

# Historical Biogeography: The New Synthesis

Since Darwin first noted the impact of past ice ages on the distribution of organisms, biogeographers have debated whether Pleistocene glaciations shaped evolutionary patterns. A new synthesis of population genetics and palaeoclimatology promises unprecedented insights into Pleistocene evolutionary history.

## Christopher Irwin Smith

Seventeen thousand years ago, global temperatures were 5°C cooler than today, glaciers covered much of Earth's temperate regions, and the oceans were 100 meters below the current sea level. Temperate organisms existed in isolated southern refugia, and the tropical forests of the Amazon basin were fragmented into small, disparate patches. At the end of the ice age, rapid climate changes produced dramatic, worldwide shifts in the distribution of plants and animals, from tropical forests to the Arctic Ocean. In 1859, Darwin [1] speculated that these past climate changes, and particularly the isolation of organisms in glacial refugia, might have promoted the formation of new species. Since then, understanding the impacts of past climate changes, including the Pleistocene glaciations, on the evolutionary process has become a major subdiscipline in biology — historical biogeography or 'phylogeography'.

Whether the Pleistocene glaciations promoted speciation and diversification of terrestrial organisms remains a fundamental and controversial question in phylogeography. Whereas some authors have argued that range fragmentations during glacial periods may have served as a 'speciation pump' that caused species to diverge while isolated in small refugia [2,3], many recent studies suggest that most evolutionarily distinct groups diverged from their nearest relatives long before the Pleistocene glaciations [4–7]. As they recently reported in *Current Biology*, Carstens *et al.* [8] took a novel synthetic approach to this question — combining analyses of DNA sequence data with

coalescent simulations and paleoclimate models — which has provided dramatic new evidence of the role of the Pleistocene glaciations in driving evolutionary diversification.

The last twenty years have seen an explosive increase in phylogeography studies, prompted in large measure by the increasing affordability of polymerase chain reaction (PCR) and DNA sequencing technology [9]. Although these studies have demonstrably improved our understanding of population genetic processes in natural populations, throughout the early 1990s phylogeography remained a largely descriptive discipline. Lacking clear null-models of how genetic diversity should be distributed geographically, or a statistical framework with which to test the predictions of those models, many investigators had to resort to *ad hoc* stories to explain phylogeographic patterns. Some studies took a more quantitative approach by using molecular clocks to estimate divergence times between taxa [2], but this method requires both that mutations accumulate at a constant rate and that a reliable estimate of the mutation rate is available — which is rarely the case. Indeed, recent work [10] suggests that weak purifying selection may cause wide variation in substitution rates over different time scales, making it even more difficult to test phylogeographic hypotheses using a molecular clock. These problems have led some to predict a bleak future for biogeography as a discipline.

However, phylogeographers have recently gained two new powerful tools with which to explore past spatial and evolutionary changes. The first of

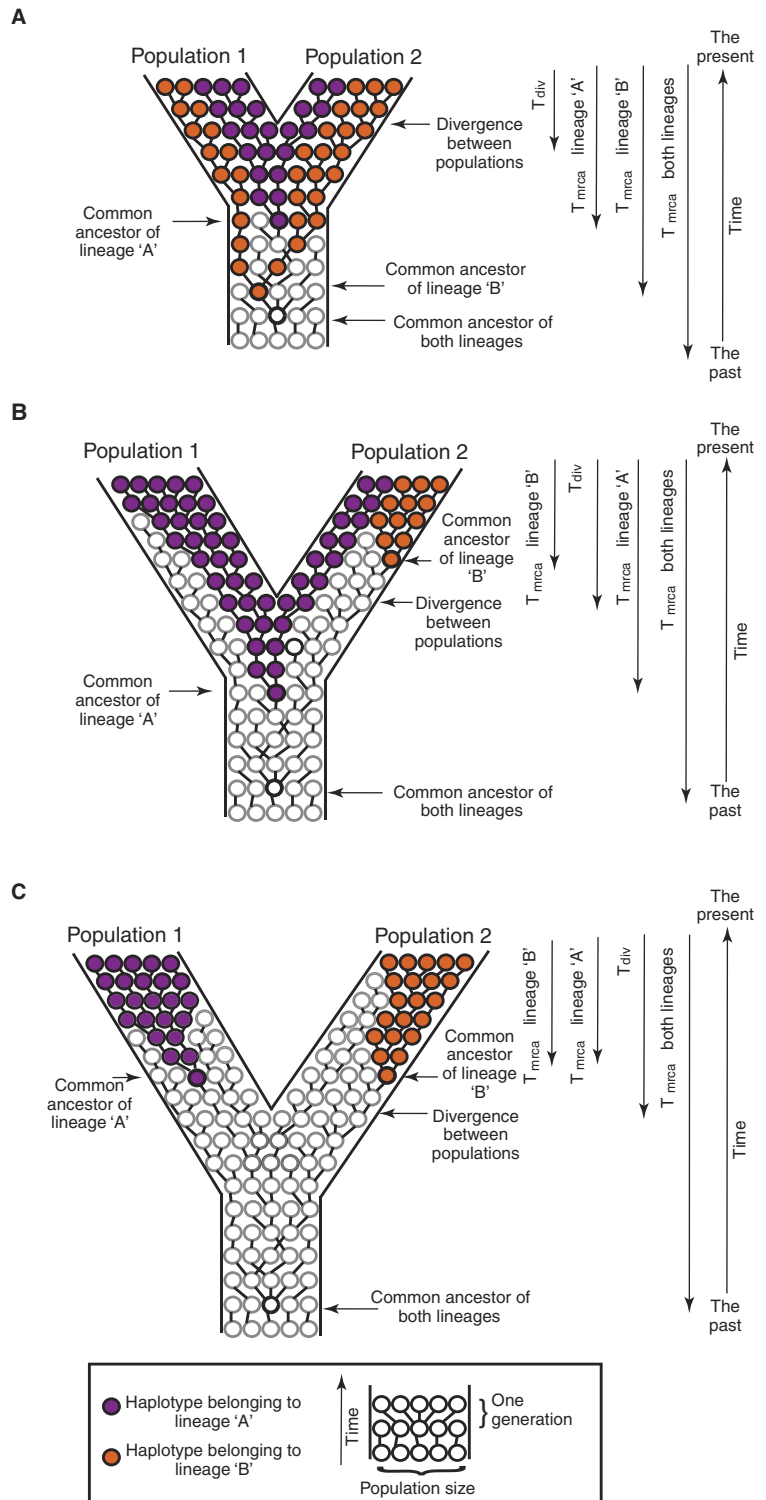
these, ecological niche modelling, combines known distribution data from museum specimens with global climate data to predict all of the areas where a species could exist, given its ecological requirements [11]. By projecting these niche models onto reconstructions of the climate during the last glacial maximum, it is possible to identify areas where particular species might have weathered the ice age [12].

The second, coalescent theory — a division of population genetics based on predictions of the neutral theory — uses probabilistic models to describe the genealogical history of gene lineages through time. By combining predictions from coalescent theory with statistical computing, it is now possible to analyse DNA sequence data and estimate specific population genetic parameters, such as the magnitude of population growth following the end of the ice age [13], rates of migration and gene flow between sub-populations [14], or the number of generations since populations diverged [15]. Using coalescent approaches, it is becoming increasingly practical to test specific questions about how the Pleistocene glaciations shaped the distribution and population genetics of species using robust statistical methods — an approach termed 'statistical phylogeography' [16].

Carstens *et al.* [8] combined these approaches to examine the phylogeographic history of *Melanoplus marshalli*, a species of flightless grasshoppers endemic to the Rocky Mountains of North America. These insects currently occur in high-elevation, mountain-top meadows in Colorado and Utah, but during the last ice age their current habitats were covered in alpine glaciers. To determine where these grasshoppers existed in the past, Carstens *et al.* [8] used ecological niche modelling and palaeoclimate data to identify areas that would have offered hospitable environments at the last glacial maximum. The reconstructed palaeodistribution showed that 17,000 years ago, the grasshoppers

Figure 1. The expected number of deep coalescence events declines as the time since divergence increases.

In this example, two generations after an ancestral population splits in two (A), there are two deep coalescence events. Both daughter populations contain haplotypes belonging to lineage 'A' and lineage 'B', and the time to the most recent common ancestor of each lineage ( $T_{mrcal}$ ) is greater than the time to divergence between the populations ( $T_{div}$ ). Six generations after divergence (B), there is one deep coalescence event. Lineage 'B' has gone extinct in population 1, but lineage 'A' still occurs in both populations and the common ancestor of lineage 'A' predates the divergence between the populations. Eight generations following divergence (C), there are no deep coalescence events. Lineage 'A' has fixed in population 1, lineage 'B' has fixed in population 2, and the time to common ancestry in both lineages is less than the time to divergence between populations.



may have been separated into two isolated refugia — one along the southern edge of the Colorado Plateau in central Arizona and New Mexico, and another in south-eastern Colorado.

To determine whether this apparent isolation could have

promoted evolutionary divergence, and to corroborate the paleodistribution inferred from the ecological niche modelling, Carstens *et al.* [8] used a novel statistical test based on coalescent theory to analyse DNA sequence data from the grasshoppers.

Rather than relying on a molecular clock to determine whether the genetic divergence between extant populations occurred before or after the last ice age, they used a simulation approach to determine the number of deep coalescence events that should be expected

under different demographic histories.

Coalescent theory states that all genes in a population share a common ancestor. How long ago that common ancestor existed is the time to coalescence, or the time to the most recent common ancestor. When a single population diverges into two, initially many genes lineages will have common ancestors that existed prior to divergence of the populations; that is, the time to coalescence of any particular gene lineage will be greater than the time to divergence. These are termed 'deep coalescence' events. As the time since divergence increases, the expected number of deep coalescence events declines, until all of the gene copies in each population share a common ancestor that existed more recently than the divergence between the two populations (Figure 1).

Using data simulations, Carstens *et al.* [8] compared the number of deep coalescence events seen in their data with the number that would be expected if populations diverged either at the onset of the last ice age (~100,000 years ago), or since the ice age ended (~17,000 years ago). These data simulations showed that, if the grasshopper populations had diverged after the last ice age, there should have been many more deep coalescence events than were actually observed in DNA

sequence data from the grasshoppers.

Although phylogeography has fallen out of fashion in recent years, the emerging climate crisis has made understanding past climate changes more important than ever. By integrating palaeoclimatology with coalescent theory, Carstens *et al.* [8] have set a new benchmark for historical biogeography that foreshadows an exciting future for the field. This new synthesis will unite investigators from population genetics, ecology, and climatology into a new science of biogeography that will continue to flourish through the next century.

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Department of Biological Sciences,  
University of Idaho, Moscow, Idaho  
83844-3051, USA.  
E-mail: csmith@uidaho.edu

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## Polarized Cell Growth: Double Grip by CDK1

Precise coupling of cell growth and cell-cycle progression is crucial for achieving cell homeostasis. A recent study sheds light on two distinct roles of cyclin-dependent kinase 1 (CDK1) in promoting polarized cell growth in budding yeast.

Giulia Rancati and Rong Li

Cell-size homeostasis is an important requirement for cell proliferation. Many efforts have been devoted to tackling this classic problem, but it remains unclear how cell growth is coordinated with cell division [1].

In the current view, cell growth and cell-cycle control are considered separate processes that are linked through dependency mechanisms. Most published studies have focused primarily on two questions: how a cell-size threshold is set; and how this threshold impinges upon the

cell-cycle regulatory system governed by cyclin-CDK complexes. The budding yeast *Saccharomyces cerevisiae* has been a useful model for studying the coupling between growth and cell-cycle progression. Existing evidence suggests that yeast cells assess their growth status by measuring the rate of translation as a function of cell volume [1]. A threshold translation rate allows accumulation of G1 cyclin, which leads to activation of CDK1 and entry into S phase through complex mechanisms. In addition, inhibition of CDK1 activity before S-phase entry permits cell growth, albeit in an isotropic fashion [2,3].