Spatio-temporal climate change contributes to latitudinal diversity gradients

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Abstract

The latitudinal diversity gradient (LDG), in which the number of species increases from the poles to the Equator, ranks among the broadest and most notable biodiversity patterns on Earth. The pattern of species-rich Tropics relative to species-poor temperate areas has been recognized for well over a century, but generative mechanisms are still debated vigorously. We use simulations to test whether spatio-temporal climatic changes could generate large-scale patterns of biodiversity as a function of only three biological processes—speciation, extinction, and dispersal—omitting adaptive niche evolution, diversity-dependence, and coexistence limits. In our simulations, speciation resulted from range disjunctions, whereas extinction occurred when no suitable sites were accessible to species. Simulations generated clear LDGs that closely match empirical LDGs for three major vertebrate groups. Higher tropical diversity primarily resulted from higher low-latitude speciation, driven by spatio-temporal variation in precipitation rather than in temperature. This suggests that spatio-temporal changes in low-latitude precipitation prompted geographic range disjunctions over Earth history, leading to high rates of allopatric speciation that contributed to LDGs. Overall, we show that major global biodiversity patterns can derive from interactions of species' niches (fixed *a priori* in our simulations) with dynamic climate across complex, existing landscapes, without invoking biotic interactions or niche-related adaptations.

Introduction

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

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

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

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

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

Results

Latitudinal diversity gradients

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

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

To evaluate the role of climate change *versus* time-independent spatial climate variation alone, we ran a series of simulations in which climate was held constant. These simulations did not produce low-latitude peaks in diversity (Figs. S19–21). Results therefore underline the key role of spatial and temporal variation in climate in generating LDGs in our simulations.

Rates of speciation and extinction

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

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

Geographic patterns

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

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

Dispersal dynamics

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

Climate dynamics

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

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

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

Comparisons with empirical patterns

We calculated cell-by-cell Pearson correlation coefficients (r) between simulated diversity and empirical diversity for three clades (birds, mammals, amphibians) using standardized, global diversity maps (Table S1). In most cases, our simulated diversity patterns correlated positively with diversity patterns for birds, mammals, and amphibians; negative correlations resulted in only a few cases in simulations considering broad-niched species (Table S1). Strongest correlations were recovered for simulations using species with narrow niches and poor dispersal abilities ($r^2 > 0.16$ for mammals). Correspondence between simulated diversity and bird and mammal diversity was higher than expected based on null distributions generated by reshuffling simulated diversity values within each latitudinal band in a series of 100 replicates (Fig. S52 and Table S2). Correlations were weaker than expected for amphibians when considering species with broad niches and poor dispersal abilities (Table S2).

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

We quantified similarity between simulated and empirical latitudinal diversity curves using Fréchet distances, which measures similarity between two curves while considering the location and ordering of the points along the curves. Simulated latitudinal diversity curves were remarkably similar to empirical diversity curves, although high-latitude diversity in the Northern Hemisphere was over-predicted for species with broad niches (Figs. 2; Figs. S5–6). Simulated diversity curves were most similar to empirical diversity curves when considering species with narrow niches and poor dispersal abilities, and most dissimilar when considering species with broad niches regardless of dispersal ability (Table S3). Overall, simulated diversity curves were most similar to the mammal diversity curve (Fig. 4 and Table S3). Indeed, we found shorter Fréchet distances between mammals and simulated diversity using species with narrow niches, than when comparing mammals, birds, and amphibians to each other. Considering all niche and dispersal combinations together, Fréchet distances from our simulations to mammals or birds were usually no greater than the distance between birds and amphibians (Table S3), suggesting that the simulations are closely replicating large-scale attributes of empirical diversity patterns.

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

Discussion

We simulated a world in which the three factors affecting biological diversity—speciation, extinction, and dispersal—responded only to realistic climate dynamics over the terrestrial global landscape. Starting from no diversity gradient, the great majority of our simulations yielded higher diversity at low latitudes, particularly for species with narrow niches. This result is consistent with previous, independent sets of simulations that employed similar frameworks for South America[28, 29]. Speciation rates, rather than extinction rates, were the primary control on these patterns, being markedly elevated in the Tropics, which is congruent with previous findings that suggest the Tropics as a cradle of biological diversity[10, 15, 19, 24, 49]. Dispersal into the Tropics did not contribute significantly to the strength of the LDG, since species dispersed from lower to higher latitudes at higher rates under all dispersal and niche combinations; in this sense, our simulations supported the ‘out of the Tropics’ model[19, 44, 50]. Given that species diversity scales with area[51, 52], and that land area is reduced at lower latitudes, rescaling diversity curves to available area further amplified low-latitude peaks in diversity for all niche and dispersal scenarios, and eliminated peaks in diversity at higher latitudes for species with broad niches. Results were not dependent on the presence or absence of continental ice sheets.

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

Our simulated biodiversity patterns and real-world diversity hotspots were similar, at least at coarse scales, except for Southeast Asia, Australia, and New Guinea (Fig. 4). Observed differences between simulated and empirical patterns may reflect model misspecification, or more ancient (pre-Eemian) processes not integrated into our simulations, such as tectonic changes and environmental perturbations. Geographic range-size frequency distributions also replicated the right-skewed nature of empirical distributions, except that a greater proportion of simulated species had larger ranges. This skew is not surprising, since virtual species were accorded relatively broad niches (i.e., 21° and 31°C temperature breadth for narrow and broad niche species, respectively) that were not limited by biotic interactions. Larger ranges, however, should not affect interpretations of simulated results or LDG mechanisms in a systematic fashion. Indeed, reduction in species' range sizes, either from narrowing tolerance limits or from biotic interactions, may further facilitate climate-driven tropical range fragmentation and more effective isolation of those range fragments (increasing speciation potential).

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

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

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

We do not suggest that Eemian (i.e., last glacial cycle) speciation alone is responsible for the modern LDG. The Earth, of course, was already populated by a rich biota at 120 Ka. Rather, we hypothesize that interactions between spatio-temporal dynamics of climate, real-world geography, and species operated similarly on geologic timescales[31, 69, 70], which could have contributed to the maintenance of LDGs observed today. This effect would explain the correspondence of our simulated biodiversity patterns to empirical biodiversity patterns. Importantly, our hypothesis can be further interrogated as new and more dense climatic data become available for earlier time periods. Current understanding of paleoclimate dynamics is that they have fluctuated continuously over various timescales[71, 72, 73]. In our simulations, spatio-temporal heterogeneity in precipitation at low latitudes generated higher rates of allopatric speciation. Although this pattern was derived from Late Pleistocene climate dynamics, low-latitude variability in precipitation has likely occurred throughout much of Earth history, and has been suggested as a driver of hominin evolution in southeastern Africa[74]. Atmospheric moisture is a strongly non-linear function of temperature, meaning that small variations in temperature are amplified by the moisture cycle. Consequently, high variability in precipitation is expected in warm climates, such as the low-latitude Tropics[63]. A logical corollary, of course, is that during periods of extreme warmth globally, such as the Late Cretaceous and Early Eocene, precipitation may have been variable everywhere, not only at low latitudes. Based on our proposed mechanism, then, speciation rates would have been high across latitudes, providing a process-based explanation for the dampened diversity gradients often reported for these time periods[12, 13, 75, 76, 77, 78, 79].

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

The above discussions lead to reflections on the reality and utility of our simulations. Our model is simple, but this simplicity was purposeful and explicitly designed. For example, we invoked no changes in species' niche traits through time or at splitting events. That is, we assumed niche stability during the lifetime of each lineage simulated. Niche stability and phylogenetic conservation are realistic assumptions for the time scale of our analysis[23, 32, 33, 34, 35, 36], and have even been proposed as a mechanism for the modern LDG[9, 23, 32, 42]. However, evolution in species' niche tolerances does occur over longer time scales and may additionally enhance the LDG[29]. Furthermore, we invoked no biotic interactions in our simulations, and we considered only a set of trait values for dispersal and niche breadth: simulations cast in the context of other dispersal and niche traits may show different patterns. Although biotic interactions could contribute to LDGs[8, 64, 81, 82], we do not consider them here for two reasons: (i) to examine the extent to which abiotic factors alone offer a mechanism to explain observed patterns of diversity; and (ii) because modelled competition was found to have little effect on resulting geographic patterns of species' richness[29].

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

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

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

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

Methods

Simulations

We used a cellular automaton algorithm to simulate patterns of speciation, extinction, and dispersal in response to a dynamic climate over the last 120,000 years (Table 1). The framework builds on previous models[28, 94, 95] to simulate the interaction of virtual species with spatio-temporal variation in temperature and precipitation. Simulations were initiated under interglacial climatic conditions (Eemian, Late Pleistocene, 120 Ka ago) and run forward in time to the present-day using current continental configurations (Fig. 4). Each initial lineage had the potential to go extinct or speciate. Speciation and extinction were driven by changing climatic conditions: speciation occurred when ranges were fragmented via isolation of suitable areas for at least 10,000 years (see justification below), and extinction occurred when all occupied suitable areas were eliminated, and the species was unsuccessful at colonizing newly-suitable regions. The simulation protocol is outlined in the Supplementary Materials and is illustrated in Fig. 1. Soft code for the simulation is provided in Appendix 1.

A virtual species began the simulation at a site of origin chosen randomly from within terrestrial areas globally, which were divided into 1°x1° grid cells (15,254 cells total). Cell occupation was controlled by species' abiotic tolerances and dispersal ability in relation to climatic conditions manifested in the cell. The temperature and precipitation values of the initial starting cell defined the centre of that species' niche. We applied symmetrical deviations to this point[28, 94] based on two niche breadths (narrow and broad), corresponding to temperature and precipitation tolerances of 21°C and 31°C and 4 mm/day and 7 mm/day, respectively. These niche breadths were derived from empirical temperature and precipitation tolerances of agriculturally-important plant species[96], in which ~18% of species were characterised as having 'tropical' distributions. Narrow and broad niche breadths were defined using the lower and upper quartiles, respectively, of niche breadths in this database[94]. Representation of species' tolerances (fundamental ecological niches) was limited by the climatic combinations existing at a given time step, referred to as the existing niche[97]. Existing niches were further limited by species' ability to access suitable cells, determined by assigned dispersal ability and initial distributions. Seasonality was considered indirectly in the model because maximum and minimum temperatures differ more markedly at higher latitudes[98].

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

Climatic attributes of individual cells fluctuated through time and resulted in conditions that were favorable or unfavorable for a species at a given time depending on whether the cell value fell within the species' climatic niche. Dynamic climate change trajectories over the last 120 Ka were derived from transient climate simulations using state-of-the-art, coupled atmosphere-ocean-vegetation models (HadCM3) developed at the Hadley Centre[102]. Three climate parameters constrained species' tolerances: mean monthly maximum temperature, mean monthly minimum temperature, and mean monthly maximum precipitation, under three scenarios related to ice sheets (discussed below). Minimum monthly precipitation is zero for nearly all localities on Earth and was therefore not included (precipitation, of course, cannot fall below zero). We also considered simulations when species' tolerances were constrained using mean annual precipitation and mean annual temperature. Resulting patterns were broadly equivalent to simulations using maximum and minimum climate layers, and therefore we focus here only on the latter.

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

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

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

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

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

Following Qiao et al[94], daughter species have identical niches and dispersal abilities as their parent species. That is, no evolution of niche or dispersal traits occurs through time, which invokes the fewest assumptions regarding demographic processes, genetic/phenotypic plasticity, and evolvability during speciation. Niche evolution was purposefully avoided to isolate the effects of the spatial distribution of climate through time on the latitudinal structure of diversity. In natural systems, niche breadth and dispersal ability will vary among species; how this variation may affect macroecological patterns is not treated here, but has been discussed elsewhere[29]. Populations that separated and re-merged in less than 10,000 years were not regarded as distinct species. Once produced, daughter species immediately began to search and occupy all suitable cells within their dispersal reach, and were not prohibited from cell occupation by presence of another species. In this sense, biotic interactions were not included in our simulations: species were not excluded from suitable areas based on presence of other species, nor did presence of other species affect extinction probability. Again, excluding the effects of biotic interactions was deliberate to reduce confounding variables, whilst examining whether biodiversity patterns can be explained by a few simple processes.

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

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

Simulations without climate change

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

Patterns of diversity by latitude

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

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

Speciation and extinction by latitude

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

Geographic patterns

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

Dispersal dynamics

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

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

Climate dynamics

The spatio-temporal dynamics of climate change drove speciation and extinction in the simulation framework. We quantified the relative contributions of the three climatic parameters (maximum precipitation, maximum temperature, and minimum temperature) to speciation and extinction across latitudes. For speciation, we determined the relative contribution of each climate parameter to unsuitable regions (i.e., the barriers) between populations, which prompted allopatric speciation. Barriers were identified by generating a convex hull around the distributional area of diverging populations at the time of speciation using the centre of each cell: cell centres within this convex hull, but not within the distribution of either population, were considered part of the ‘barrier’ that promoted speciation. This region, however, could be unoccupied because of dispersal constraints, or because one or more climatic parameters were outside the tolerance limits for a given species. We analysed only the latter scenario, removing from consideration any pixel that was suitable but unoccupied due to dispersal limitations. For each ‘barrier’ pixel in a speciation event, we documented unsuitability with respect to the three climatic parameters, indicating the pixel was outside the species’ niche and therefore causing range fragmentation and ultimately speciation. This process was repeated for 1000 random speciation events every 5000 years (for a total of 50 time steps). Each pixel associated with speciation was assigned three values representing the proportion of speciation events in that pixel caused by: (i) unsuitability in maximum precipitation, (ii) unsuitability in maximum temperature, and (iii) unsuitability in minimum temperature. Note that these values need not sum to unity, since a pixel could be unsuitable in multiple climate dimensions. Mean proportions were calculated for each climate variable in each latitudinal band and time step, for all niche breadth and dispersal combinations (Fig. 6; Figs. S45–S47).

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

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

Comparison with empirical patterns

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

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

We standardized both empirical and simulated diversity maps on a scale from 0 to 1 by dividing by the highest diversity value in each. This step allowed us to compare the shape of curves and relative distribution of diversity, rather than the absolute magnitude of species counts, since total number of species differs amongst groups (for example, ~10,000 in birds and only ~5,400 in mammals exist globally) and is arbitrary in our simulations. Using the standardized maps, we quantified similarity between our simulations and empirical diversity patterns in four ways: (1) We calculated correlations (Pearson's *r*) between simulated diversity and empirical diversity on a cell-by-cell basis (Table S1). We compared the level of correlation to null expectations, generated by reshuffling the simulated diversity values within each 1° latitudinal band and quantifying correlations between these reshuffled maps and the empirical maps. This process was repeated 100 times to generate a count of instances in which the strength of correlation was lower using the reshuffled maps (Fig. S52; Table S2). Note that the amphibian diversity map lacked data in some regions (Fig. 4), which were excluded from analyses. (2) We calculated model residuals by subtracting simulated diversity from empirical diversity to examine regions in which the simulations over- or under-predicted richness (Fig. S53). Analyses were performed using the 'raster' package in R[120]. (3) We quantified similarity between simulated and empirical latitudinal diversity curves using Fréchet distances (Fig. 2), which measure similarity between two curves while considering the location and ordering of the points along the curves. The metric is often described in terms of a person walking a dog on a leash, with the person walking along one curve and the dog along another[121]. The dog and person are able to vary their speeds, or even stop, but not go backwards. The Fréchet metric is the minimum leash length required to complete the traversal of both curves. We calculated this metric between all pair-wise combinations of simulated diversity curves and empirical diversity curves using the ‘Frechet’ function in the SimilarityMeasures package for R 3.3.1[122] (Table S3). We additionally used Kolmogorov-Smirnov two-sample tests to compare similarities between all pair-wise combinations of simulated diversity curves and empirical diversity curves. These tests suggested statistically-significant differences among all diversity gradients ($p < 0.0001$), including among empirical clades (e.g., between birds and mammals), and thus we do not dwell further on these results. Finally, (4) we compared geographic range-size frequency distributions (Fig. S54). We assessed the similarity of the range-size frequency distributions for virtual species at the end of the simulations with range-size frequency distributions for species of birds, mammals, and amphibians. Each species’ distribution was represented as a polygon in a vector GIS shapefile. Shapefiles for each species in the three groups were rasterized from the IUCN (mammals and amphibians) and BirdLifeInternational (birds) to 1° resolution. A species was considered to occupy a given cell if any part of that species’ range intersected the cell; the total number of occupied cells was then summed across the species’ range. We repeated this process for each virtual, bird, mammal, and amphibian species. Range-size frequency distributions for birds, mammals, and amphibians were then compared statistically to simulated range-size frequency distributions by niche × dispersal × climate scenario combination using Kolmogorov-Smirnov two-sample tests in R 3.1.1. Given our ability to generate many more species than are often observed in empirical groups (405,480 in total), 10,000 simulated species were selected randomly from each niche × dispersal × climate scenario combination for comparison to the empirical patterns, in each of a series of 100 replicates.

Acknowledgments

We thank Robert Colwell (U Connecticut) and Fabien Condamine (CNRS) for comments that greatly improved our contribution. We are indebted to Dan Hill (Leeds, UK), Paul Wignall (Leeds, UK), and Roger Benson (Oxford, UK) for thoughtful discussions that informed this manuscript. H.Q. was supported by the National Key Research and Development Project of China (2017YFC1200603), Natural Science Foundation of China (31772432). EES acknowledges funding from an EAR NSF Postdoctoral Fellowship and Leverhulme Grant no. DGR01020. CEM acknowledges funding from NSF #1601878. All data are available via Dryad: doi:10.5061/dryad.m6h850q. Note that the soft code for the simulations is provided in Appendix 1 and freely available for use.

Author contributions

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

The authors declare no competing interests.

Supplementary Materials

Supplementary Simulation Protocol

Supplementary Tables (S1–S5)

Supplementary Figures (S1-S60)

Table and Figures

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

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

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

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

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

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

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

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