 2003; Field *et al.*, 2009;
239 Wang *et al.*, 2011) and were used in previous studies assessing the relative importance of
240 evolutionary and ecological effects on species richness (e.g. Algar *et al.*, 2009; Qian *et al.*, 2015).
241 Mean temperatures for all 12 months and their derivations BIO1–BIO11 in the WorldClim
242 database (Hijmans *et al.*, 2005; <http://www.worldclim.org>) were all strongly correlated in our
243 data, but the minimum coldest-month temperature (BIO6, hereafter ‘minimum temperature’) is
244 the most appropriate for assessing freezing tolerance and cold tolerance more generally (e.g.
245 Algar *et al.*, 2009; Hawkins *et al.*, 2014; Qian *et al.*, 2015). We therefore used this variable in
246 testing all the predictions relating to temperature (i.e. all the predictions in Table 1 except 1b, 4a,
247 4b and 5a). To test predictions 2a, 2b, 3a and 3c we also used mean annual temperature (BIO1,
248 hereafter ‘mean temperature’), mean annual potential evapotranspiration (‘PET’, calculated
249 using the method of Willmott *et al.*, 1985; see Gavin & Hu, 2006), temperature seasonality (BIO4)
250 and the maximum warmest-month temperature (‘maximum temperature’; BIO5). As a
251 preliminary analysis, we examined the bivariate relationships between all the response and
252 temperature variables.

253 Mean annual precipitation is commonly used to measure water availability in species
254 richness studies (e.g. Field *et al.*, 2009; Algar *et al.*, 2009; Qian *et al.*, 2015) and we used it to test
255 predictions relating to current climate (5b and 5c in Table 1). To test water stress-related
256 conservatism (predictions 4a–c), water availability during the (main) growing season and,
257 particularly, measures of water stress are more appropriate. We obtained various water-related
258 variables, measuring water deficit, water surplus, actual evapotranspiration, precipitation and
259 precipitation seasonality, including WorldClim BIO12–BIO19. We initially examined bivariate
260 relationships between all the response and water variables, but only entered a few water
261 variables into our modelling, based primarily on theoretical reasoning and secondarily on the
262 bivariate relationships: mean annual precipitation (BIO12, for comparison with previous studies),
263 annual water deficit, warmest-quarter precipitation (BIO18), driest-month precipitation (BIO14),
264 water surplus in summer (specifically August, which showed stronger relationships with some
265 response variables than water surplus in other summer months). Appendix S3 lists all
266 environmental variables obtained and initially examined, and their sources.

267

268 *Data analysis*

269 We first examined whether the observed values of NRI and PSV differ from null expectation. For
270 each of the 57 forest plots, we generated 1000 null assemblages by randomly shuffling the
271 species on the tips of the phylogeny. From these null assemblages we computed the mean NRI
272 and PSV for each plot, to create the variables NRI_{null} and PSV_{null} .

273 We took three approaches to assessing the relationships between species richness and
274 the evolutionary and ecological variables. First, we used Pearson's correlation to quantify the

275 bivariate relationships between variables (multiple R for quadratic relationships). Second, for
276 prediction 5b (Table 1) we conducted partial regressions (Legendre & Legendre, 1998) to
277 partition the variance in species richness into four portions: uniquely accounted for by (a)
278 ecological variables (current climate), (b) evolutionary variables (NRI and PSV), (c) jointly
279 accounted for by the ecological and evolutionary variables, and (d) accounted for by none of the
280 variables. We used SAM version 4.0 (Spatial Analysis in Macroecology; Rangel *et al.*, 2010) for
281 correlation and regression analyses, including variance partitioning. Using this software, we
282 checked for spatial structure in the residuals.

283 Third, we used path analysis (within structural equation modelling, 'SEM') to estimate the
284 direct effects of these variables on species richness (predictions 5a and 5b), and the indirect
285 effect of climate routed through evolutionary history (prediction 5c). The framework of our path
286 analyses is based on Algar *et al.* (2009) and Qian *et al.* (2015), in which species richness was the
287 response, climate variables were exogenous and NRI and PSV were endogenous variables. Unlike
288 those studies, we did not transform species richness because this produced good normality and
289 homoscedasticity, better in both respects than using any of the common transformations. We
290 used Amos (<http://amosdevelopment.com>) for our SEM analyses.

291

292 **Results**

293 The number of angiosperm tree species per genus varied from 1 to 22 (Fig. 1). As expected, PD
294 was strongly correlated with species richness of angiosperm trees ($r = 0.918$), which was strongly
295 correlated with latitude ($r = -0.880$; Fig. 2A), and PD was strongly correlated with latitude ($r = -$
296 0.881). Similarly, standardized PD (accounting for species richness), was strongly correlated with

297 latitude (Fig. 2B), and with minimum temperature (Table 2), as expected (Table 1, prediction 1a).
298 NRI and PSV were negatively correlated with each other ($r = -0.832$), and both were correlated
299 with latitude (Fig. 2C, D). Both were also correlated with species richness (Table 2), in line with
300 prediction 1b except that the negative species richness–NRI correlation was not very strong.
301 Species richness was lower in colder climates (Table 2), consistent with prediction 1c. Values of
302 NRI and PSV derived from the null assemblages were not significantly correlated with species
303 richness, latitude, minimum temperature or mean annual precipitation (P ranging from 0.142 to
304 0.805).

305 The freezing tolerance and chilling tolerance versions of TCH predict that minimum
306 temperature correlates more strongly with species richness, NRI and PSV than do other
307 temperature variables (Table 1, prediction 3a), while other forms of the continuous TCH predict
308 no such difference (prediction 2b). With species richness and NRI, minimum temperature was
309 slightly more correlated than the other temperature variables (Table 2), with two exceptions
310 (temperature seasonality for species richness and mean annual temperature for NRI), both of
311 which were extremely co-linear with minimum temperature ($|r| = 0.99$; Table 2). PSV was no
312 more strongly correlated with minimum temperature than with other temperature-related
313 variables. The proportion of variation accounted for by (minimum) temperature was lower for
314 evolutionary history than for species richness: in regressions with minimum temperature as the
315 only explanatory variable, r^2 was 0.841 with species richness as response, 0.729 for PSV² and
316 0.576 for NRI (Table 2, Fig. 3).

317 The continuous and freezing tolerance TCHs are also distinguished by their predictions
318 about whether relationships between temperature (especially minimum temperature) and

319 species richness, NRI and PSV show threshold-like behaviour (prediction 2a vs 3b and 3c). For
320 species richness, the relationship with minimum temperature (and with the highly co-linear
321 temperature seasonality) showed some evidence of a threshold (Fig. 3A, B). Evidence for
322 threshold-like relationships between temperature and either NRI or PSV was weak at best; the
323 most non-linear relationship for each is shown in Fig. S2. However, all significantly clustered
324 communities (i.e. those forest plots with NRI > 1.96, the critical Z-score for significance at $P =$
325 0.025 in a one-tail test) experience minimum temperatures below freezing, most well below
326 freezing (Fig. S2A).

327 There was little evidence for species in more water-stressed forest plots being more
328 closely related (see Table 1, prediction 4a). Mean annual precipitation did correlate positively
329 with standardized PD (Table 3), but became non-significant when minimum temperature was
330 accounted for ($P=0.58$; multiple regression with standardized PD as response, minimum
331 temperature and its square fit as covariates, $N=36$). Further, standardized PD was uncorrelated
332 with warmest-quarter precipitation and actually positively correlated with water deficit (though
333 only marginally significant; Table 3). Relationships between water variables and both NRI and PSV
334 were mostly non-significant or weak (Table 3); neither NRI nor PSV correlated significantly with
335 the most direct measure of water stress, annual water deficit, in contradiction to prediction 4b.

336 For species richness, relationships with water variables were stronger, but still weaker
337 than with temperature variables (Tables 2, 3), and importantly the correlation with water deficit
338 was not significant. Of the water variables, mean annual precipitation was the strongest correlate
339 of species richness, but was also strongly correlated with minimum temperature (Table 3) and
340 only uniquely accounted for 1.6% of the variance in species richness in partial regression (data

341 not shown). Partitioning the species-richness variance between that accounted for by minimum
342 temperature (quadratic) and the water-stress variables, annual water deficit was not significant
343 ($P=0.175$). Warmest-quarter precipitation correlated quite strongly with species richness (Table
344 3), accounting for 45% of the variance, almost all of which overlapped with minimum
345 temperature (Fig. 4A), in line with prediction 4c. Similarly, all the variance in PSV^2 that warmest-
346 quarter precipitation could account for overlapped with minimum temperature (no significant
347 independent contribution). In contrast, for NRI, both water-stress variables were significant in
348 the variance partitioning, together accounting for 9% of the variance in NRI, none of which was
349 shared with minimum temperature (Fig. 4B). Here, the warmest-quarter precipitation had a
350 positive partial correlation with NRI—rather surprisingly in the same direction (positive
351 correlation with NRI) as water deficit. In the path analysis, none of the water-stress variables
352 added significantly to the models shown (Figs 5, S4).

353 Predictions 5a–c (Table 1) concern the amount of shared, and unique, explained variance
354 between evolutionary and climatic (ecological) variables. We tested these predictions using
355 partial regressions (Figs 4C, S3) and by comparing the direct and indirect effects on species
356 richness as modelled in path analysis (Figs 5, S4). Overall explained variance was high (84–90%),
357 but in the partial regressions the variables measuring evolutionary history (NRI and PSV) uniquely
358 accounted for very little (1–3%). Shared explained variance always exceeded 50% of the total
359 variance, and the unique contribution of the climate variables was approximately one third of the
360 total. Similarly, in each path analysis, the direct effects of the evolutionary history variables were
361 weak, though they were significant, while the direct effect of minimum temperature was strong

362 (Figs 5, S4). The indirect effect of climate, routed through evolutionary history, was also quite
363 strong.

364

365 **Discussion**

366 Minimum temperature appeared to primarily control tree species richness, via both a threshold-
367 like freezing effect and a linear relationship in climates without freezing. This one climatic
368 variable accounted for 84% of the variation in species richness. Adding variables measuring
369 evolutionary history (NRI and PSV) and/or water surplus (August) raised this only slightly (to 87–
370 90%; Figs 4–5, Appendix S2), but more than half of the total variance was shared between
371 climate and evolutionary history. Thus, around two thirds of the climate–species richness
372 correlation may be attributable to niche conservatism. The core predictions of the tropical
373 conservatism hypothesis (TCH) were all met (predictions 1a–c and 5a, Table 1), while our findings
374 also indicate an important direct role of minimum temperature (predictions 5b–c not met).

375 The strongest models involved a quadratic relationship between minimum temperature
376 and species richness, in which species richness was very low when minimum temperature was
377 below about -10°C, rapidly increasing at higher minimum temperatures. Minimum temperature
378 could also account for much of the variation in NRI and PSV. These results are consistent with the
379 freezing tolerance TCH (predictions 3a–c), and also with the chilling tolerance version of the
380 continuous TCH (prediction 2a but not 2b). Water variables tended not to add much explanatory
381 power to any of these models, in these mostly mesic forest plots, and overall there was little
382 support for water-stress conservatism (predictions 4a–c).

383 Before proceeding, we note that our R^2 values are very high for fine-grained plot data
384 (Field *et al.*, 2009). Concern exists that very strong spurious relationships between richness,
385 climate and phylogenetic metrics can result from repeated co-occurrences of species across plots
386 (B.A. Hawkins, pers. comm.). On average, each species occurred in only 3.8 of our 57 plots (mean:
387 3.79, standard deviation: 3.89), so we consider this potential problem to be minimal in our
388 analysis.

389

390 *Tropical conservatism (predictions 1–3)*

391 Consistent with the TCH, minimum temperature outperformed other temperature variables that
392 were not excessively co-linear with it, in accounting for species richness. Similarly, Wang *et al.*
393 (2011), found that species richness covaried more with minimum temperature than their other
394 five temperature-related variables in 2500-km² cells across China—accounting for 10% more of
395 the variation (69%) than mean annual temperature (59%). Thus, the two studies, focusing on very
396 different spatial scales, are consistent with each other and with the notion that freezing
397 tolerance is important in structuring species richness patterns (Latham & Ricklefs, 1993; Wiens &
398 Donoghue, 2004)—but also with any limitation associated with minimum temperatures, such as
399 chilling tolerance. At approximately the same scale (grain and latitudinal extent) as our study,
400 Hawkins *et al.* (2014) examined TCH predictions for clade age of angiosperm tree species in forest
401 plots in the USA. They found clade age correlated more strongly with minimum temperature than
402 mean or maximum temperature, and it correlated very strongly with cold tolerance. Taken
403 together, these findings support the notion that the TCH can account for a considerable part of
404 the relationship between climate and tree species richness and composition at the plot level.

405 We found evidence for threshold-like behaviour in the relationship between minimum
406 temperature and species richness (Fig. 3A): above minimum temperature values of about -5°C ,
407 species richness values were much higher than below -15°C (unfortunately we had no data
408 between these two values)—consistent with the fact that water containing solutes freezes at
409 slightly lower temperatures than 0°C . Above -5°C , the relationship was continuous (near-linear;
410 Fig.3A), suggesting that freezing tolerance is not the only temperature-related effect on species
411 richness, and that a continuous, positive relationship with temperature exists—superimposed on
412 a threshold. Further research should be focused on this. Minimum temperature linearly related
413 to both NRI and PSV above -5°C , with no evidence for thresholds. Overall, then, while our results
414 are consistent with freezing tolerance as an important structuring force in tree assemblages, they
415 also emphasize a more continuous effect of (minimum) temperature.

416

417 *Water-stress conservatism (predictions 4)*

418 Water variables generally added little to minimum temperature in accounting for species
419 richness, NRI or PSV (Table 3; Figs. 4–5, see also Figs. S3–S4 in Appendix S2). The desiccation-
420 related link between cold tolerance and drought tolerance (see Introduction) was expected to
421 lead to shared explained variance between minimum temperature and water-stress variables
422 (prediction 4c). However, water deficit was not even significantly correlated with species richness,
423 NRI or PSV (Table 3). Overall, we found no compelling evidence for trade-offs or correlations
424 among niche axes within niche conservatism. Our study forests were mostly mesic, though
425 annual water deficit ranged up to 150 mm and 9 of the 57 plots had 5 or 6 months of water
426 deficit; these relatively water-stressed plots did not have high residuals from fits with minimum

427 temperature, suggesting little effect of water stress. Further, the water variable adding most to
428 minimum temperature in accounting for both species richness and NRI was a measure of summer
429 water surplus (Appendix S2), not water stress.

430 Putting our results together with others from Asia and the New World, we find little
431 evidence for water-stress conservatism being a strong factor in determining the species richness
432 and composition of angiosperm trees at continental extents. Wang *et al.* (2011), analyzing a
433 gradient from deserts to tropical rainforests in China, found that minimum temperature
434 accounted for 9% more of the variation in species richness than did the best water-related
435 variable. Hawkins *et al.* (2014) found that minimum temperature was a much stronger predictor
436 of clade age of angiosperm tree species in USA forest plots than annual precipitation,
437 precipitation of the driest or warmest quarters, or soil moisture. Moles *et al.* (2014) concluded
438 that plant traits correlated more strongly with mean annual temperature than mean annual
439 precipitation. We interpret these results as consistent with ideas of resource-based increase in
440 the capacity to support more species (e.g. Wright, 1983; Currie & Paquin, 1987; Lavers & Field,
441 2006). Additional research, focusing on more water-stressed areas, is needed to investigate this
442 further.

443

444 *Beyond niche conservatism (predictions 5)*

445 The path analyses (Figs 5, S4) suggest some variance in species richness is due to direct effects of
446 evolutionary history on species richness. This is consistent with the idea that current climate
447 sorts species according to tolerances built up over their evolutionary history, these phylogenetic
448 patterns in turn partly determining species richness (Wiens & Donoghue, 2004). It is not clear

449 from the various forms of niche conservatism hypothesis why (minimum) temperature should
450 correlate so much less strongly with NRI and PSV than with species richness—the opposite to
451 Qian *et al.* (2015), who found minimum temperature correlated much more strongly with PSV
452 than species richness or NRI for North American angiosperm trees in 1° grid cells. The necessarily
453 imperfect correlation between current minimum temperature and past minimum temperature
454 may be part of the explanation. Regardless, a substantial proportion of the variation in species
455 richness was accounted for by minimum temperature directly, with no apparent connection to
456 evolutionary history. Thus, at most, niche conservatism explains only part of the species
457 richness–climate correlation. Further, Boucher-Lalonde *et al.* (2014) found that, while bird
458 species richness in 10,000-km² grid cells in the Americas seasonally tracks environment,
459 individual species’ seasonal geographical distributions do not—implying minimal role for niche
460 conservatism in accounting for species richness patterns. Clearly, niche conservatism can only be
461 part of the explanation for species-richness patterns (Wiens & Graham, 2005).

462 Algar *et al.* (2009, their Fig. 3) and Qian *et al.* (2015, their Fig. 2) both used path analysis to
463 separate direct effects of climate on species richness from indirect effects via evolutionary
464 history. They drew opposing conclusions: Algar *et al.* (2009) found minimal direct effects of
465 evolutionary history, while Qian *et al.* found strong ones. Our parallel analyses (Figs S3A, S4A)
466 produced results intermediate between the two, while suggesting a possible freezing-related
467 threshold. It is likely that the balance of direct current climate and evolutionary history effects in
468 explaining species richness and its patterning varies with taxon, scale and study region.

469 Absolute numbers of species should be differentiated from spatial species-richness
470 patterns. In two regions with the same richness–temperature correlation, the number of species

471 at a given temperature may be much higher in one region than the other (Latham & Ricklefs,
472 1993). Although our study is limited to one region, the distinction is important because it affects
473 possible explanations for direct effects of climate on species richness. One possibility invokes
474 carrying capacity for species richness (e.g. Brown, 2014), perhaps set by productivity or
475 combinations of resource states (Lavers & Field, 2006). Although the carrying capacities may not
476 be absolute (Etienne *et al.*, 2012), such explanations require better understanding of why
477 carrying capacities are apparently so different in different parts of the world with very similar
478 climates.

479 Other candidates exist for explaining direct effect of current climate on species richness
480 without involving (deep-time) evolutionary history. Climate may affect dispersal and its balance
481 with ecological specialization (Jocque *et al.*, 2010), for example. Another interesting possibility is
482 that climate determines stochastic immigration and extinction rates (Boucher-Lalonde *et al.*,
483 2012). Evolutionary history may have resulted in different-sized species pools in different
484 biogeographical realms, and, if rates of immigration to (and/or local extinction within) areas
485 within these realms are modified by climate, then richness–climate correlations may emerge that
486 result directly from climate (Boucher-Lalonde *et al.*, 2014). The degree to which these
487 correlations are modified by local environmental filtering (e.g. Qiao *et al.*, 2015) based on
488 conserved niches may vary with scale, taxon and study region.

489

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495

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615 **SUPPORTING INFORMATION**

616 Additional Supporting Information may be found in the online version of this article:

617

618 Appendix S1 Map showing where the 57 forest plots used in the present study were sampled.

619 Appendix S2 Additional analyses and results.

620 Appendix S3 Environmental variables obtained and their sources.

621

622 **BIOSKETCHES**

623 **Hong Qian's** research is multidisciplinary and particularly lies at the interface of ecology and

624 biogeography (www.researchgate.net/profile/Hong_Qian3).

625 **Richard Field's** main interests are in biodiversity patterns, conservation biogeography

626 (particularly with reference to tropical rainforests) and island biogeography.

627

628 H.Q. and R.F. conceived the ideas, conducted most of the statistical analyses, and wrote the

629 paper. S.C. collected the plant data. Both J.Z. conducted the phylogenetic analyses. All authors

630 contributed to revisions.

631

632 Editor: Peter Linder

633

634 **Tables**

635 Table 1. Specific predictions tested herein. The predictions are grouped by numbers
 636 corresponding to the hypotheses or debate investigated, subdivided by letters into a set of
 637 specific predictions for each. ‘TCH’ = tropical conservatism hypothesis; ‘PSV’ = phylogenetic
 638 species variability; ‘NRI’ = net relatedness index; ‘minimum temperature’ = minimum
 639 temperature of the coldest month.
 640

Hypothesis or debate	Predictions
1. TCH (core predictions)	1a. Species in forest plots with lower temperatures are more closely related (i.e. phylogenetically clustered). 1b. Species richness correlates strongly with PSV (positively) and NRI (negatively). 1c. Species richness is lower in colder climates.
2. Continuous TCH	2a. Continuous bivariate relationships between temperature variables and (i) species richness, (ii) PSV, (iii) NRI. 2b. Minimum temperature no more correlated with species richness, PSV or NRI than other temperature variables. [Not true for the chilling tolerance version of the hypothesis.]
3. Freezing tolerance (threshold) TCH	3a. Species richness, PSV and NRI correlate more strongly with minimum temperature than with other temperature variables. [Also true for chilling tolerance version of the continuous TCH.] 3b. Minimum temperature has a threshold-like relationship with species richness, PSV and NRI. 3c. Threshold-like relationships with species richness, PSV and NRI are less clear for other temperature variables than for minimum temperature.
4. Water-stress conservatism	4a. Species in more water-stressed forest plots are more closely related. 4b. Water stress correlates negatively with species richness and PSV, and positively with NRI. 4c. Water stress overlaps with minimum temperature in accounting for variation in species richness, PSV and NRI.
5. Evolutionary history vs other mechanisms for species richness–current climate correlations	5a. Evolutionary history has strong direct effects on species richness. 5b. Current climate explains little additional variation in species richness once evolutionary history is accounted for. 5c. Current climate has strong indirect effects on species richness, routed through evolutionary history, and weak direct effects.

641

642 Table 2. Pearson's correlation coefficients among species richness (SR), standardized
 643 phylogenetic diversity (PD_{std}), net relatedness index (NRI), phylogenetic species variability (PSV,
 644 transformed by being squared) and the five temperature (or related) variables analyzed: mean
 645 annual temperature (MeanT), mean annual potential evapotranspiration (PET), temperature
 646 seasonality (T_{seas}), maximum temperature of the warmest month (MaxT) and minimum
 647 temperature of the coldest month (MinT). N = 57 except correlations involving PD_{std}, where N =
 648 36. $P < 0.001$ for all the relationships shown.
 649

	SR	PD _{std}	NRI	PSV ²	MeanT	PET	T _{seas}	MaxT
PD _{std}	0.723 ^a							
NRI	-0.650 ^b	-0.813						
PSV ²	0.742	0.879	-0.869					
MeanT	0.893 ^b	0.816	-0.757 ^b	0.859				
PET	0.859	0.786 ^b	-0.737	0.871 ^b	0.950			
T _{seas}	-0.921 ^b	-0.820	0.724 ^b	-0.811	-0.962	-0.864		
MaxT	0.655	0.577	-0.659	0.739	0.826	0.880	-0.646	
MinT	0.917 ^b	0.838	-0.759 ^b	0.854	0.991	0.912 ^c	-0.985	0.759

650 ^a When correlated with log(SR), $r = 0.812$

651 ^b Quadratic fit

652 ^c When modelled as quadratic with MinT + MinT² as explanatory, (multiple) $r = 0.968$

653

654

655 Table 3. Pearson's correlation coefficients among species richness (SR), standardized
 656 phylogenetic diversity (PD_{std}), net relatedness index (NRI), phylogenetic species variability (PSV,
 657 transformed by being squared) and the water-related variables analyzed: annual water deficit
 658 (Water def.), precipitation of the warmest quarter ($Precip_{warm}$), the surplus of precipitation over
 659 potential evapotranspiration in August (Sur_{Aug}) and mean annual precipitation ($Precip_{annual}$).
 660 Minimum temperature of the coldest month (MinT), as the most important temperature variable
 661 (Tables 1,2) is included to indicate the degree of correlation between temperature and water
 662 variables. N = 57 except correlations involving PD_{std} , where N = 36. Non-significant relationships
 663 ($P > 0.05$) are indicated by 'ns'; $P < 0.001$ for all other relationships shown, except where
 664 otherwise indicated.
 665

	SR	PD_{std}	NRI	PSV ²	Water def.	$Precip_{warm}$	$Surplus_{Aug}$	$Precip_{annual}$
PD_{std}	0.723 ^a							
NRI	-0.650 ^b	-0.813						
PSV ²	0.742	0.879	-0.869					
Water def.	ns	0.338 ^d	ns	ns				
$Precip_{warm}$	0.674 ^b	ns	ns	0.521	-0.357 ^e			
$Surplus_{Aug}$	0.415	ns	ns	ns	ns	0.506		
$Precip_{annual}$	0.814 ^c	0.655	-0.557	0.762	ns	0.848	0.283 ^f	
MinT	0.917 ^b	0.838	-0.759 ^b	0.854	ns	0.579	ns	0.855

666 ^a When correlated with $\log(SR)$, $r = 0.812$

667 ^b Quadratic fit

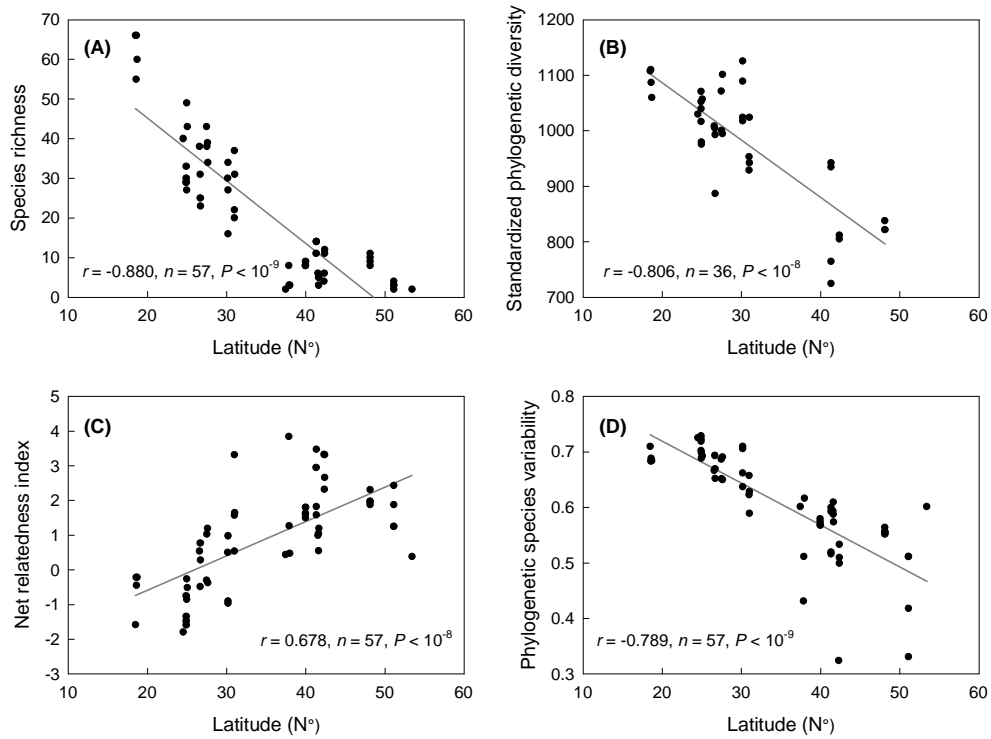
668 ^c When correlated with $\log(SR)$, $r = 0.882$

669 ^d $P = 0.043$

670 ^e $P = 0.007$

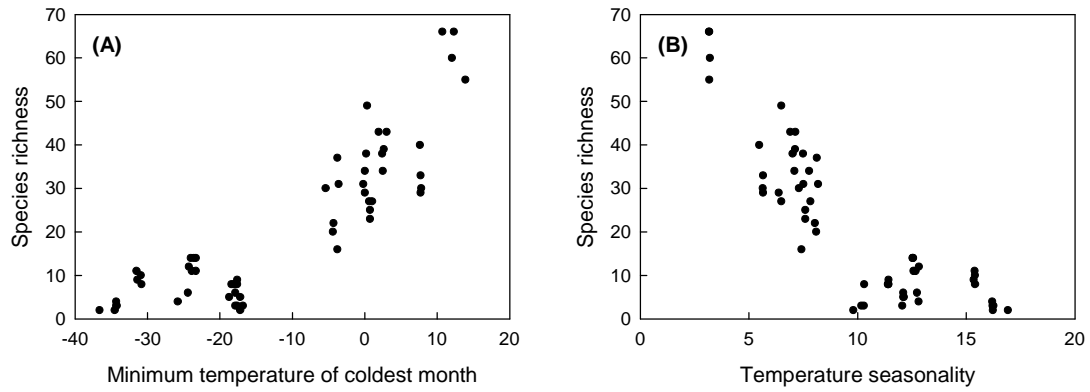
671 ^f $P = 0.033$

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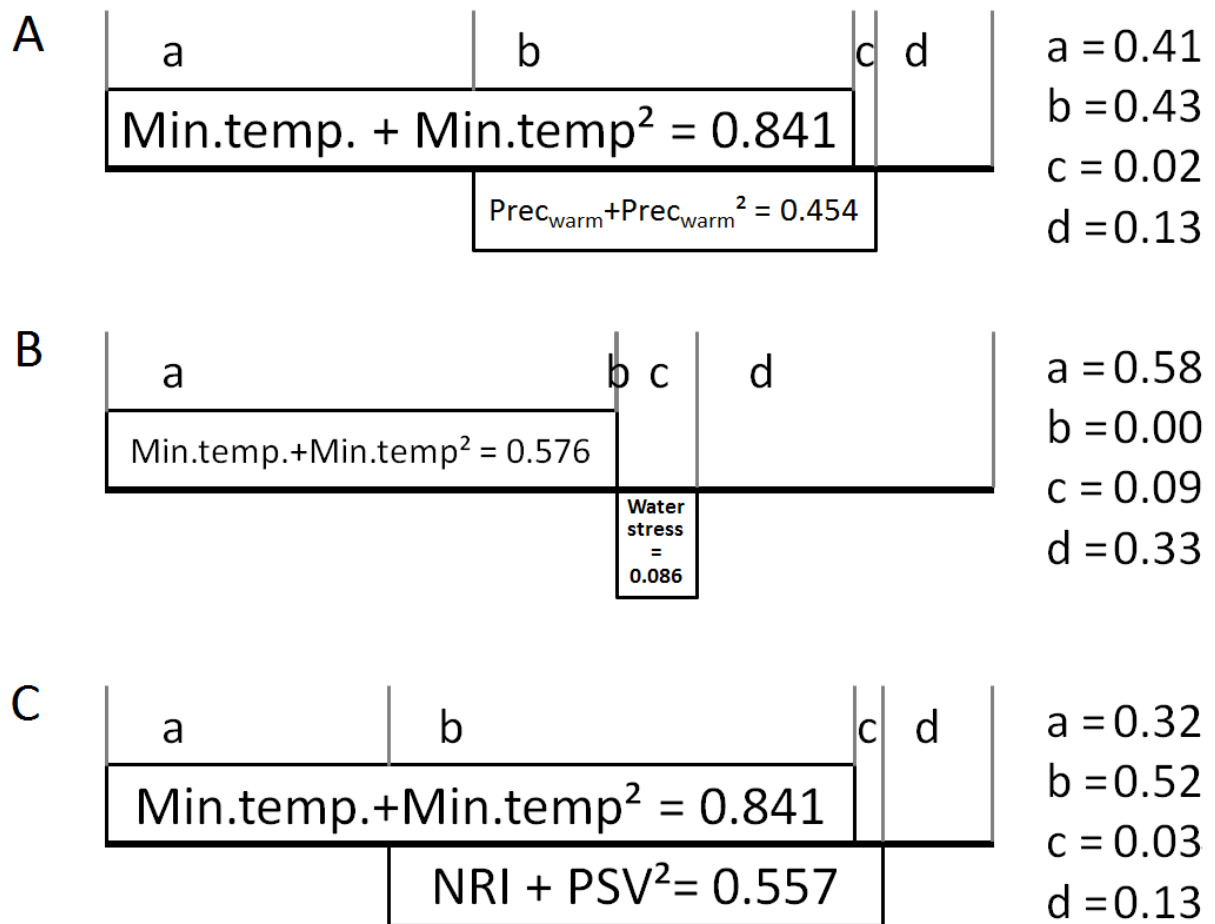
682
 683 Figure 2 Latitudinal trends in (A) species richness, (B) standardized phylogenetic diversity, (C) net
 684 relatedness index and (D) phylogenetic species variability for the angiosperm tree communities
 685 examined in this study.
 686

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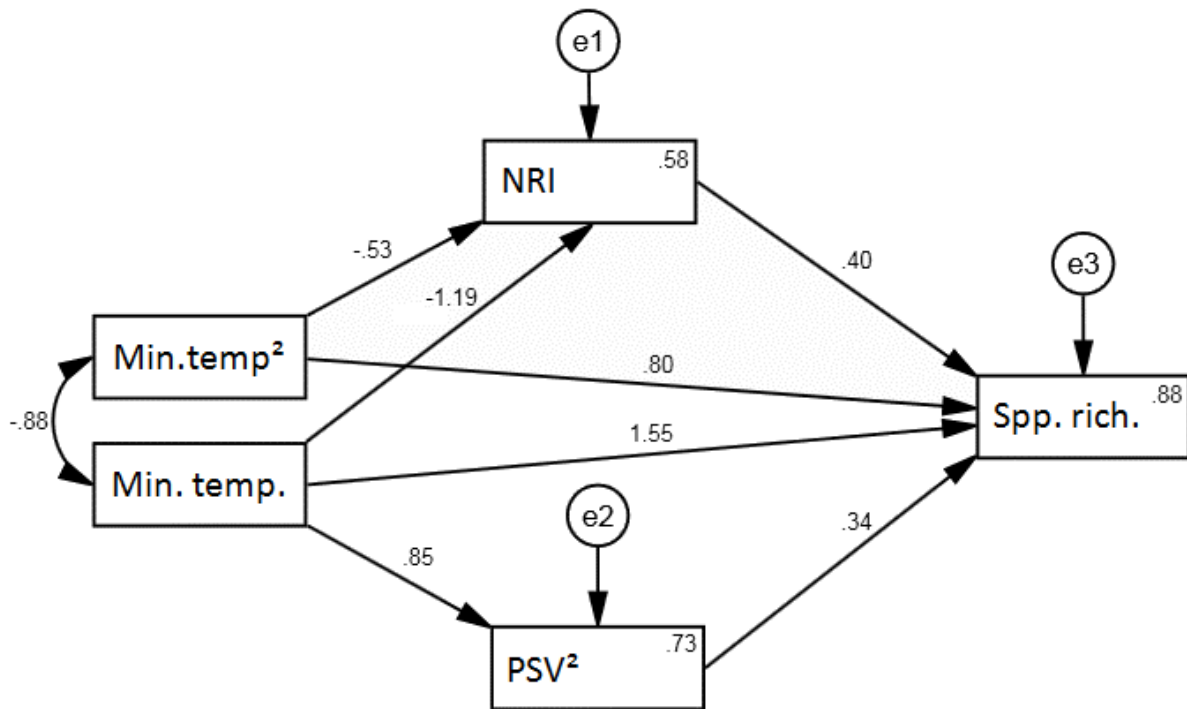


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Figure 3 Evidence regarding threshold-like behaviour in the relationships between species richness and (A) minimum temperature and (B) temperature seasonality. In both graphs, N = 57 forest plots.



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 694
 695 Figure 4 Partial regression results—partitioning the variance: (A) in species richness between
 696 temperature (above the thick line) and water-stress (below the line) variables; (B) in NRI between
 697 temperature and water-stress variables; (C) in species richness between climatic and
 698 evolutionary variables, where climate is represented only by minimum temperature. In each case,
 699 the variance in the response variable is partitioned into four portions: (a) uniquely accounted for
 700 by variable set 1 (above the thick line); (b) accounted for jointly by variable sets 1 and 2; (c)
 701 uniquely accounted for by variable set 2 (below the thick line); and (d) unexplained variance.
 702 Explanatory variables are ‘Min.temp.’ = minimum temperature of the coldest month, ‘Prec_{warm}’ =
 703 warmest-quarter precipitation, ‘water stress’ = both Prec_{warm} and annual water deficit, ‘NRI’ = net
 704 relatedness index and ‘PSV’ = phylogenetic species variability.
 705
 706



707
 708
 709 Figure 5 Structural equation model examining the influence on species richness ('Spp. Rich.';
 710 untransformed) of climatic and evolutionary variables, where climate is represented only by
 711 minimum temperature ('Min. temp.') and evolutionary history is represented by net relatedness
 712 index ('NRI') and phylogenetic species variability ('PSV'; transformed by squaring it). Minimum
 713 temperature is modelled as having a quadratic relationship with NRI and species richness but a
 714 linear relationship with PSV². For direct effects (single-headed arrows), values are standardized
 715 partial regression coefficients; non-significant direct effects were removed. For double-headed
 716 arrows (between exogenous variables), values are covariances. For endogenous variables (with
 717 error terms), the values given in their top-right corners are R²s showing the proportion their
 718 variation accounted for.
 719