

Correspondence

Cradles of diversity
are unlikely relics
of regional climate
stabilityDamien A. Fordham^{1,2,*},
Stuart C. Brown¹, Tom M.L. Wigley^{1,3},
and Carsten Rahbek^{2,4}

The stability of regional climates on millennial timescales is theorised to be a primary determinant of nearby diversification [1–5]. Using simulated patterns of past temperature change at monthly timescales [6], we show that the locations of climatically stable regions are likely to have varied considerably across and within millennia during glacial–interglacial cycles of the Late Quaternary. This result has important implications for the role of regional climate stability in theories of speciation, because long-term climate refugia are typically presumed to be ‘cradles’ of diversity (areas of high speciation) only if they remain stable across Milankovitch climate oscillations [1–5], which operate on multi-millennial time scales [7].

Long-term stability of the mean climate state is considered a crucial factor responsible for spatiotemporal variations in biodiversity. By providing relatively stable environmental conditions in the face of large-scale climate oscillations, it is postulated that these refuges allow older species to survive (‘arks’ of diversity) and new lineages to be generated [5]. Therefore, climate stability not only enables survival of relictual taxa, but also promotes morphological differentiation of radiating taxa, resulting in aggregates of taxa with restricted distributions [3]. Changes in mean climate states that have been, at most, minor are generally thought to be essential for *in situ* persistence for species with small geographical ranges [4]. A low propensity for range movement, and high local survival, results in species becoming specialised to local abiotic and biotic conditions and therefore more vulnerable to larger mean climate state changes.

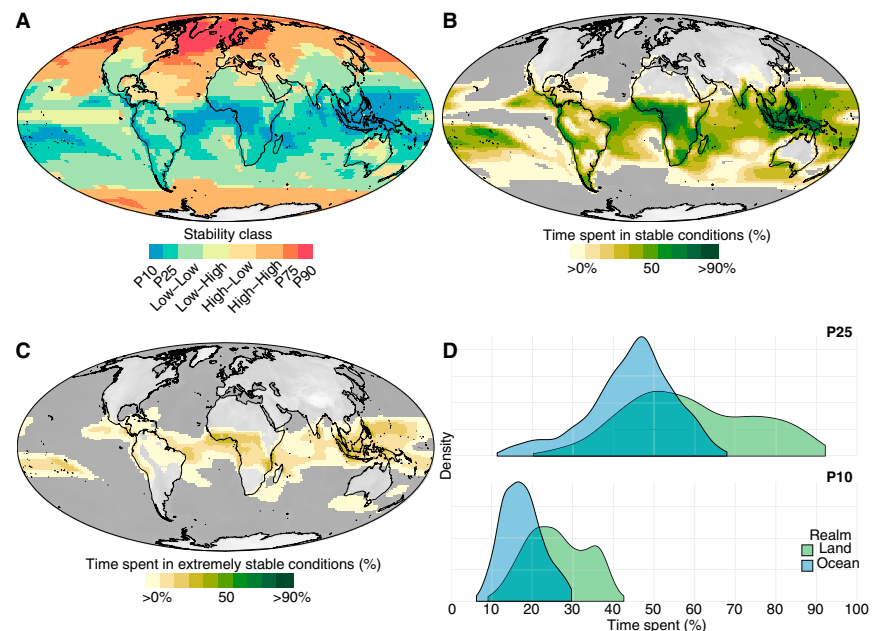


Figure 1. Location and persistence of Late Quaternary climate refugia during periods of rapid global mean temperature change.

(A) Map of climate stability broken into eight classes, using percentiles of median trend and variability (SD) calculated separately for land and ocean: $\leq 10^{\text{th}}$ (percentile for trend and SD) (P10); $> 10^{\text{th}}$ and $\leq 25^{\text{th}}$ (P25); (iii) $> 25^{\text{th}}$ and $\leq 50^{\text{th}}$ (Low–Low); $\leq 50^{\text{th}}$ for trend and $\geq 50^{\text{th}}$ for variability (Low–High); $> 50^{\text{th}}$ for trend and $\leq 50^{\text{th}}$ for variability (High–Low); $> 50^{\text{th}}$ and $\leq 75^{\text{th}}$ (High–High); $> 75^{\text{th}}$ and $\leq 90^{\text{th}}$ (P75); (viii) $> 90^{\text{th}}$ (P90). (B) Percentage of time spent in ‘stable’ ($\leq 25^{\text{th}}$ percentile for trend and SD) and (C) ‘extremely stable’ ($\leq 10^{\text{th}}$ percentile for trend and SD) climate conditions. (D) Percentage of time spent in ‘stable’ (top) and ‘extremely stable’ (bottom) climate conditions for class breaks (P25 and P10) shown in (A), for land (green) and ocean realms (blue). See Data S1 for raster files.

Because regional climates have changed markedly on decadal and centennial timescales over the past glacial–interglacial cycle [6], a spatially detailed picture of climate change on these timescales is an essential prerequisite for assessing whether climate stability leads to reduced extinction rates and high levels of speciation that, in turn, shape species richness patterns. Using annual means of monthly surface temperature from the Community Climate System Model ver. 3 TRaCE-21ka climate simulation (accessed via PaleoView [6]) and pre-industrial control runs from an ensemble of Atmosphere–Ocean General Circulation Models (AOGCM), we firstly identify centuries of rapid global mean temperature change (based on the century timescale linear trend magnitude) between the Last Glacial Maximum (LGM; 21,000 BP) and large-scale industrialisation (100 BP; i.e., 1850 AD). Then, we map the location (Figure 1A) and persistence (Figure 1B,C) of areas of stable

temperature (climate refugia) during these episodes of rapid change in global mean temperature.

We defined regions of stable climate in the following way. We quantified climate stability for each $2.5^{\circ} \times 2.5^{\circ}$ grid cell ($n = 10,368$ cells, covering the globe) based on the ‘local’ linear trend magnitude and variability (standard deviation, SD, about the trend) in annual mean temperature for maximally overlapping century windows (21,000 BP to 100 BP). For each century of rapid global mean temperature change since 21,000 BP (see Supplemental Experimental Procedures), we calculated the value for temperature trend magnitude and SD for each grid cell and determined the 10th and 25th percentiles across grid cells, for land and ocean realms separately. For any given grid cell and time point, the climate was defined as ‘stable’ if both the temperature trend and SD are \leq the 25th percentile, and as ‘extremely stable’ if both are \leq the 10th percentile. We then used this time

series to calculate the percentage of time a grid cell spent in 'stable' or 'extremely stable' climate conditions. We also calculated the median trend magnitude and median SD for each grid cell (i.e., across the time series of trend magnitude and SD values) and used these gridded values to determine the 10th, 25th, 50th, 75th and 90th percentiles. Our approach is described in detail in the Supplemental Experimental Procedures.

We estimate that, historically, 22% of terrestrial and 19% of marine environments experienced climatic conditions that were 'stable' during rapid changes in global mean temperature over the past ~21,000 years (Figure 1A). These areas of relative climate stasis, which were largely restricted to tropical regions (68% of land and 56% of ocean cells between 20°S and 20°N were classed as having historically 'stable' climates), were not, however, continuously stable (Figure 1B). Our estimates of the time spent in 'stable' climatic conditions range, across grid cells, from 21% to 92% on land and 11% to 68% in the ocean (Figure 1D). The highest values occurred in the tropics of south-east Asia and central Africa (Figure 1B), likely promoting regional persistence and, potentially, gradual speciation [3]. Moreover, within these regions of relative climate stasis, the location of 'extremely stable' climates also varied through time (Figure 1C,D). These results were relatively insensitive to variation ($\pm 10\%$) in the percentile thresholds used to define 'stable' and 'extremely stable' climates (Figure S1).

Our high temporal resolution paleoclimate simulations show a latitudinal gradient in climate stability since 21,000 BP (Figure 1A), with climatically stable regions generally occurring in the tropics (P10 and P25 in Figure 1A), in accordance with the Climate Stability Hypothesis for the latitudinal gradient of diversity [8]. More importantly, however, these simulations show that the persistence of climate-related refugia is strongly determined by centennial-scale climate fluctuations (Figure 1B,C), which are likely to have caused repeated population crashes, range shifts and gene flow during periods of widespread climate change [2].

This new result questions the role of Late Quaternary climate stability in promoting heterogeneity in speciation at regional scales in the tropics and beyond. Since major speciation events tend to require > 100,000 years to occur [9] and, as we show here, the location of climate refugia are highly unlikely to be fixed across (or potentially, even within) Milankovitch climate oscillations, it is doubtful that 'cradles' of diversity are primarily a relic of an invariant mean climate state during the late Quaternary. This is because the climate of past glacial–interglacial cycles was interrupted by century-to-millennial-scale warming and cooling events [10], which caused widespread (but, importantly, not ubiquitous) climate variations [7].

Notably, much of the early theory linking the accumulation and evolution of taxa to the effect of worldwide climate fluctuations on environmentally stable areas was generated at local spatial resolutions (the scale of individual valleys in mountain ranges [3]), accounting for the degree of topographic diversity of a landscape [4]. While topography could indeed buffer the effect of orbital and millennial climate fluctuations at fine spatial resolutions, our coarser resolution results remain pertinent, since rates of diversification at continental to global scales are most often attributed to regional-scale differences in ecoclimatic stability [1,2,5].

By simulating the spatial pattern of climate change and variability during the Late Pleistocene and Holocene, at a high temporal resolution, we have shown that regions of climatic stability rarely stay in fixed locations. Our results provide new impetus to revisit theories linking the impact of past global climate fluctuations to the processes of diversification, and more specifically the potential role that areas with Late Quaternary climate stability had in moulding the shape of present-day patterns of species richness, range-size-frequency-distributions, areas of endemism and biodiversity hotspots.

SUPPLEMENTAL INFORMATION

Supplemental information includes two figures, a data file, methods and references, and can be found at <https://doi.org/10.1016/j.cub.2019.04.001>.

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AUTHOR CONTRIBUTIONS

D.A.F. and C.R. conceived the idea. D.A.F., S.C.B. and T.M.L.W. did the analysis. All authors contributed to writing the manuscript.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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¹The Environment Institute and School of Biological Sciences, University of Adelaide, South Australia 5005, Australia. ²Center for Macroecology, Evolution, and Climate, Natural History Museum of Denmark, University of Copenhagen, Universitetsparken 15, 2100 Copenhagen O, Denmark. ³Climate and Global Dynamics Laboratory, National Center for Atmospheric Research, Boulder, CO 80307-3000, USA. ⁴Department of Life Sciences, Imperial College London, Ascot SL5 7PY, UK. *E-mail: damien.fordham@adelaide.edu.au