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# 1 Spatio-temporal climate change contributes to latitudinal 2 diversity gradients

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## 18 19 20 **Abstract** 21

22 The latitudinal diversity gradient (LDG), in which the number of species increases from the  
23 poles to the Equator, ranks among the broadest and most notable biodiversity patterns on  
24 Earth. The pattern of species-rich Tropics relative to species-poor temperate areas has been  
25 recognized for well over a century, but generative mechanisms are still debated vigorously.  
26 We use simulations to test whether spatio-temporal climatic changes could generate large-  
27 scale patterns of biodiversity as a function of only three biological processes—speciation,  
28 extinction, and dispersal—omitting adaptive niche evolution, diversity-dependence, and

29 coexistence limits. In our simulations, speciation resulted from range disjunctions, whereas  
30 extinction occurred when no suitable sites were accessible to species. Simulations generated  
31 clear LDGs that closely match empirical LDGs for three major vertebrate groups. Higher  
32 tropical diversity primarily resulted from higher low-latitude speciation, driven by spatio-  
33 temporal variation in precipitation rather than in temperature. This suggests that spatio-  
34 temporal changes in low-latitude precipitation prompted geographic range disjunctions over  
35 Earth history, leading to high rates of allopatric speciation that contributed to LDGs. Overall,  
36 we show that major global biodiversity patterns can derive from interactions of species'  
37 niches (fixed *a priori* in our simulations) with dynamic climate across complex, existing  
38 landscapes, without invoking biotic interactions or niche-related adaptations.

39  
40

## 41 42 **Introduction**

43  
44 As the broadest and most notable biodiversity pattern known, the latitudinal diversity  
45 gradient (LDG) ranks amongst the most striking features of life on Earth<sup>1</sup>. The LDG has been  
46 observed in both terrestrial<sup>2, 3</sup> and marine<sup>4, 5</sup> realms, in plants<sup>6, 7</sup> and animals<sup>8, 9, 10</sup>, and to  
47 varying degrees throughout geological time<sup>11, 12, 13</sup>. However, despite over a century of study  
48 and analysis, consensus on causal mechanisms has yet to be reached<sup>1, 3, 14, 15, 16</sup>.

49 In the simplest sense, LDGs can be explained *only* by particular combinations of  
50 differential speciation rates (Tropics as a cradle; <sup>17, 18, 19</sup>), extinction rates (Tropics as a  
51 museum; <sup>18, 20, 21</sup>), and/or dispersal rates into the Tropics<sup>22, 23</sup>. The causal mechanisms behind  
52 such differential rates<sup>8, 10, 15, 24</sup>, however, remain uncertain. Although over 40 ecological and  
53 evolutionary explanations have been proposed<sup>1, 14, 15, 25</sup>, most researchers agree that a near-  
54 ubiquitous pattern should have a consistent mechanistic explanation applicable across  
55 different life histories and habitats<sup>26</sup>.

56           Here, we explore whether spatio-temporal climate dynamics can produce elevated  
57 diversity at low latitudes, offering a simple explanation for LDGs. We propose that  
58 fluctuating climate conditions yield higher rates of range fragmentation at low latitudes  
59 compared to high latitudes<sup>27, 28, 29, 30, 31</sup>. Range fragmentation isolates populations, which  
60 results in allopatric speciation if populations remain separated for sufficiently-long periods of  
61 time. Isolation and speciation may be facilitated by species' inability to adapt quickly to  
62 changing climatic conditions<sup>23, 32, 33, 34, 35, 36</sup> (Fig. 1). Our specific hypothesis, then, is that  
63 spatio-temporal dynamics of climate change generate higher rates of allopatric speciation at  
64 low latitudes, contributing to LDGs.

65           We follow recent work<sup>22, 28, 29, 31, 37, 38, 39</sup> to extend process-based simulations to  
66 terrestrial areas globally<sup>40, 41</sup>. Rangel et al.<sup>29</sup> showed that such simulations can replicate many  
67 real-world biodiversity patterns, and tested the role of orographic features such as the Andes  
68 in structuring biodiversity spatially. We diverge from that work<sup>29</sup> by specifying in our  
69 simulations only two species traits—niche breadth and dispersal ability—and incorporating  
70 only influences of the abiotic environment, without invoking additional processes such as  
71 biotic interactions or niche evolution<sup>9, 23, 32, 42</sup>. These simplifying assumptions were made to  
72 explore the sufficiency of abiotic processes in explaining observed biodiversity patterns<sup>26</sup>.

73           Using process-based, spatially- and temporally-explicit simulations<sup>40, 41, 43</sup> from the  
74 Eemian (last interglacial) to present, we recorded the spatial pattern of diversity generated at  
75 the end of each simulation (Table 1). We additionally noted the location and frequency of the  
76 speciation, extinction, and dispersal events that generated this biodiversity, to explore their  
77 relative contributions to LDGs and the potential climatic drivers behind these  
78 macroevolutionary dynamics.

79

## 80 **Results**

81 *Latitudinal diversity gradients*

82           Mean latitudinal diversity was quantified by selecting one simulation from each 1°  
83 latitudinal band in a series of 100 bootstrap replicates. As a consequence, global diversity  
84 was initially equivalent across latitudes (i.e., one ‘species’ per latitudinal band) at the start of  
85 simulations. However, when diversity was quantified from selected seeds after simulations  
86 completed, species diversity was maximum at the Equator and lower at higher latitudes (Fig.  
87 2). This pattern was most pronounced among species with narrow niches and poor dispersal  
88 abilities, and under climate scenarios in which ice sheets were included as biogeographic  
89 constraints (Fig. 2; Figs. S1–4). Species with better dispersal ability and/or broader niches  
90 showed flattened latitudinal diversity curves, and we even noted a middle-latitude diversity  
91 bump in scenarios in which ice sheets were not considered (Figs. S1, S5 & S6). Scaling  
92 species numbers to area available in latitudinal bands steepened the LDGs (Figs. S7–12) and  
93 removed the higher-latitude peaks for species with broad ecological niches (Figs. S9 & S10).

94           Simulated New World diversity provided much of the elevated low-latitude diversity  
95 for the global LDG. Higher tropical diversity was observed under all scenarios in the New  
96 World (Figs. S13–15), though the most dramatic LDG resulted from species with poor  
97 dispersal abilities and narrow niche breadths (Fig. S15). Europe and Africa showed more  
98 dampened LDGs, with higher tropical diversity only among species with poor dispersal  
99 abilities and/or narrow niche breadths. Asia and Australia were characterized by reverse  
100 gradients in all scenarios, with higher diversity at higher latitudes. Scaling numbers of species  
101 on a per-unit-area basis in latitudinal bands resulted in yet-steeper New World diversity  
102 gradients (Figs. S16–18), and higher-latitude diversity peaks in broad-niched species were  
103 dampened or eliminated.

104           To evaluate the role of climate change *versus* time-independent spatial climate  
105 variation alone, we ran a series of simulations in which climate was held constant. These

106 simulations did not produce low-latitude peaks in diversity (Figs. S19–21). Results therefore  
107 underline the key role of spatial and temporal variation in climate in generating LDGs in our  
108 simulations.

109

#### 110 *Rates of speciation and extinction*

111 Speciation rates showed latitudinal patterns that were dependent on interactions  
112 between niche breadth and dispersal ability (Fig. 3, Figs. S22–24). At low latitudes,  
113 speciation rates were higher for species with narrow niche breadths, regardless of dispersal  
114 ability (Fig. 3, Fig. S23); species with broad niches, regardless of dispersal ability, showed  
115 the opposite pattern (Fig. S24). This niche-breadth dependency was consistent across climate  
116 scenarios. As expected, inclusion of ice sheets dampened high-latitude speciation rates.  
117 Scaling to area available in latitudinal bands resulted in significantly higher tropical  
118 speciation rates in all niche and dispersal combinations (Figs. S25–27).

119 Extinction rates were either elevated at high latitudes or similar across latitudes, in all  
120 combinations of niche breadth, dispersal ability, and climate scenario (Fig. 3, Figs. S28–30).  
121 The only scenario in which extinction rates were higher at lower latitudes (0–8°S latitude)  
122 was for species with narrow niche breadth and poor dispersal ability (Fig. S30). Scaling to  
123 area available in latitudinal bands did not change overall patterns of extinction rates (Figs.  
124 S31–33). Speciation outpaced extinction in the simulations, resulting in increased diversity  
125 over time (Fig. S34).

126

#### 127 *Geographic patterns*

128 Geographic patterns of diversity, speciation, and extinction were examined globally  
129 on a cell-by-cell basis. We found high levels of diversity equatorially in Brazil and central  
130 Africa in all scenarios (Fig. 4, Fig. S35). Southeast Asia, however, was more depauperate.

131 Simulations returned hotspots of diversity at high latitudes in northern Europe and Asia for  
132 broad-niched species (Fig. S35). Diversity hotspots were caused primarily by elevated  
133 speciation: high speciation rates coincided with areas of high diversity, whereas extinction  
134 rates were low and diffuse throughout terrestrial areas globally (Fig. S35).

135

### 136 *Dispersal dynamics*

137 We documented the frequency of shifts from temperate to tropical biomes and *vice*  
138 *versa* to test the role of dispersal in generating diversity gradients<sup>19, 44</sup>. More lineages  
139 dispersed from the Tropics to temperate regions than *vice versa* in our simulations, even  
140 when holding the number of species considered constant in each biome<sup>45</sup>. Results were  
141 consistent regardless of whether we counted numbers of initial lineages (Fig. 5; Figs. S36–  
142 38), total numbers of species dispersing from each initial lineage (Figs. S39–41), or the  
143 number of dispersal events from a standardized number of species in each biome (Figs. S42–  
144 44). The dominance of tropical-to-temperate dispersal over temperate-to-tropical dispersal  
145 was statistically significant ( $P < 0.001$ ; one-tailed Mann Whitney  $U$ -tests) in all scenarios.

146

### 147 *Climate dynamics*

148 We assessed temperature and precipitation as potential causal agents in vicariant  
149 events separating populations for a sufficiently-long period to induce speciation. Precipitation  
150 was responsible for most low-latitude speciation events, regardless of niche or dispersal  
151 combination (Fig. 6; Figs. S45–S47). Temperature, however, became an equally-important  
152 driver of speciation around 30–35°N, and a more important driver by around 50–55°N.  
153 Extinction was caused by changes in both temperature and precipitation, although the relative  
154 contribution of temperature was higher at high latitudes (Fig. 6; Figs. S48–S50).

155 Spatio-temporal climate patterns were congruent with the above analyses that  
156 implicate precipitation as the primary driver of elevated low-latitude speciation. The  
157 magnitude of precipitation change was greater at low latitudes over the last 120 Ka, whereas  
158 the magnitude of temperature change was greater at high latitudes over the same time period.  
159 This relationship can be quantified by correlating latitude with the mean standard deviation of  
160 climate change amongst cells within those latitudes over the last 120 Ka; the relationship was  
161 negative for precipitation ( $r = -0.80$ ), but positive for maximum and minimum temperature ( $r$   
162  $= 0.65$  and  $0.83$ , respectively). This pattern indicates that variation in precipitation decreases  
163 with latitude, but variation in both maximum and minimum temperature increases with  
164 latitude.

165 Temporal changes in precipitation were spatially heterogeneous at low latitudes. That  
166 is, some equatorial regions experienced significant change in precipitation over the last 120  
167 Ka, whereas adjacent regions experienced relatively little change. This heterogeneity is  
168 illustrated by significant peaks and troughs in the standard deviation of precipitation values at  
169 low latitudes (Fig. S51a). Conversely, temperature did not fluctuate significantly over the last  
170 120 Ka in equatorial regions, but did change at high latitudes. Unlike precipitation, these  
171 high-latitude temporal fluctuations were not spatially heterogeneous but occurred over  
172 continuous and broad regions (Fig. S51b,c).

173

#### 174 *Comparisons with empirical patterns*

175 We calculated cell-by-cell Pearson correlation coefficients ( $r$ ) between simulated  
176 diversity and empirical diversity for three clades (birds, mammals, amphibians) using  
177 standardized, global diversity maps (Table S1). In most cases, our simulated diversity  
178 patterns correlated positively with diversity patterns for birds, mammals, and amphibians;  
179 negative correlations resulted in only a few cases in simulations considering broad-niched



180 species (Table S1). Strongest correlations were recovered for simulations using species with  
181 narrow niches and poor dispersal abilities ( $r^2 > 0.16$  for mammals). Correspondence between  
182 simulated diversity and bird and mammal diversity was higher than expected based on null  
183 distributions generated by reshuffling simulated diversity values within each latitudinal band  
184 in a series of 100 replicates (Fig. S52 and Table S2). Correlations were weaker than expected  
185 for amphibians when considering species with broad niches and poor dispersal abilities  
186 (Table S2).

187 Simulated diversity was subtracted from empirical diversity on a cell-by-cell basis to  
188 examine regions where simulations over- or under-predicted diversity. Diversity patterns  
189 were replicated closely across broad swaths of global terrestrial regions. However, our  
190 simulations generally tended to under-predict diversity in South America and over-predict  
191 diversity in central Africa (Fig. S53). Europe and Asia tended to be characterized by too-high  
192 simulated diversity for species with broad niches.

193 We quantified similarity between simulated and empirical latitudinal diversity curves  
194 using Fréchet distances, which measures similarity between two curves while considering the  
195 location and ordering of the points along the curves. Simulated latitudinal diversity curves  
196 were remarkably similar to empirical diversity curves, although high-latitude diversity in the  
197 Northern Hemisphere was over-predicted for species with broad niches (Figs. 2; Figs. S5–6).  
198 Simulated diversity curves were most similar to empirical diversity curves when considering  
199 species with narrow niches and poor dispersal abilities, and most dissimilar when considering  
200 species with broad niches regardless of dispersal ability (Table S3). Overall, simulated  
201 diversity curves were most similar to the mammal diversity curve (Fig. 4 and Table S3).  
202 Indeed, we found shorter Fréchet distances between mammals and simulated diversity using  
203 species with narrow niches, than when comparing mammals, birds, and amphibians to each  
204 other. Considering all niche and dispersal combinations together, Fréchet distances from our

205 simulations to mammals or birds were usually no greater than the distance between birds and  
206 amphibians (Table S3), suggesting that the simulations are closely replicating large-scale  
207 attributes of empirical diversity patterns.

208 We also assessed similarity between geographic range-size frequency distributions in  
209 our simulations and those of birds, mammals, and amphibians. As in empirical range-size  
210 frequency distributions<sup>46, 47, 48</sup>, simulated range-size frequency distributions were right-  
211 skewed (Fig. S54). Although range-size frequency distributions were within the same general  
212 magnitude as empirical groups, simulated species tended to have larger geographic ranges.  
213 Consequently, the distribution for simulated species for all niche  $\times$  dispersal  $\times$  climate  
214 scenario combinations differed significantly from empirical distributions based on  
215 Kolmogorov-Smirnov two-sample tests ( $p$ -value  $< 0.001$ ). However, range-size frequency  
216 distributions for empirical distributions also differed significantly ( $p < 0.001$ ) from one  
217 another.

218

## 219 **Discussion**

220 We simulated a world in which the three factors affecting biological diversity—  
221 speciation, extinction, and dispersal—responded only to realistic climate dynamics over the  
222 terrestrial global landscape. Starting from no diversity gradient, the great majority of our  
223 simulations yielded higher diversity at low latitudes, particularly for species with narrow  
224 niches. This result is consistent with previous, independent sets of simulations that employed  
225 similar frameworks for South America<sup>28, 29</sup>. Speciation rates, rather than extinction rates,  
226 were the primary control on these patterns, being markedly elevated in the Tropics, which is  
227 congruent with previous findings that suggest the Tropics as a cradle of biological diversity<sup>10,</sup>  
228 <sup>15, 19, 24, 49</sup>. Dispersal into the Tropics did not contribute significantly to the strength of the  
229 LDG, since species dispersed from lower to higher latitudes at higher rates under all dispersal

230 and niche combinations; in this sense, our simulations supported the ‘out of the Tropics’  
231 model<sup>19, 44, 50</sup>. Given that species diversity scales with area<sup>51, 52</sup>, and that land area is reduced  
232 at lower latitudes, rescaling diversity curves to available area further amplified low-latitude  
233 peaks in diversity for all niche and dispersal scenarios, and eliminated peaks in diversity at  
234 higher latitudes for species with broad niches. Results were not dependent on the presence or  
235 absence of continental ice sheets.

236 Simulated diversity was consistent with the well-documented, empirical patterns of  
237 steeper diversity gradients and higher overall diversity in the New World<sup>2</sup> and in species with  
238 poor dispersal abilities<sup>53</sup>. This outcome is remarkable, since no target diversity pattern was  
239 sought, and we started each simulation with a world with only one species per latitudinal  
240 band. Moreover, simulations replicated the shape of empirical LDG curves with high fidelity,  
241 including a northern latitude diversity drop at  $\sim 20^\circ$  that has been documented in empirical  
242 studies (Fig. 4)<sup>54, 55</sup>, and higher numbers of specialist species at low latitudes<sup>16, 56, 57</sup> (Fig.  
243 S55). Simulated diversity patterns diverged most from those of amphibians, which is  
244 unsurprising, given that amphibians typically have narrow niches and low dispersal potential,  
245 probably lower than that in our simulations<sup>58, 59</sup>. Amphibians possess a mean latitudinal range  
246 of  $\sim 4.2^\circ$ , compared to  $12.4^\circ$ ,  $21.9^\circ$ , and  $22.2^\circ$  for mammals, our aggregate simulations, and  
247 birds, respectively.

248 Our simulated biodiversity patterns and real-world diversity hotspots were similar, at  
249 least at coarse scales, except for Southeast Asia, Australia, and New Guinea (Fig. 4).  
250 Observed differences between simulated and empirical patterns may reflect model  
251 misspecification, or more ancient (pre-Eemian) processes not integrated into our simulations,  
252 such as tectonic changes and environmental perturbations. Geographic range-size frequency  
253 distributions also replicated the right-skewed nature of empirical distributions, except that a  
254 greater proportion of simulated species had larger ranges. This skew is not surprising, since

255 virtual species were accorded relatively broad niches (i.e., 21° and 31°C temperature breadth  
256 for narrow and broad niche species, respectively) that were not limited by biotic interactions.  
257 Larger ranges, however, should not affect interpretations of simulated results or LDG  
258 mechanisms in a systematic fashion. Indeed, reduction in species' range sizes, either from  
259 narrowing tolerance limits or from biotic interactions, may further facilitate climate-driven  
260 tropical range fragmentation and more effective isolation of those range fragments  
261 (increasing speciation potential).

262         Analysis of the spatio-temporal dynamics of precipitation and temperature and their  
263 relationships to speciation and extinction revealed that tropical diversity was primarily a by-  
264 product of precipitation (Fig. 6). Patterns of precipitation are spatially and temporally  
265 heterogeneous at low latitudes (Fig. S51)<sup>60, 61, 62, 63</sup>, and this heterogeneity served to fragment  
266 species' ranges, resulting in isolation and eventual lineage splitting. Extinction, however, was  
267 caused by variation in temperature and precipitation across latitudes, although the relative  
268 contribution of temperature to extinction was higher at high latitudes (Fig. 6). High-latitude  
269 extinction driven by Cenozoic cooling may further sharpen LDGs<sup>10, 27, 64, 65, 66</sup>. This argument  
270 is essentially equivalent to the 'Tropics as older' hypothesis, which proposes that climatic  
271 stability at low latitudes resulted in dampened extinction rates at low latitudes<sup>50, 67, 68</sup>.

272         Diversity peaks were obtained at high latitudes for species with broad niches, with  
273 high rates of extra-tropical speciation driven primarily by spatio-temporal dynamics of  
274 temperature (Fig. 6). Wider and more continuous temperature barriers at high latitudes (Fig.  
275 S51) were able to isolate effectively generalist species, but were less effective at fragmenting  
276 ranges of species with narrow niches. That is, spatio-temporal temperature changes at high  
277 latitudes were not sufficiently patchy to generate range disjunctions for narrow-niched  
278 species, though note that the relative contribution of temperature to speciation was high at  
279 high latitudes for *both* narrow- and broad-niched species.

280           Recent, parallel simulations<sup>29</sup> that also examined the influence of climatic  
281 heterogeneity on diversification concluded that temperature, rather than precipitation, drove  
282 speciation and extinction. Rangel and colleagues<sup>29</sup> examined correlations between mean  
283 annual climate values and mean speciation rates over the South American continent in a time-  
284 series analysis, rather than examining directly the contribution of each climate variable to  
285 speciation and extinction in a mechanistic, per-event and spatially-explicit context as we did  
286 here (see ‘climate dynamics’ Methods section). Employing the correlational methodology of  
287 Rangel et al<sup>29</sup>, we obtain a significant role for precipitation and also for temperature (Table  
288 S4). These divergent patterns may stem from the temporal scale of study (Rangel and  
289 colleagues<sup>29</sup> covered eight glacial-interglacial cycles, whereas our study covered only one),  
290 or the inclusion of different processes.

291           We do not suggest that Eemian (i.e., last glacial cycle) speciation alone is responsible  
292 for the modern LDG. The Earth, of course, was already populated by a rich biota at 120 Ka.  
293 Rather, we hypothesize that interactions between spatio-temporal dynamics of climate, real-  
294 world geography, and species operated similarly on geologic timescales<sup>31, 69, 70</sup>, which could  
295 have contributed to the maintenance of LDGs observed today. This effect would explain the  
296 correspondence of our simulated biodiversity patterns to empirical biodiversity patterns.  
297 Importantly, our hypothesis can be further interrogated as new and more dense climatic data  
298 become available for earlier time periods. Current understanding of paleoclimate dynamics is  
299 that they have fluctuated continuously over various timescales<sup>71, 72, 73</sup>. In our simulations,  
300 spatio-temporal heterogeneity in precipitation at low latitudes generated higher rates of  
301 allopatric speciation. Although this pattern was derived from Late Pleistocene climate  
302 dynamics, low-latitude variability in precipitation has likely occurred throughout much of  
303 Earth history, and has been suggested as a driver of hominin evolution in southeastern  
304 Africa<sup>74</sup>. Atmospheric moisture is a strongly non-linear function of temperature, meaning that

305 small variations in temperature are amplified by the moisture cycle. Consequently, high  
306 variability in precipitation is expected in warm climates, such as the low-latitude Tropics<sup>63</sup>. A  
307 logical corollary, of course, is that during periods of extreme warmth globally, such as the  
308 Late Cretaceous and Early Eocene, precipitation may have been variable everywhere, not  
309 only at low latitudes. Based on our proposed mechanism, then, speciation rates would have  
310 been high across latitudes, providing a process-based explanation for the dampened diversity  
311 gradients often reported for these time periods<sup>12, 13, 75, 76, 77, 78, 79</sup>.

312         Diverse factors have been implicated in producing biodiversity patterns, and  
313 particularly the LDG<sup>1, 14, 15, 25</sup>, and these factors could further enhance and refine spatial  
314 patterns of biodiversity. For example, we did not examine effects of niche evolution<sup>29</sup>, area-  
315 productivity dynamics<sup>80</sup>, increased biotic interactions and competition<sup>29, 64, 81, 82</sup>, diversity-  
316 dependent speciation and extinction processes<sup>8</sup>, or higher energy to accelerate mutation  
317 rates<sup>83</sup> and/or promote species coexistence<sup>84</sup> on biodiversity patterns. Moreover, whilst mid-  
318 domain effects<sup>85</sup> may contribute to LDGs, they did not contribute significantly to our  
319 simulated patterns, because we did not recover diversity gradients in simulations that allowed  
320 virtual species to search and occupy suitable areas, but which invoked no climate change<sup>86</sup>  
321 (Figs. S19–S21).

322         The above discussions lead to reflections on the reality and utility of our simulations.  
323 Our model is simple, but this simplicity was purposeful and explicitly designed. For example,  
324 we invoked no changes in species' niche traits through time or at splitting events. That is, we  
325 assumed niche stability during the lifetime of each lineage simulated. Niche stability and  
326 phylogenetic conservatism are realistic assumptions for the time scale of our analysis<sup>23, 32, 33,</sup>  
327 <sup>34, 35, 36</sup>, and have even been proposed as a mechanism for the modern LDG<sup>9, 23, 32, 42</sup>.  
328 However, evolution in species' niche tolerances does occur over longer time scales and may  
329 additionally enhance the LDG<sup>29</sup>. Furthermore, we invoked no biotic interactions in our

330 simulations, and we considered only a set of trait values for dispersal and niche breadth:  
331 simulations cast in the context of other dispersal and niche traits may show different patterns.  
332 Although biotic interactions could contribute to LDGs<sup>8, 64, 81, 82</sup>, we do not consider them here  
333 for two reasons: (i) to examine the extent to which abiotic factors alone offer a mechanism to  
334 explain observed patterns of diversity; and (ii) because modelled competition was found to  
335 have little effect on resulting geographic patterns of species' richness<sup>29</sup>.

336 We assessed terrestrial realms only, though LDGs are also manifested in marine  
337 environments<sup>4, 22, 87</sup>. Spatio-temporal changes in precipitation, of course, are not directly  
338 applicable to marine LDGs, but the same general mechanism of spatio-temporal climate  
339 dynamics driving allopatric speciation across real-world seascapes could be responsible for  
340 LDGs<sup>22</sup>.

341 Our results may also depend on the relatively coarse spatial grain of the simulations  
342 ( $1^\circ \times 1^\circ$ ), as grain is known to affect species richness patterns<sup>88, 89, 90, 91</sup>. The resolution of our  
343 simulations was constrained by the spatial resolution of climate data available: analyses at  
344 finer scales may produce different results. For example, we did not examine the effect of  
345 topography-driven climate heterogeneity on biodiversity patterns in mountainous regions.  
346 Topographic, and therefore climatic, heterogeneity could further augment LDGs by  
347 prompting allopatric speciation<sup>29</sup>. This mechanism, however, is unlikely to contribute  
348 significantly to global-scale LDG patterns, because topographic heterogeneity is not higher at  
349 low latitudes (Fig. S56); an argument, of course, which assumes that diversity is promoted in  
350 the same way by topographic heterogeneity across latitudes (see <sup>92</sup>). Regardless, the 'climatic  
351 flattening' of mountains caused by the coarse resolution of our climate model data does not  
352 affect interpretation of the importance of climate parameters in driving evolutionary  
353 processes (i.e., precipitation being responsible for low-latitude speciation), since patterns of  
354 heterogeneity in temperature and precipitation are likely to be affected similarly<sup>93</sup>.

355 Finally, it is unavoidable that our simulations are influenced by the availability of  
356 climate data. The climate data we have used represent a full, transient global climate  
357 trajectory from the last interglacial period to present. No other general circulation model  
358 outputs of this nature (i.e., temporally continuous) are available to our knowledge, nor is the  
359 fully-coupled HadCM3 model we have used available for earlier time periods. We eagerly  
360 await the availability of data on transient changes in climate deeper into the Pleistocene and  
361 Pliocene in order to make additional, crucial assessments of the relative roles of Pleistocene  
362 and pre-Pleistocene climate dynamics in generating biological diversity.

363 Our simulations provide quantitative, process-based support for environmental  
364 variability as an underlying mechanism for LDGs, proposed previously in landmark papers<sup>28</sup>,  
365 <sup>29</sup>. Using virtual-world simulations with minimal biological assumptions, we were able to  
366 replicate the shape and strength of the diversity gradient at global and continental scales.  
367 Hence, we show that the spatial implications of climate change across real-world landscapes  
368 can drive the creation of LDGs, under the assumption of static ecological niches. In this  
369 sense, a small number of simple geographic and biological processes are sufficient to explain,  
370 either alone or in tandem with others, the generation and maintenance of a major spatial  
371 pattern of biodiversity.

372

373

## 374 **Methods**

### 375 *Simulations*

376 We used a cellular automaton algorithm to simulate patterns of speciation, extinction,  
377 and dispersal in response to a dynamic climate over the last 120,000 years (Table 1). The  
378 framework builds on previous models<sup>28, 94, 95</sup> to simulate the interaction of virtual species  
379 with spatio-temporal variation in temperature and precipitation. Simulations were initiated



380 under interglacial climatic conditions (Eemian, Late Pleistocene, 120 Ka ago) and run  
381 forward in time to the present-day using current continental configurations (Fig. 4). Each  
382 initial lineage had the potential to go extinct or speciate. Speciation and extinction were  
383 driven by changing climatic conditions: speciation occurred when ranges were fragmented  
384 via isolation of suitable areas for at least 10,000 years (see justification below), and  
385 extinction occurred when all occupied suitable areas were eliminated, and the species was  
386 unsuccessful at colonizing newly-suitable regions. The simulation protocol is outlined in the  
387 Supplementary Materials and is illustrated in Fig. 1. Soft code for the simulation is provided  
388 in Appendix 1.

389         A virtual species began the simulation at a site of origin chosen randomly from within  
390 terrestrial areas globally, which were divided into  $1^{\circ}\times 1^{\circ}$  grid cells (15,254 cells total). Cell  
391 occupation was controlled by species' abiotic tolerances and dispersal ability in relation to  
392 climatic conditions manifested in the cell. The temperature and precipitation values of the  
393 initial starting cell defined the centre of that species' niche. We applied symmetrical  
394 deviations to this point<sup>28, 94</sup> based on two niche breadths (narrow and broad), corresponding  
395 to temperature and precipitation tolerances of 21°C and 31°C and 4 mm/day and 7 mm/day,  
396 respectively. These niche breadths were derived from empirical temperature and precipitation  
397 tolerances of agriculturally-important plant species<sup>96</sup>, in which ~18% of species were  
398 characterised as having 'tropical' distributions. Narrow and broad niche breadths were  
399 defined using the lower and upper quartiles, respectively, of niche breadths in this database<sup>94</sup>.  
400 Representation of species' tolerances (fundamental ecological niches) was limited by the  
401 climatic combinations existing at a given time step, referred to as the existing niche<sup>97</sup>.  
402 Existing niches were further limited by species' ability to access suitable cells, determined by  
403 assigned dispersal ability and initial distributions. Seasonality was considered indirectly in

404 the model because maximum and minimum temperatures differ more markedly at higher  
405 latitudes<sup>98</sup>.

406 Each species was assigned a dispersal function, reflecting its ability to search outside  
407 of its present range for habitable cells. Dispersal in the simulation was stochastic, and  
408 represented the process of exploration, with possible colonization and range expansion; this  
409 definition therefore differs from other definitions of dispersal at local scales (e.g., movements  
410 of individuals). We considered two levels of dispersal ability, both defined by exponential  
411 decay curves of the probability that a species will disperse a certain number of cells. From a  
412 given occupied cell, a species was allowed to search, at maximum, four (good dispersers) or  
413 two (poor dispersers) cells in a single simulation step, corresponding to distances of >400 km  
414 and >200 km, respectively. Species searched for suitable cells simultaneously from all cells  
415 currently occupied, and each cell was assigned a different probability of dispersal. If a  
416 species was allowed to disperse two or more cells in a given time step, they could jump over  
417 unsuitable regions to encounter more spatially remote but suitable cells elsewhere. As such,  
418 dispersal could occur at least occasionally between continents. Dispersal values are provided  
419 in Table S5, based loosely on known dispersal abilities of empirically-derived seed-dispersal  
420 capacities in plants<sup>99, 100</sup>. Considerable uncertainty remains regarding the distances to which  
421 plants are able to disperse and colonize areas<sup>100</sup>. However, restricting most dispersal events to  
422 one (~100 km in size) or no cells per time step (100 years) was considered a close match to  
423 reality, since, for example, models for invasive tree species in South Africa estimate rates of  
424 up to ~700 m·yr<sup>-1</sup><sup>101</sup>.

425 Climatic attributes of individual cells fluctuated through time and resulted in  
426 conditions that were favorable or unfavorable for a species at a given time depending on  
427 whether the cell value fell within the species' climatic niche. Dynamic climate change  
428 trajectories over the last 120 Ka were derived from transient climate simulations using state-

429 of-the-art, coupled atmosphere-ocean-vegetation models (HadCM3) developed at the Hadley  
430 Centre<sup>102</sup>. Three climate parameters constrained species' tolerances: mean monthly maximum  
431 temperature, mean monthly minimum temperature, and mean monthly maximum  
432 precipitation, under three scenarios related to ice sheets (discussed below). Minimum  
433 monthly precipitation is zero for nearly all localities on Earth and was therefore not included  
434 (precipitation, of course, cannot fall below zero). We also considered simulations when  
435 species' tolerances were constrained using mean annual precipitation and mean annual  
436 temperature. Resulting patterns were broadly equivalent to simulations using maximum and  
437 minimum climate layers, and therefore we focus here only on the latter.

438         The HadCM3 climate model was originally developed at the UK Met Office and used  
439 in previous IPCC future climate projections. The version used here has been described and  
440 evaluated by comparison with observational datasets<sup>102</sup>. Simulations were run at 62 time  
441 slices, covering the last 120 Ka, at a frequency of every 1000 years back to 22 Ka, every  
442 2000 years back to 80 Ka, and every 4000 years back to 120 Ka. The climate model was  
443 driven with appropriate boundary conditions for orbital configuration, greenhouse gases  
444 derived from ice core records, and ice-sheet volume and topography/bathymetry derived from  
445 sea level reconstructions (method described in Eriksson et al.<sup>103</sup>). The climate models, which  
446 include interactive vegetation, are described in Singarayer et al<sup>104</sup> and Davies-Barnard et  
447 al<sup>105</sup>. For the purposes of this study, relevant climate outputs were downscaled from 2.50 x  
448 3.75° horizontal resolution to 1° resolution using bicubic interpolation, using the climate  
449 anomaly method so that predicted modelled changes in climate were added (or using the ratio  
450 for precipitation) to an observed present day climatology<sup>62</sup>. This method removes any  
451 systematic bias from the climate model. These data were then interpolated linearly to 100-  
452 year time steps, resulting in 1201 equal-duration time slices for each of three climatic layers  
453 used in the simulation.

454 Simulations were run under three scenarios of ice sheet prevalence: (1) no ice sheet;  
455 (2) ice sheet present; and (3) varying probability of ice. In the ice sheet model, each cell was  
456 assigned a certain percent coverage of ice (from 0 to 100%). In the ‘probability of ice’  
457 scenario, the percent coverage value was used as a probability of elimination of the  
458 populations occupying that cell. In the ‘ice sheet present’ scenario, a cell that became covered  
459 in any percentage of ice resulted in complete elimination of the populations living there. The  
460 ice sheet extent was derived from Davies-Barnard et al.<sup>105</sup>, and was calculated based on the  
461 Ice5G ice sheet reconstruction<sup>106</sup>. Ice sheet extent information is available in 1000-year  
462 intervals from 26–21 Ka and thereafter every 500 years to present. Reconstruction of ice  
463 sheet extent for older periods is difficult, because older evidence has been eroded by ice  
464 during the glacial maximum. Consequently, we approximated ice sheet extent prior to 26 Ka  
465 by matching sea level. For instance, observed sea level depression is estimated to be 50 m at  
466 75 Ka and also at 12 Ka. Hence, we allocated the same ice mask for both periods. These ice  
467 masks were then interpolated linearly in both space and time to produce maps every 100  
468 years. Ice sheet extent and mean global value for each time step and parameter over the last  
469 120 Ka are provided in Fig. S57.

470 In all simulations, species occupied immediately any suitable cell that they  
471 encountered via dispersal, and remained there until the cell became unsuitable due to climate  
472 change. This process imitates natural range dynamics of species, which are thought often to  
473 begin small<sup>107, 108</sup>. Climate change modified distributions of suitable cells uniquely for each  
474 species (i.e., dependent on niche dimensions); species tracked suitable cells through these  
475 changes as a function of their dispersal ability. One consequence of climate change was the  
476 fragmentation of suitable areas, resulting in either newly-isolated populations or elimination  
477 of all occupied suitable areas (Fig. 1). The former resulted in speciation if populations were  
478 isolated for a sufficient length of time (see below), whereas the latter resulted in extinction.

479 Figure 1 provides a schematic of how this process works within our simulation framework.  
480 Simulations also produced a complete phylogeny from each individual starting lineage; these  
481 data are stored, although not used in the current analysis.

482 Minimum isolation time for speciation to occur was set arbitrarily at 10,000 years. In  
483 nature, of course, speciation may take longer<sup>109</sup> or shorter<sup>110, 111</sup> than 10,000 years, but this  
484 duration is not unreasonable based on both paleontological and neontological data<sup>112, 113, 114,</sup>  
485 <sup>115</sup>. Importantly, we chose a time-to-speciation that was proportional to the time steps  
486 available in the climate dataset to generate appreciable numbers of speciation events at the  
487 scale of climate change steps. The climate model used here represents a full, transitory global  
488 climate trajectory from the last interglacial period to present—no other general circulation  
489 model outputs of this nature (i.e., temporally ‘continuous’) are available to our knowledge,  
490 nor is the HadCM3 model available for earlier periods. Importantly, other parallel  
491 simulations by Rangel et al<sup>29</sup> found that time-to-speciation did not have significant effects on  
492 model results.

493 Following Qiao et al<sup>94</sup>, daughter species have identical niches and dispersal abilities  
494 as their parent species. That is, no evolution of niche or dispersal traits occurs through time,  
495 which invokes the fewest assumptions regarding demographic processes, genetic/phenotypic  
496 plasticity, and evolvability during speciation. Niche evolution was purposefully avoided to  
497 isolate the effects of the spatial distribution of climate through time on the latitudinal  
498 structure of diversity. In natural systems, niche breadth and dispersal ability will vary among  
499 species; how this variation may affect macroecological patterns is not treated here, but has  
500 been discussed elsewhere<sup>29</sup>. Populations that separated and re-merged in less than 10,000  
501 years were not regarded as distinct species. Once produced, daughter species immediately  
502 began to search and occupy all suitable cells within their dispersal reach, and were not  
503 prohibited from cell occupation by presence of another species. In this sense, biotic

504 interactions were not included in our simulations: species were not excluded from suitable  
505 areas based on presence of other species, nor did presence of other species affect extinction  
506 probability. Again, excluding the effects of biotic interactions was deliberate to reduce  
507 confounding variables, whilst examining whether biodiversity patterns can be explained by a  
508 few simple processes.

509         Extinction occurred when all occupied suitable habitat (i.e., cells) for a species  
510 disappeared and the species was unsuccessful at colonizing new areas. We applied no  
511 specific demographic model or inferred minimum population survivorship threshold<sup>94</sup>, such  
512 as might derive from the existence of Allee effects. A strict extinction criterion was used  
513 because it also invoked the fewest assumptions, and because the relatively coarse spatial  
514 resolution of the simulation (i.e., 110 km x 110 km at the Equator) was likely broad with  
515 respect to individual life histories.

516         In all, 2000 initial species locations were chosen randomly (Fig. S58) and tested under  
517 all combinations of niche breadth (narrow and broad), dispersal ability (poor and good), and  
518 climate scenario (no ice, ice, and probability of ice), resulting in 24,000 unique virtual  
519 species simulations. Each of these 24,000 simulations started as a point in space: at the end of  
520 each simulation, the final spatial pattern of diversity was quantified, including all extant  
521 species that had evolved over the course of the simulation. We additionally documented the  
522 location and frequency of the speciation and extinction events that generated this  
523 biodiversity. Although we considered 2000 initial seed points for each ecological  
524 combination, patterns of diversity were analyzed using standard numbers of seed points in  
525 each latitudinal band (discussed below), such that no diversity gradient existed at the  
526 beginning of each analysis (Fig. S59).

527

528 *Simulations without climate change*

529           The above simulation framework was repeated under constant climate conditions  
530 from 120 Ka using the ‘no ice’ climate model. Species could occupy suitable cells based on  
531 their niches and dispersal abilities, but climate remained static over the course of the 120 Kyr  
532 simulation (note that temperature seasonality was still considered implicitly, since there is  
533 greater disparity between maximum and minimum temperatures at high latitudes). No  
534 speciation or extinction occurred in the simulations, since these processes are driven by  
535 spatio-temporal dynamics of climate change. These ‘no climate change’ simulations served  
536 as a null model against which to compare patterns resulting from spatio-temporal dynamics  
537 of climate, and thus relied on the same initial seeds and parameters as the original  
538 simulations.

539

#### 540 *Patterns of diversity by latitude*

541           Global terrestrial areas were seeded randomly with incipient species, such that some  
542 latitudes differed in numbers of species simulated, reflecting different land areas. To account  
543 for this uneven initial starting diversity, we drew randomly one simulation from each 1°  
544 latitudinal band for a series of 100 bootstrap replicates. This process standardized initial  
545 diversity by latitude (i.e., one initial seed or ‘species’), which was necessary since we did not  
546 wish to *a priori* generate latitudinal diversity gradients (Fig. S59). From each bootstrap  
547 replicate, we quantified the number of species at each degree of latitude at the end of the  
548 simulations, a process repeated for every dispersal × niche × climate scenario combination.  
549 Mean and median latitudinal diversity and associated 95% confidence intervals from the 100  
550 bootstrap replicates are shown in Fig. 2 and Figs. S1–6. Note that variance among bootstrap  
551 samples may depend on longitudinal extent of each latitudinal band (Fig. S58). We also  
552 present results scaled to unit land area available per latitudinal band (Figs. S7–12).

553 Regional biodiversity patterns were assessed using the bootstrap framework described  
554 above for Eurafrika (Europe & Africa), Australasia (Australia and Asia), and the Americas  
555 for both raw diversity (Figs. S13–15) and diversity scaled to area (Figs. S16–18). These  
556 analyses considered only 139 latitudinal bands (from -55° to 83°), removing highest latitudes  
557 because land area was minimal and lacked initial species seeds.

558

#### 559 *Speciation and extinction by latitude*

560 Using the bootstrap framework described above, we quantified speciation and  
561 extinction rates by latitude by pulling randomly one simulation from each 1° latitudinal band  
562 for a series of 100 bootstrap replicates. Two methods were used to determine *where*  
563 speciation events occurred: (1) cells were included if they were within the distribution of the  
564 two diverging populations at the time of speciation; or (2) each unoccupied, empty cell (i.e.,  
565 the barrier) between diverging populations was included. For the latter method, we calculated  
566 a convex hull around the distributional areas of the diverging populations at the time of  
567 speciation. The cells within this convex hull, but not within the distribution of either  
568 population, were counted as the area of speciation. The two methods produced almost  
569 identical results, so we present results for only the latter. We document where an extinction  
570 event occurred using the entire historical distribution of the species, as the distribution prior  
571 to extinction was often represented by only one cell. Using this framework, we generated  
572 characterizations of speciation (Fig. 3; Figs. S22–24) and extinction (Fig. 3; Figs. S28–30)  
573 per latitude for the different niche × dispersal × climate scenario combinations, and also  
574 scaling both metrics to per-unit area in each latitudinal band (Figs. S25–27 and S31–33).

575

#### 576 *Geographic patterns*



577 Global patterns of biodiversity, speciation, and extinction were examined on a per-cell  
578 basis. Maps were generated by selecting one simulation per latitudinal band. Numbers of  
579 events (presence of species, extinction or speciation events) were then tabulated for each cell  
580 globally (Fig. 4; Fig. S35). This process was repeated 100 times, and the results summed  
581 across replicates. Speciation and extinction were considered using the same framework  
582 outlined above (Fig. S35).

583

#### 584 *Dispersal dynamics*

585 We documented the frequency of shifts from temperate to tropical biomes and vice  
586 versa to examine the role of dispersal in generating diversity gradients. Tropical and  
587 temperate regions were delineated as those regions having mean annual temperatures greater  
588 and less than 18°C, respectively<sup>116, 117</sup> (Fig. S60). In the first two analyses, we selected  
589 randomly 10 simulations per biome per replicate over a series of 100 bootstrap replicates. We  
590 counted either (1) the number of initial incipient lineages with *any* species that originated in  
591 the tropics and dispersed to temperate regions and *vice versa*. Using this method, a maximum  
592 of 10 dispersal events could be counted for species dispersing from temperate to tropical  
593 regions or *vice versa* per bootstrap (Figs. S36–38); or (2) the total number of any species that  
594 dispersed from the tropics to temperate regions and *vice versa* from these initial incipient  
595 lineages (Fig. 5; Figs. S39–41). Higher out-of-the-tropics expansion becomes likely if  
596 diversity is higher in the tropics<sup>45</sup>, so we standardized the number of potential dispersal  
597 events from tropical to temperate regions and *vice versa* in a third analysis. In this method,  
598 we selected randomly 1000 species that were ‘born’ (i.e., simulations initiated) in tropical  
599 regions and counted the proportion of those species that dispersed from the tropics to  
600 temperate regions in a series of 100 bootstrap replicates; this process was then repeated for  
601 species born in, and selected randomly from, temperate regions (Figs. S42–44).

602 In addition to defining tropical areas by temperature, we considered ‘tropical’ regions  
603 as areas within +/- 23.5° latitude, regardless of climate. Dispersal analyses were repeated  
604 using this latitudinal definition of biomes. Results, however, were similar and therefore are  
605 not shown.

606

#### 607 *Climate dynamics*

608 The spatio-temporal dynamics of climate change drove speciation and extinction in  
609 the simulation framework. We quantified the relative contributions of the three climatic  
610 parameters (maximum precipitation, maximum temperature, and minimum temperature) to  
611 speciation and extinction across latitudes. For speciation, we determined the relative  
612 contribution of each climate parameter to unsuitable regions (i.e., the barriers) between  
613 populations, which prompted allopatric speciation. Barriers were identified by generating a  
614 convex hull around the distributional area of diverging populations at the time of speciation  
615 using the centre of each cell: cell centres within this convex hull, but not within the  
616 distribution of either population, were considered part of the ‘barrier’ that promoted  
617 speciation. This region, however, could be unoccupied because of dispersal constraints, or  
618 because one or more climatic parameters were outside the tolerance limits for a given species.  
619 We analysed only the latter scenario, removing from consideration any pixel that was suitable  
620 but unoccupied due to dispersal limitations. For each ‘barrier’ pixel in a speciation event, we  
621 documented unsuitability with respect to the three climatic parameters, indicating the pixel  
622 was outside the species’ niche and therefore causing range fragmentation and ultimately  
623 speciation. This process was repeated for 1000 random speciation events every 5000 years  
624 (for a total of 50 time steps). Each pixel associated with speciation was assigned three values  
625 representing the proportion of speciation events in that pixel caused by: (i) unsuitability in  
626 maximum precipitation, (ii) unsuitability in maximum temperature, and (iii) unsuitability in

627 minimum temperature. Note that these values need not sum to unity, since a pixel could be  
628 unsuitable in multiple climate dimensions. Mean proportions were calculated for each climate  
629 variable in each latitudinal band and time step, for all niche breadth and dispersal  
630 combinations (Fig. 6; Figs. S45–S47).

631         The same framework was used to assess the relative contributions of the three climate  
632 variables to extinction across latitudes. We considered the climate conditions in the time step  
633 in which the species disappeared (i.e., no longer occupied any pixels), but determined which  
634 of the climate variables caused extinction by looking to the pixels occupied in the time step  
635 immediately preceding the extinction event. In each of these previously-occupied pixels, we  
636 assigned values representing the proportion of extinction events in that pixel caused by: (i)  
637 unsuitability in maximum precipitation, (ii) unsuitability in maximum temperature, and (iii)  
638 unsuitability in minimum temperature. Mean proportions were calculated for each climate  
639 variable in each latitudinal band and time step analysed (Fig. 6; Fig. S48–S50). As with  
640 speciation, we considered the effect of niche breadth and dispersal combinations.

641         In addition to assessing the relative contribution of the three climate variables to  
642 speciation and extinction, we quantified spatio-temporal variability of each climatic  
643 parameter over the last 120 Ka. Variability was measured as the standard deviation of  
644 conditions in a particular cell across the 120 Ka (Fig. S51) using the ‘no ice’ climate  
645 scenario, since the other scenarios use the ice sheet only as a ‘mask’ to remove occupied  
646 cells.

647

#### 648 *Comparison with empirical patterns*

649         We compared simulation results to empirical patterns of global terrestrial diversity for  
650 birds, mammals, and amphibians, because diversity data for these taxa were readily available  
651 worldwide, which was not the case for plants (i.e., no global database was available to us).

652 Diversity maps were derived from BiodiversityMapping.org<sup>118, 119</sup>, which in turn obtained  
653 data from BirdLife International and NatureServe (birds) and the IUCN (mammals and  
654 amphibians; <http://www.iucnredlist.org>). We coarsened maps from 10 km x 10 km resolution  
655 to match the 1° resolution of our simulations using bilinear interpolation.

656 We standardized both empirical and simulated diversity maps on a scale from 0 to 1  
657 by dividing by the highest diversity value in each. This step allowed us to compare the shape  
658 of curves and relative distribution of diversity, rather than the absolute magnitude of species  
659 counts, since total number of species differs amongst groups (for example, ~10,000 in birds  
660 and only ~5,400 in mammals exist globally) and is arbitrary in our simulations. Using the  
661 standardized maps, we quantified similarity between our simulations and empirical diversity  
662 patterns in four ways: (1) We calculated correlations (Pearson's  $r$ ) between simulated  
663 diversity and empirical diversity on a cell-by-cell basis (Table S1). We compared the level of  
664 correlation to null expectations, generated by reshuffling the simulated diversity values  
665 within each 1° latitudinal band and quantifying correlations between these reshuffled maps  
666 and the empirical maps. This process was repeated 100 times to generate a count of instances  
667 in which the strength of correlation was lower using the reshuffled maps (Fig. S52; Table  
668 S2). Note that the amphibian diversity map lacked data in some regions (Fig. 4), which were  
669 excluded from analyses. (2) We calculated model residuals by subtracting simulated diversity  
670 from empirical diversity to examine regions in which the simulations over- or under-  
671 predicted richness (Fig. S53). Analyses were performed using the 'raster' package in R<sup>120</sup>. (3)  
672 We quantified similarity between simulated and empirical latitudinal diversity curves using  
673 Fréchet distances (Fig. 2), which measure similarity between two curves while considering  
674 the location and ordering of the points along the curves. The metric is often described in  
675 terms of a person walking a dog on a leash, with the person walking along one curve and the  
676 dog along another<sup>121</sup>. The dog and person are able to vary their speeds, or even stop, but not

677 go backwards. The Fréchet metric is the minimum leash length required to complete the  
678 traversal of both curves. We calculated this metric between all pair-wise combinations of  
679 simulated diversity curves and empirical diversity curves using the ‘Frechet’ function in the  
680 SimilarityMeasures package for R 3.3.1<sup>122</sup> (Table S3). We additionally used Kolmogorov-  
681 Smirnov two-sample tests to compare similarities between all pair-wise combinations of  
682 simulated diversity curves and empirical diversity curves. These tests suggested statistically-  
683 significant differences among all diversity gradients ( $p < 0.0001$ ), including among empirical  
684 clades (e.g., between birds and mammals), and thus we do not dwell further on these results.  
685 Finally, (4) we compared geographic range-size frequency distributions (Fig. S54). We  
686 assessed the similarity of the range-size frequency distributions for virtual species at the end  
687 of the simulations with range-size frequency distributions for species of birds, mammals, and  
688 amphibians. Each species’ distribution was represented as a polygon in a vector GIS  
689 shapefile. Shapefiles for each species in the three groups were rasterized from the IUCN  
690 (mammals and amphibians) and BirdLifeInternational (birds) to 1° resolution. A species was  
691 considered to occupy a given cell if any part of that species’ range intersected the cell; the  
692 total number of occupied cells was then summed across the species’ range. We repeated this  
693 process for each virtual, bird, mammal, and amphibian species. Range-size frequency  
694 distributions for birds, mammals, and amphibians were then compared statistically to  
695 simulated range-size frequency distributions by niche × dispersal × climate scenario  
696 combination using Kolmogorov-Smirnov two-sample tests in R 3.1.1. Given our ability to  
697 generate many more species than are often observed in empirical groups (405,480 in total),  
698 10,000 simulated species were selected randomly from each niche × dispersal × climate  
699 scenario combination for comparison to the empirical patterns, in each of a series of 100  
700 replicates.

701

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711 Appendix 1 and freely available for use.

712

713 **Author contributions**

714 EES designed the study, EES and HQ performed the analyses, J. Singarayer and PV provided  
715 climate data and analysis, EES and HQ analyzed the results. EES wrote the first draft of the  
716 manuscript, and all authors (CEM, ATP, JS, J. Singarayer, PV, HQ) contributed to revisions.

717

718 The authors declare no competing interests.

719

720 **Supplementary Materials**

721 Supplementary Simulation Protocol

722 Supplementary Tables (S1–S5)

723 Supplementary Figures (S1-S60)

724

725

726 **Table and Figures**

727

728

729 **Table 1.** Model parameters and their permutations used in the simulations. A detailed  
730 explanation of all scenarios and parameters are provided in the main text methods.

731

732 **Figure 1.** Schematic of the process of speciation and extinction in the simulation framework.  
733 Speciation occurs in response to range fragmentation driven by climate change. Speciation  
734 will occur only if populations remain isolated for at least 10,000 years. Extinction is also  
735 climatically mediated, and occurs when a species is no longer able to occupy suitable cells or  
736 suitable cells do not exist. See ‘Simulation Protocol’ in the Supplementary Materials for  
737 further details.

738

739 **Figure 2.** Standardized mean number of species per 1° latitudinal band with standard error  
740 bars. Simulated results are shown only for the ‘no ice’ climate scenario for all dispersal and  
741 niche combinations, and for species with narrow niches and poor dispersal abilities. Results  
742 were similar for other climate scenarios, albeit even closer matches to empirical diversity  
743 curves, shown in Figs. S1-6 and scaled to area in Figs. S7-12.

744

745 **Figure 3.** Mean speciation (top) and extinction (bottom) rate per latitudinal band with  
746 associated 95% confidence intervals across 100 bootstrap replicates. Values include all  
747 speciation and extinction events that occurred over the 120-kyr simulation for species with  
748 narrow niches aggregated across both dispersal abilities. Three climate scenarios are shown,  
749 which are explained in detail in the Methods. Parallel graphics with speciation and extinction  
750 rates scaled to area are given as Figs. S25–27 and S31–33.

751  
752

753 **Figure 4.** Distribution of bird, mammal, and amphibian species, as well as virtual species  
754 with narrow niches and poor dispersal abilities in the present day. Simulated results are  
755 shown only for the ‘no ice sheet’ climate scenario, but patterns do not differ significantly for  
756 other climate scenarios. Extant vertebrate data were derived from  
757 BiodiversityMapping.org<sup>118, 119</sup>. Latitudinal diversity curves were generated by quantifying  
758 mean diversity in each 1° latitudinal band with associated standard deviations. Note the  
759 variability among the three empirical diversity maps and curves.

760  
761

762 **Figure 5.** Frequency of shifts from temperate to tropical biomes and *vice versa* by virtual  
763 species across 100 bootstrap replicates for all dispersal and niche combinations (for other  
764 dispersal and niche combinations, see Figs. S36–44). Results show the total number of  
765 species that dispersed from the tropics to temperate regions and *vice versa* from initial  
766 incipient lineages. Three climate scenarios are shown, which are explained in detail in the  
767 Methods.

768  
769

770 **Figure 6.** Mean contribution of climate parameters to speciation (top) and extinction  
771 (bottom) in each 1° latitudinal band with associated 95% confidence intervals that reflect  
772 temporal variation during the simulation. Each pixel associated with speciation and extinction  
773 was assigned three values representing the proportion of events in that pixel caused by (i)  
774 unsuitability in maximum precipitation, (ii) unsuitability in maximum temperature, and/or  
775 (iii) unsuitability in minimum temperature. Note that these values need not sum to unity,  
776 since a pixel could be unsuitable in all three climate dimensions. Mean proportions were  
777 calculated for each climate variable in each latitudinal band and in each time step. Results are  
778 shown for all dispersal and niche combinations. No confidence intervals are shown for  
779 extinction, as variability was so high that it obscured mean patterns. Max precip = maximum  
780 precipitation; max temp = maximum temperature, and min temp = minimum temperature.  
781 Other niche and dispersal scenarios are shown in Figs. S45–50.

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