
Chapter 11

Plant Species Migration as a Key Uncertainty in Predicting Future Impacts of Climate Change on Ecosystems: Progress and Challenges

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11.1 Introduction

The prediction of climate change impacts on ecosystems is a challenging problem that has been addressed by both modeling and experimental approaches. The many varied experimental (e.g., Beier et al. 2004) and observational approaches (e.g., Parmesan and Yohe 2003) to investigating ecosystem and species responses to climate change are not addressed here. Modeling approaches also vary widely in approach and scale, from local “patch” scale simulation of system processes and competitive interactions (Shugart et al. 1992; Solomon 1986) to global scale simulation of vegetation functional and structural types (Prentice et al. 1992; Woodward et al. 1995). At “intermediate” geographic scales of landscapes and regions one modeling approach taken has been species-based, with the unit of simulation being the species’ geographic range (Guisan and Zimmermann 2000; Huntley et al. 1995; Peterson 2001). Simulation approaches at local and global scales mentioned above are strongly process-oriented. They ignore species range preferences evident at the intermediate landscape and regional scale, and by default assume that a global species or functional pool is available to colonize each site, should environmental conditions be suitable at that site. This has largely concealed a key uncertainty in predicting ecosystem responses to climate change – that which is governed by the underlying spatial rearrangements of species’ geographic ranges.

It is widely accepted that climate change impacts on natural species and communities will affect the geographic ranges of species (Parmesan and Yohe 2003; Walther et al. 2002). Indeed, early signs of climate change may be identified by species range shifts (Walther et al. 2001), strongly supporting the idea that range shifts are likely to continue in a larger number of species, and enhancing the possibility for new species invasions (Mooney and Hobbs 2000). What are the implications for predicting vegetation change in response to climate change? Importantly, species in existing plant communities are unlikely to possess similar migration capabilities, and as a result of differential migration and persistence, the communities of the future are unlikely to maintain the composition of those of today with novel com-

munities likely to emerge (Neilson et al. 2005; Pitelka et al. 1997). Clearly, predictions of changing ecosystem function need to account for the species-specific range shifts that may result, apart from the direct conservation need to identify which species are not likely to migrate, and may therefore suffer range reductions and the threat of extinction (Thomas et al. 2004; Thuiller 2004). Considerations of migration and geographic range shift therefore have two direct applications – to modellers of ecosystem function whose models are underpinned by the presence of species with particular functional traits as ecosystem components, and to conservation planners who need to assess threats to biodiversity (Hannah et al. 2002).

The migration capabilities of organisms depend fundamentally both on the distances offspring move from their parents (dispersal) and on the number of offspring a parent produces (Skellam 1951). A great variety of processes is responsible for moving diaspores (Ridley 1930), hence predicting the distances that diaspores move is no trivial task (Higgins et al. 2003; Nathan et al. 2003). Similarly, the diverse range of processes that determines the number of offspring that individuals produce means that forecasting rates of population increase is a complex task (Neubert and Caswell 2000). Research on predicting migration rates has more recently sought to understand the extent to which migration rates are demographically or dispersal limited (Clark et al. 2003).

It is clear that the structure and composition of the world’s vegetation can be broadly correlated with climate regime, but it is far more complex to derive from this observation the mechanisms that may drive range shifts as climate changes. This is for three main reasons: First, it is not known what proportion of the world’s species have current geographic ranges which are directly controlled by climate and not by other determinants such as disturbance regime (Bond et al. 2003), human land-use (Hobbs 2000), or strong inter-species interactions (either mutualistic or antagonistic) (Davis et al. 1998). Such factors are at most only indirectly linked to climate. Second, even if we knew precisely how climate controlled species ranges, it would remain a substantial challenge to predict how ranges might change dynamically due to lags in adult mortality and range contractions, which might delay range responses as climate changes. Third,

human impacts that have fragmented the landscape and altered populations of biological dispersal vectors (Janzen and Martin 1982) have introduced barriers and filters to the dispersal and establishment of propagules. Many of these factors will retard migration rates (Collingham et al. 1996; Higgins et al. 2003; Schwartz et al. 2001). Other human activities, such as human mediated dispersal (Hodkinson and Thompson 1997) may accelerate spread rates. Plant species migration therefore represents a major uncertainty in the prediction of vegetation response to climate change (Higgins et al. 2003).

In spite of the problems identified above, there has been significant progress in modeling plant species' ability to migrate, driven by the need to project threats both of invasions by alien species and climate change to biodiversity (Clark et al. 2003). In this chapter, we review this progress in broad terms, and identify some key challenges and opportunities that remain.

11.2 Will Migration Be Necessary for Species Persistence?

Four broad responses may follow when populations of sessile organisms are confronted with a change in environmental conditions that compromise their physiological performance, namely local extinction, *in situ* persistence, *in situ* adaptation over generations (also termed an orthoselective response), and migration (Barnosky 1987). These responses are not all mutually exclusive, but may occur concurrently. For example, genetic patterns documented in several tree species reveal the synergistic effect of apparently recent (post-glacial) concurrent migration and selection in spatially separated populations (Cwynar et al. 1987; Davis and Shaw 2001).

In situ persistence is essentially a first line of defense for sessile organisms that can be accomplished either through high levels of tolerance and a long life span of the vegetative stage, or longevity and dormancy of propagules. Many species of extreme environments have evolved significant abilities to persist under adverse or unpredictable conditions, such as the propagules of desert annuals (van Rheede van Oudtshoorn and van Rooyen 1999), or long-lived trees (Bond and Midgley 2001). Persistence may allow many species of extreme environments to maintain a presence in the landscape long after suitable climate conditions have changed. Indeed, it now seems as though populations situated at the so-called "rear edge" of a species' geographic range undergoing a spatial shift are particularly important for the persistence of genetic diversity and evolution of species (Hampe and Petit 2005).

Genetic selection and adaptation is possibly an underappreciated control of species response to climate change (Davis and Shaw 2001), bearing in mind that rapid

genetic change via selection under future anthropogenic climate change is possibly only relevant for the shortest-lived plant species. Nonetheless, selection by past climate change may determine current-day spatial variation in physiological optima of broad-ranging species in ways which affect predictions of species responses to climate change. For example, the response of the evergreen gymnosperm *Pinus contorta* to climate change and atmospheric CO₂ rise reverses from being positive throughout its range (if a single optimum genotype is assumed to inhabit the entire species range), to becoming slightly to strongly negative given the current distribution of varying genotypes (Rehfeldt et al. 1999). Nowak et al. (1994) illustrate a range of migration and adaptive responses to Pleistocene-Holocene change in woody plant species of the northwestern Great Basin, and demonstrate the clear existence of "orthoselective" species. These are species that possess high levels of genetic variation that permit their *in situ* persistence during periods of climate change through local selection of pre-adapted genotypes. The factors that determine adaptive plasticity are likely complex and species-specific, and it is too early to be able to generalize about how this response will emerge as anthropogenic climate change continues, but the topic deserves more attention in the context of species persistence.

There is currently no analysis available of what proportion of local, regional or global floras may persist or adapt to climate change *in situ*, but it is widely recognised that migration to keep pace with suitable climate conditions is a necessary response in organisms that lack extreme stress tolerance, longevity or genetic plasticity. Indeed, the rate and amount of climate change may ultimately exceed the capacity of either of these *in situ* responses. Studies of paleo-records strongly suggest that migration has been a widespread response to climate change in Pleistocene floras (e.g., Davis 1976; Davis 1983; Huntley 1990; Huntley and Birks 1983; Webb 1981; Webb 1992) and faunas (Graham 1992) and early monitoring efforts have identified incipient range shifts already occurring in response to recent climatic changes (Parmesan et al. 1999; Parmesan and Yohe 2003).

Spatially distinct genetic patterns in lodgepole pine in western Canada have been ascribed to migration accompanied by selection during post-glacial times (Cwynar et al. 1987), and Davis and Shaw (2001) illustrate several examples of concurrent genetic adaptation and migration, most conclusively for Scots Pine which has migrated extensively in northern Europe since the Last Glacial Maximum, and now shows physiological responses to climate cues that vary depending on the geographic provenance of the species. Thus, a combination of migration and concurrent selection has interacted to allow this species to occupy a range that is potentially wider than if the species had remained genetically homogeneous across its range.