

## NEWS AND COMMENTARY

### Biodiversity

# A climate for colonization

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Evolutionary questions necessarily involve a consideration of time. Genetic studies of populations usually work with a few generations, while earth structure and geography deal in millions of years. Such disparate disciplines and time scales are components to understanding the evolution and significance of our present biota, and in recent years they have begun to be combined more effectively, as in the burgeoning field of phylogeography (Avise, 2000; Hewitt, 2001). Population genetic processes, gene lineages and trees, geographic genotype distribution, Quaternary fossil distributions and palaeoclimate measures are impacting on, and feeding off, each other to produce more satisfying explanations – and sometimes startling revelations. In a recent paper, Enrique Lessa, Joseph Cook and James Patton combined their interests to advance this synergy (Lessa *et al.*, 2003). Using coalescent population genetic models, they looked for genetic signals of demographic expansion after the last ice age in current populations of American mammals. Notably, this allowed for a quantitative comparison of such postglacial population changes in various species from two distinct biogeographic regions. In line with some hypotheses and predictions, it seems that North American Temperate species have expanded greatly to fill their present range, while in Tropical Amazonia, species show much weaker genetic signals of expansion, indicating larger populations and less change in range through the Late Pleistocene.

Advances in palaeoclimatology provide a startling picture of major ice age cycles lasting 100 thousand years over the last 0.9 million years, with nested millennial oscillations and shorter flickers of drastically changing conditions (Alley, 2000). These changes caused shifts in the ranges of species as they tracked the climate and environment to which they were adapted. This is most clearly seen – and easily analyzed – in Arctic and Temperate regions, which were covered in ice sheets and permafrost. The fossil record shows that many

species now occupying these regions survived in warmer refugia to the south. As the climate warmed rapidly after the Last Glacial Maximum (LGM; 24–18 thousand years ago), these species responded by expanding their ranges. Different expansion dynamics are predicted to leave distinct genetic signatures – thus rapid, Pioneer colonization by founders will reduce allelic diversity and produce patches of genotypic homogeneity, while slower, Phalanx advance by populations will tend to retain diversity (Nichols and Hewitt, 1994; Ibrahim *et al.*, 1996). There is currently considerable interest in colonization genetics, in both ancient and modern invasions (Petit *et al.*, 2001; Clark and McLachlan, 2003). Broad genetic surveys across Europe have shown that genotypes present in the southern ice age refugia are now spread across the north in distinct patterns, and that many postglacial populations show reduced genetic diversity (Hewitt, 2001).

Other regions, however, have different geography, climate and geological history, which will have variously affected range changes and hence the genetic structure and phylogeny of their own species. Thus, North America, while of similar size and latitude as that of Europe, differs significantly in the orientation of its mountain chains, its connection through Central America to the Tropics and in the greater extent of its LGM ice sheets (Hewitt, 1993). Nonetheless, a survey of some 41 North American fishes showed that populations in previously glaciated regions likewise had lower genetic variation and greater areas of homogeneity, likely produced by postglacial colonization (Bernatchez and Wilson, 1998). Similar genetic signals are being discovered in other North American species, including the voles, shrews, squirrels and bears analyzed by Lessa and colleagues. To find genetic evidence of expansion, the authors used two tests based on coalescence models of the genetic variation expected in populations under different demographic conditions. The tests were a Metropolis-Hastings Monte

Carlo algorithm in the program Flucuate (Kuhner *et al.*, 1998), which produces a maximum likelihood estimate 'g' of population growth, and Fu's 'Fs' statistic designed to test neutrality that is very sensitive to population growth (Fu, 1997). Significantly, these tests indicated great expansion in the northern parts of the four mammal species ranges that were previously glaciated, while populations in more southern parts and nearer to likely refugia show lower growth parameters. The NW Pacific region of North America, in which the northern parts of these species ranges occur, has been the subject of phylogeographic studies in a number of plants and other animals (Brunsfield *et al.*, 2001). The geography and genetic structure of several of these studies indicate postglacial colonization, and could be similarly analyzed, as could those existing and accumulating for Eastern North America.

The Tropics contain most species diversity, yet there are few genetic studies to illuminate this. One exception is for some small mammals in Western Amazonia. These groups show high variation within populations, and 11 of these species are used in this comparative analysis. With the same two coalescent tests, the signal of expansion is much weaker in all species, except the rice rat, which is perhaps a recent colonizer. Overall, the contrast with the Temperate species is remarkable, and indicates very different population processes through the Quaternary. Fossil pollen studies are also lacking in the Tropics, and there is uncertainty about forest structure over the ice ages (Collinvaux *et al.*, 2000). It seems possible that during the colder, drier stadia, tree species descended in altitude and survived in a patchy network, rather than being restricted to a few refugia. Such a spatial structure would tend to retain genetic diversity, and is supported by these genetic results that record only modest expansion and suggest that larger structured populations survived. This retention of genetic diversity is particularly marked in Tropical mountain regions, which have been proposed as engines of speciation (Fjeldsa and Lovett, 1997). Often, genetic lineages within and among related species are very distinct, suggesting that speciation has been proceeding in these regions from the Pliocene and through the ice ages (Hewitt, 2001). The wet Tropics of NE Australia are also the subject of considerable phylogeographic study (Moritz, 2002), including climatic range

reconstruction to identify refugia (Hugall *et al.*, 2002), and these likewise suggest lineage divergence from the Pliocene.

As the acuity of genetic analyses of past events increases, they may be gainfully applied to phylogeographic data from other regions of the globe. As well as the Tropics, Arctic and Montane biota are now being studied, but information from deserts and oceans is scant. It is important to understand how genetic diversity was molded through the climatic cycles of the Quaternary. Clarifying the structure and location of refugia during climatic change can significantly inform our management of the world's biodiversity.

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