

Climate change and the migration capacity of species

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In a recent paper, McLachlan *et al.* presented evidence that migration rates of two tree species at the end of the last glacial (c. 10–20 thousand years ago) were much slower than was previously thought. These results provide an important insight for climate-change impacts studies and suggest that the ability of species to track future climate change is limited. However, the detection of late-glacial refugia close to modern range limits also implies that some of our most catastrophic projections might be overstated.

The migration rate debate

Studies that predict the potential impacts of future climate change on biodiversity usually consider two scenarios regarding the ability of species to track the changing conditions: either unlimited or no dispersal [1–3]. In reality, the migration capacity of species is likely to fall somewhere between the two; however, the degree to which species can achieve rapid large-scale migrations is still poorly understood [4]. New molecular evidence reported recently by McLachlan *et al.* [5] suggests that migration rates of two North American tree species (American beech *Fagus grandifolia* and red maple *Acer rubrum*) at the end of the last glacial [c. 10–20 thousand years ago (ka)] were much slower than has previously been deduced from the fossil pollen record. These findings provide an important warning as to the limited potential for species to keep pace with future climate change.

Predicting migration rates

Interpretations of fossil pollen data have suggested that rapid migration, of the order of 100–1000 m y⁻¹, was typical for tree populations responding to postglacial warming in North America [6] and Europe [7]. These rates are difficult to explain using our current knowledge of tree demography and seed dispersal; a problem commonly termed ‘Reid’s paradox’ in recognition of the difficulties faced by Victorian botanist Clement Reid when trying to understand the postglacial spread of oaks into the UK [8]. Long-distance dispersal via diverse mechanisms, including transportation of seeds in updrafts and by birds in nest material, has been implicated as a possible explanation for the paradox [4,8,9].

However, alternative theories propose that colonization was achieved by local dispersal from isolated populations that persisted in microclimates during periods when the

regional climate was unsuitable [10,11]. Such low-density populations do not show up in the pollen record, but might have been present well beyond the reconstructed range margins that have been used to infer rapid migration rates. By studying genetic structures within modern populations, McLachlan *et al.* [5] have added significant weight to the theory that colonization was driven by local dispersal from disjunct glacial refugia (Box 1).

Implications for future projections

Estimates of the migration rates that will be required for plant species to keep pace with human-induced climate warming over the coming century are commonly > 1000 m y⁻¹ [12]. The supposed rapid postglacial migration of trees is often cited as reason for optimism that such rates might be attainable, yet the postglacial rates estimated by McLachlan *et al.* [5] are an order of magnitude slower (< 100 m y⁻¹) than those required. If our cause for optimism is unfounded, trees will be unable to keep up with the changing climate and we might expect future impacts of climate change on biodiversity to adhere closest to the ‘no dispersal’ scenario used in impacts models.

For example, Thomas *et al.* [2] estimated species-level extinction risk from climate change for 1103 endemic animals and plants from sample regions that cover ~20% of the surface of the Earth. Using projections of maximum expected climate warming for 2050, the authors estimated the percentage of species ‘committed to extinction’ to be 21–23% with unlimited dispersal, compared with 38–52% with no dispersal. Based on our revised understanding of migration capacity, the extinction risk from climate change could be expected to be more at the ominous end of this spectrum.

It’s not all bad news

Although McLachlan *et al.* [5] provide yet more warning as to the potentially severe effects of climate change on biodiversity, there is an important additional interpretation of their findings. If postglacial colonization from isolated refugial populations was common, then the concept that species respond to climate change by undergoing large-scale distribution shifts to track optimal conditions might be erroneous. Instead, the ability of species to maintain low-density isolated populations for long periods of time while the regional climate is unsuitable becomes of paramount importance. This ability provides a fundamental challenge to the ‘bioclimate

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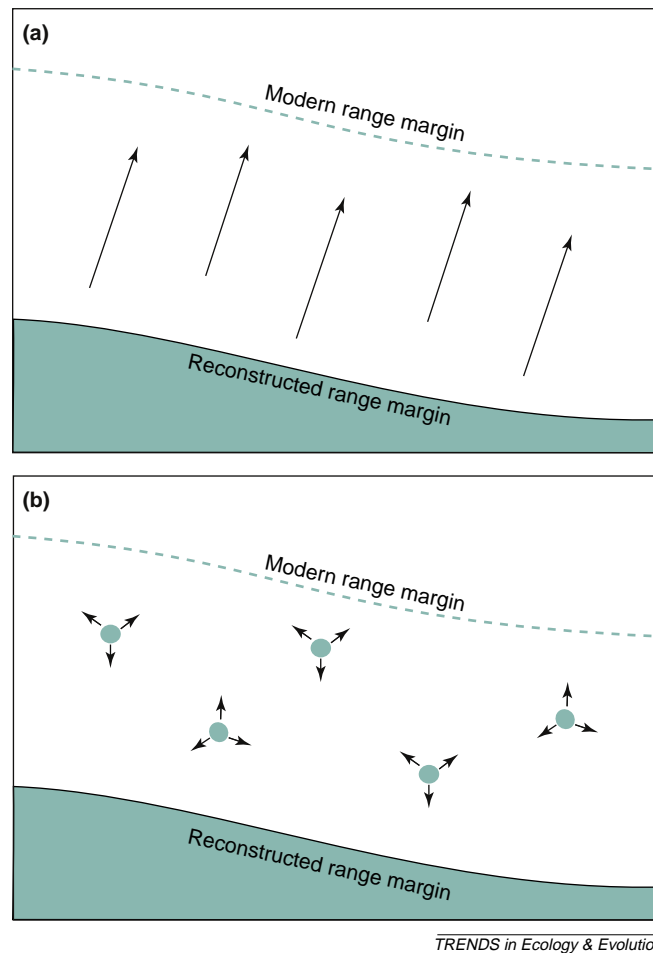
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Box 1. Fossil pollen versus molecular data

Fossil pollen recovered from sediments has been widely used to estimate range margins over successive time intervals during the last late glacial (c. 10–20 ka [6,7]). These reconstructed range margins suggest that past rates of tree migration have been as fast as 100–1000 m y^{-1} . However, a significant weakness of the fossil pollen record is that the absence of pollen in samples of sediment does not rule out the possibility of small low-density populations [5].

McLachlan *et al.* [5] used chloroplast DNA surveys of American beech *Fagus grandifolia* and red maple *Acer rubrum* from eastern North America to analyze genetic variation across the present-day range of species to provide a record of late-glacial migration routes that is independent of the fossil record. Because it is likely that modern cpDNA haplotypes pre-date postglacial colonization (mutation rates in the chloroplast genome are low), and because there is little gene flow into established populations, the modern geographical distribution of cpDNA haplotypes can be used to infer past migration dynamics. Molecular data are particularly valuable compared with fossil pollen records because genetic structures are highly sensitive to the role of small populations, owing to the strong impacts of founding effects and genetic drift within small populations [5].

McLachlan *et al.* [5] found that genetic structure across modern ranges implies a different process of colonization to that reconstructed from fossil pollen. In particular, the new molecular evidence suggests that American beech and red maple persisted as low-density populations much further north than was previously thought, possibly within 500 m of the Laurentide ice sheet, which spread as far south as $\sim 37^{\circ}\text{N}$. The existence of refugial populations means that much slower migration rates ($< 100 \text{ m } y^{-1}$) can be inferred compared with the rapid rates suggested by the fossil pollen record. Molecular evidence thus provides an important insight to the mechanisms by which trees achieved rapid colonization in response to past rapid climate change (Figure 1).



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Figure 1. Alternative mechanisms to explain rapid colonization of trees in response to late-glacial (c. 10–20 ka) climate warming. Green shading depicts areas occupied by a species and arrows illustrate migration either through long-distance (a) or local (b) dispersal processes. (a) Migration from an advancing range margin via long-distance dispersal. This mechanism is commonly inferred from fossil pollen records, which show range expansions over large regions as the climate warmed. (b) Local dispersal from isolated populations that persisted in microclimates when the regional climate was unsuitable. The pattern of spread is like a rash, with migration proceeding from multiple localized sources.

envelope' models that are often used to project future impacts on biodiversity [13].

Bioclimate envelope models use associations between environmental variables and known distributions of species to define environmental requirements that can be projected under scenarios of future climate change. The models predict large-scale distribution shifts and are

usually run at coarse spatial resolutions, for example across $50 \times 50 \text{ km}$ cells [3]. By averaging climates over large cells, the models do not incorporate localized microclimates within which low-density populations can persist. Thus, just as the fossil pollen record is too coarse to identify small populations, bioclimate envelope models might be too coarse to incorporate a key mechanism by

which species can persist through rapid changes in climate. The result will be overly pessimistic predictions of extinction risk from climate change.

Prospects

New research is constantly improving our understanding of the responses of species to climate change, yet often reminds us that current knowledge is inadequate, and that predictions of future impacts are fraught with uncertainty. To improve predictions of climate-change impacts on biodiversity, new modeling approaches are required that address fine-scale impacts and that can identify potential refuges from conditions that are regionally unfavorable. Unfortunately, such efforts are likely to be hampered by the difficulties of making regional climate-change predictions [14]. There is also the need to use more dynamic and mechanistic modeling approaches that integrate envelope models of environmental requirements with simulations of the dispersal of species across landscapes.

In light of McLachlan *et al.*'s study [5], such dispersal models should not rely on extraordinarily rare long-distance dispersal events to achieve rapid migrations, but should instead incorporate dispersal and life-history traits (e.g. seed production and survival) that limit migration capacity [15]. In addition, models will be required to incorporate land-use data alongside climate-change scenarios, because modern human-dominated landscapes are very different from those at the end of the last glaciation. Furthering our understanding of past responses to climate-change gives an important insight into what responses we can expect in future, yet the magnitude of impacts on biota caused by anthropogenic climate change remains difficult to predict. The article by McLachlan *et al.* [5] provides reason to think that some of our most catastrophic projections of climate-change impacts might be overstated, yet the low potential for rapid migration implied by the new analysis gives no cause for optimism.

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Root foraging theory put to the test

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Roots have a tremendous plasticity that has long fascinated plant scientists. Root proliferation into enriched soil patches is commonly considered as a way for plants to acquire patchily distributed soil resources. In a recent synthetic study involving the responses of over 100 species, Kembel and Cahill

concluded that long-standing generalizations explaining variation in root proliferation should be reconsidered.

Root proliferation and foraging precision

Systematic experimental research into root proliferation began during the 1970s, with experiments by Drew and co-workers with barley *Hordeum vulgare* [1]. Their results demonstrated that plants whose main roots were only

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