



Figure 1 Observed and simulated vegetation of east Asia during the Last Glacial Maximum and today. **a**, Pollen data for the Last Glacial Maximum, 18,000 ± 1,000 ¹⁴C yr BP, classified to top-level vegetation units (biomes) using a standard method⁸. **b**, Subrecent pollen data analysed in the same way, reflecting present vegetation patterns. **c**, Simulated vegetation during the Last Glacial Maximum, 21,000 cal yr BP (~18,000 ¹⁴C yr BP). Climate anomalies from the NCAR CCM1, with computed (mixed-layer ocean model) sea-surface temperatures⁹; vegetation simulation from BIOME4 (ref. 10). **d**, Simulated present potential natural vegetation, on the basis of twentieth-century climatology (CLIMATE 2.2). Colour scale: dark green, tropical forest, savanna and woodland; light green, temperate deciduous forest; light blue, temperate coniferous forest; dark blue, warm temperate evergreen forest; olive green, mixed (temperate and boreal) forest; brown, boreal forest; orange, non-forest.

habitat reductions in some regions occurred simultaneously with increases in others. Palaeodata from east Asia may still be broadly consistent with the allopatric-speciation hypothesis for species diversity put forward by Qian and Ricklefs¹, but only if it is recognized that population fragmentation occurred during glacial as well as interglacial periods. Although eastern North America also shows evidence of relative aridity during the Last Glacial Maximum, temperate forests there seem to have been more extensive and continuous⁷.

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Qian and Ricklefs reply — The point we wished to make was simply that the more complex geography and topography of eastern Asia compared with eastern North America, in conjunction with climate change and sea-level fluctuations, have provided greater opportunity for allopatric speciation. This explanation of the greater diversity of vascular plants in temperate regions of eastern Asia cannot yet be tested using any particular biome reconstruction, all of which are poorly resolved.

The estimated distribution of vegetation during the Last Glacial Maximum (18,000 yr BP) and at 6,000 yr BP, on the basis of fossil-pollen data¹ and climate, shows that mesic vegetation types were shifted southwards during the Last Glacial Maximum relative to their modern distributions in both eastern Asia and eastern North America^{2,3}. However, the temperate deciduous forest biome, which currently harbours many of the eastern Asian/eastern North American disjunct genera we discussed⁴, is poorly represented as a vegetation type in fossil-pollen deposits from the Last Glacial Maximum, casting doubt on the accuracy of the reconstruction by Harrison *et al.*

For example, the palaeovegetation of the Last Glacial Maximum for the vast area between 20° and 30° N and 105° and 120° E was reconstructed from only six pollen

localities, including only one from the interior of eastern Asia, which currently harbours the greatest plant diversity in the region.

It is not possible to determine whether temperate forests coalesced or fragmented during the Last Glacial Maximum without more detailed information. Nonetheless, the reconstruction by Harrison *et al.* confirms that the currently isolated temperate forests of China, Japan, and probably the Korean peninsula, were connected during the Last Glacial Maximum.

Speciation and extinction are processes of populations, not biomes. Climate change causes restructuring of forest communities, probably including the dispersion of temperate deciduous forest taxa among other vegetation types⁵. Vegetation maps cannot provide a detailed picture of past fragmentation and coalescence of particular species populations. Furthermore, because most eastern Asian/eastern North American disjunctions pre-date the onset of major glacial climate cycles in the Northern Hemisphere⁶, diversification of disjunct lineages may have begun under pre-Pleistocene climate conditions that were quite different from those in the present or in the Last Glacial Maximum. In these pre-Pleistocene conditions, eustatic sea-level changes may have been important in isolating and rejoining populations.

Reconstruction of vegetation history, combined with physiographical and climatic heterogeneity, conveys a general impression of the capacity of a region to promote or retard diversification through allopatric speciation⁷. However, the biome reconstruction by Harrison *et al.*, including their interpretation of restricted deciduous forest vegetation during glacial maxima, does not contradict the idea that the more complex landforms and climates of eastern Asia provided greater opportunities for allopatric formation of new species compared with eastern North America.

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