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 communities 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 worlds 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 CO_2 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 homogenous across its range.

It is also apparent that the relative migration capabilities of species are reflected in the global patterns of biodiversity rich regions (e.g., Myers et al. 2000). It seems likely that Pleistocene climatic oscillations between glacial and interglacial climatic conditions have repeatedly sifted local biota according to their migration capabilities, and those regions which were exposed to relatively low rates and amounts of climate change have retained higher numbers of species as endemics (Jansson 2003). This pattern strongly suggests that migration has been a key determinant of the current global distribution of biodiversity, and that high rates of migration across the board are unlikely. Indeed, in the mid-latitude western Cape region of southern Africa, the key characteristics of an endemic include the likelihood of its being ant-dispersed (McDonald and Cowling 1995).

Given expected rates of anthropogenic climate change, what migration rates are required to allow species or species assemblages to keep pace? Two approaches have been taken to address this question. The first is derived from modeling global vegetation types using Dynamic Global Vegetation Models (DGVMs), and the second from modeling individual species ranges.

11.2.1 Vegetation-Type Models

Enhanced DGVMs represent one of the key products of the GCTE project (Cramer et al. 2001), and were designed to model ecosystem processes as determined by interacting vegetation and biogeochemical cycles (e.g., Bachelet et al. 2003; Box 1996; Foley et al. 1998; Holoyac 2000; Kirilenko et al. 2000; Sitch et al. 2003; Smith et al. 2001). Because of their complexity and the resultant computational demands in running them, DGVMs that simulate global vegetation structure and function commonly run at coarse spatial scales – typically more than 2 × 2 degrees of latitude and longitude (although they may be run at a rather fine temporal scale of days to hours and even minutes for some key processes such as photosynthesis). Given that propagule dispersal by plants only approaches distances appropriate to this coarse scale under extremely rare circumstances, DGVMs were clearly never designed to estimate migration requirements under climate change scenarios, but nonetheless have been used to do so (e.g., Malcolm et al. 2002).

Analyses of the required migration rate for ten biome types (representing between 60 and 80% of the Earth's surface) simulated by two vegetation models was estimated to be predominantly in the <300 m yr^{-1} range (Malcolm et al. 2002). For a minority of biome types (representing between 10 and 20% of the Earth's surface) required migration rates of between 1 000 and 10 000 m yr^{-1} were estimated (Fig. 11.1), not exceeding by far rates of migration recorded in the paleo-record (e.g., MacDonald 1993). The lowest required migration rates were found in tropical latitudes, but this increased strongly at latitudes of 40° and higher, such that temperate and circumpolar biomes had higher required rates than did tropical and subtropical biomes.

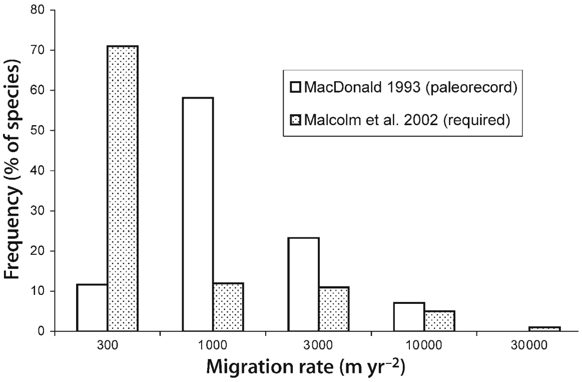

Fig. 11.1. Frequency distribution of post-glacial migration rates (from MacDonald 1993) in relation to required migration rates (from Malcolm et al. 2002). *x*-axis labels represent upper bounds of the migration rate categories

The concept behind Malcolm et al.'s (2002) analysis has been justifiably criticised (Loehle and LeBlanc 1996). Indeed, plant assemblages have never been stable through past variations in climate (Prentice 1986; Webb 1981). Many modern species assemblages do not appear to have long histories (Birks 1993; Davis 1983) and therefore communities or biomes are thought unlikely to move as an entity under changing environment conditions (Birks 1986; Huntley and Webb 1988).

Given the limitation of modeling vegetation types or biomes as whole entities, we analysed, for the purposes of this chapter, the required migration rates of individual plant functional types that define the world's biomes in the Sheffield DGVM (SDGVM, Woodward et al. 1995). In this DGVM, the geographic limits of individual functional types are defined by their physiological tolerances and performance relative to competing functional types. Biomes are then mapped using the relative composition of functional types. This approach is more justifiable than that of Malcolm et al. (2002) for a number of reasons. Most important is the fact that biomes may share functional types (and even species) with adjacent biomes, and the Malcolm et al. (2002) approach therefore overestimates required migration rates of shared functional types.

Our results for SDGVM are presented at a coarse spatial scale (Fig. 11.2) but nevertheless show that all functional types modeled show some migration to new ranges (Table 11.1), and that the most significant required migration rates are for temperate, subtropical and tropical functional types (C_3 shrub/grass, C_4 grass and deciduous broad-leaved tree functional types). Required migration rates are evenly spread with latitude, in contrast to the strong latitudinal patterning predicted by (Malcolm et al. 2002). This lack of latitudinal trend in our analysis is due partly to modeling relatively few functional types, which increases the likelihood of types being shared by

Fig. 11.2. Global map of 3.75 × 2.5° pixels which experience the arrival of a novel plant functional type as projected by the SDGVM (Woodward 1995) using a climate change scenario for ~2050 according to the GCM HadCM3 (different *colours* represent the number of novel PFTs migrating into a cell, *green* = 1 PFT, *blue* = 2 PFT, *red* = 3 PFT)

Table 11.1. Migration rates of 6 major plant functional types in terms of numbers of 2.5° pixels (median shift, mean shift and standard error), as projected by the SDGVM (Woodward 1995) using a climate change scenario for ~2050 according to the GCM HadCM3

PFT	C3	C4	Dcbl	Evbl	Dcnl	Evnl
# pixels	251	56	29	67	55	15
Median shift	4.5	3.75	3.75	2.5	2.5	2.5
Mean shift	8.33	4.50	4.93	3.47	3.77	4.37
Std error	0.47	0.37	0.68	0.20	0.29	0.81

adjacent geographic pixels. As such, these results are not directly comparable with those of (Malcolm et al. 2002). However, despite differences in approach, both analyses underline the central message that biogeochemically-based modeling approaches of vegetation predict a substantial requirement for migration of biomes and functional types to new geographic ranges.

The need to incorporate dispersal limitations into DGVM forecasts has been recognised for some time (e.g., Pitelka et al. 1997), but the challenges are substantial. A recent treatment (Neilson et al. 2005) has reiterated that, apart from the challenge of simulating dispersal realistically at such coarse spatial scale, it is difficult to assign a distribution of potential migration rates to plant functional types. This is because plant functional types group species based on functional or vegetative attributes (Smith et al. 1997), and there are not yet well known relationships between these attributes and attributes of fecundity and dispersal. Several issues need to be considered when trying to generalize species-specific knowledge about dispersal and fecundity. For example, how does dispersal ability relate to traits that define either the response to environmental factors or ecosystem functioning (Lavorel and Garnier 2002), and on what basis should functional types be split to distinguish between poor and good dispersers?

It is clear that by incorporating greater scientific understanding of plant functional types and a necessary increase in computational power, future DGVMs will resolve functional types more finely, and operate at finer spatial scale. It may, therefore, become feasible to assign dispersal and fecundity characteristics to functional types that more closely represent groups of species and even individual species, and model their migration more credibly. This step will be critical to allow DGVMs to account for lags in ecosystem response to climate change induced by migration limitations (Neilson et al. 2005), which currently introduce is ignored as an uncertainty in DGVM simulations.

11.2.2 Species-Based Models

Species-based approaches (also called niche-based models) have received increasing interest in the past decade because of their apparent ability to project the potential geographic range responses of multiple species, finally allowing some quantification of species' range shifts in response to climate change. Several recent studies have applied this class of models to generate and estimate risk of species extinctions (Thomas et al. 2004), as well as species' range shifts, species turnover, and variation in species richness (Iverson and Prasad 2002; Bakkenes et al. 2002; Thuiller 2003; Schwartz et al. 2001; Peterson 2003), under global climate change. Recent steps have included the use of species-based models to select areas for species persistence (Araújo and Williams 2000) and to assess the persistence of species in existing reserve networks in the face climate change (Araújo et al. 2004).

Despite considerable research on statistical models of species-climate relationships and their application to climate change studies, the uncertainties in forecasts of such models arising from ecological and methodological considerations have not so far been estimated. Species-based approaches have primarily been derived by developing statistical relationships between known species ranges and environmental variables taken as surrogates for physiologically relevant variables (Austin et al. 1994; Austin and Smith 1989; Guisan and Zimmermann 2000). The approach relies heavily on the concept of Hutchinson's realized niche, recently clarified by Leibold (1995) and Pulliam (2000). In this regard, the most frequent oversimplification found in the literature is the statement that, due to the observed distributions being constrained by biotic interactions, species-based approaches *de facto* quantify the realized niche of species, and never the fundamental niche (Pulliam 2000). As a direct consequence, projecting these models into climatically changed future conditions is, at least according to theory, likely to generate mistakes (Davis et al. 1998), but see Pearson and Dawson (2003) and reply from Hampe (2004).

The degree of error in predictions of niche-based models should thus be related in some way to the competitive status of the species for a given resource (weak vs. strong competitor), which in turn should allow the prediction of whether the species occupies its full fundamental niche or only part of it. Recent analyses have shown that it may be possible to include inter-specific competition in these models (Leathwick and Austin 2001; Anderson et al. 2002) but the competitive status of species can also be expected to change with a changing climate (Davis et al. 1998; Hughes 2000).

A further source of uncertainty is due to the fact that these models are static in space and time and are conceptually unable to cope with non-equilibrium situations, since they do not distinguish between the transient and equilibrium responses of species to a stochastically and dynamically changing environment (Guisan and Zimmermann 2000). As a direct consequence, they cannot theoretically include migration in a dynamic way. To cope with this limitation, recent risk assessment analyses for future climate change scenarios have commonly used two crude assumptions about migration, namely no migration beyond a species present site ("zero migration" or "null migration") and perfect migration to all sites, or "full migration" (Peterson et al. 2002; Thomas et al. 2004; Thuiller 2004). These approximations bracket the most pessimistic and optimistic estimates of future species range size, but have so far incorporated only the simplest migration limitations (i.e., migration into contiguous elements of the modeled landscape (Peterson et al. 2002)) to refine these estimates. The projected impacts of climate change on species turnover (an index of community compositional change and probably linked with ecosystem function) are very strongly influenced by the contrasting migration assumptions of zero and universal migration (Fig. 11.3), and this clearly demonstrates the current limitation in forecasting climate change impacts on biodiversity, and ecosystem structure and function, induced by uncertainties in migration rate.

11.3 Measurements and Models of Migration Rates

Much of our understanding of plant migration is derived from paleo-botanical studies of northern hemisphere regions (Davis 1976; Huntley and Birks 1983; Webb 1992). These studies indicated that several tree genera appeared to migrate rapidly from equatorward "refugial" populations of the Last Glacial Maximum (LGM), some 20 000 years ago, to occupy their current ranges several degrees of latitude poleward. Although some of these

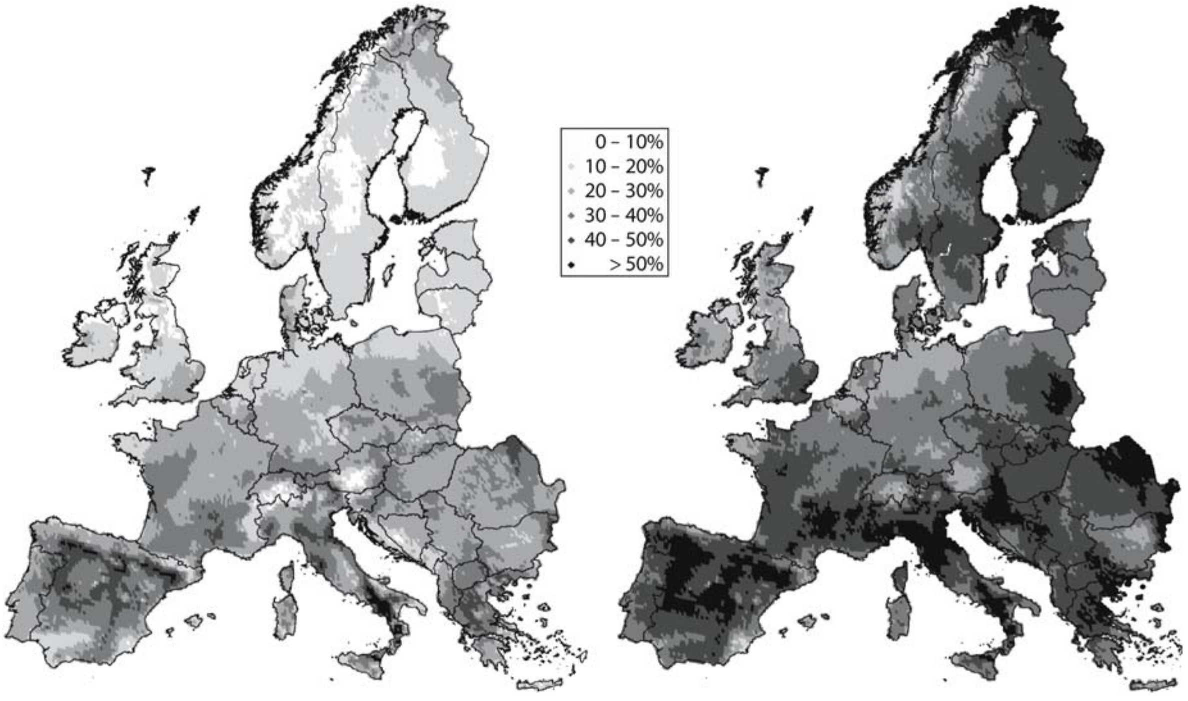

Fig. 11.3. Rate of plant species turnover in Europe for a climate scenario simulated by the GCM HadCM3 under the A1 SRES assumptions (Nakicenovic and Swart 2000), assuming either no species dispersal (*left hand panel*), or universal dispersal (*right hand panel*)

paleo-botanical studies have recently been questioned (e.g., McClachlan and Clark 2004), the balance of evidence suggests that rapid spread (>100 m yr^{-1}) is possible, at least for some species. This apparent empirical evidence for rapid migration cannot be reconciled with models of plant spread that assumed that dispersal should be approximated as a diffusion process (Skellam 1951). This conundrum (termed "Reid's paradox" by Clark et al. 1998) was resolved by re-examining the simple diffusion assumption that lies at the heart of classical models of spread. Relaxing the assumption that the distribution of seed dispersal distances is Gaussian was found to be consistent with empirical data on the distribution of seed dispersal distances. Moreover, the resulting spread rates were consistent with the rates estimated from the paleo-ecological evidence (Clark 1998; Higgins and Richardson 1999). Hence a new class of spread models have emerged that essentially all treat dispersal as a stratified process (Shigesada et al. 1995). That is, they accommodate the possibility that most diaspores move relatively short distances and that a few diaspores move relatively long distances.

The "resolution" of Reid's paradox has shifted attention away from dispersal and focused it on the other component of spread models, namely the demographic component (Clark et al. 2003). Our empirical knowledge of demographic rates suggest that most populations are neither increasing nor decreasing, that is they have population growth rates close to zero (Franco and Silvertown 2004). A population with a zero growth rate cannot spread, hence most populations for which we have empirical data on demographic rates would be predicted not to spread. However, growth rates could become positive as a result of disturbances caused by climate change, due to the opening up of new geographic areas suitable for occupation by species. Very little is known about how rapidly population growth at the margins of species' ranges will respond to an "improving" climate, and the new availability of space in adjacent areas.

Most data on demographic rates are, for practical reasons, collected from sites where the study species are common (e.g., Sagarin and Gaines 2002), but the demographic rates estimated at such sites are not representative of the conditions to which a spreading population may be exposed. Ideally demographic parameter variation needs to be estimated from the so-called "core" to the edge of species ranges – seldom done, such an approach may yield useful insights into demographic factors controlling range limits (e.g., Brewer and Gaston 2003). It seems especially at range edges that this information could contribute to a fuller understanding of the vulnerability of marginal populations to temporal variability (Vucetich and Waite 2003).

Spreading alien invasive species provide an opportunity to estimate the demographic rates that are appropriate for spread models. For instance, Higgins (2001) estimated demographic and dispersal parameters for spreading invasive plants. While much can be learned from the spread of invasive species about the potential spread of native species under climate change, several factors mean that the knowledge gained is not directly transferable. Notably, spreading alien species are often demographic super-organisms because of predator and competitor release (Keane and Crawley 2002). This suggests that to forecast the spread rate of native species under climate change we need to estimate the likelihood that predators and competitors will accompany the target species, which is clearly a complex task. Nonetheless, studies of invasive plants do reveal the complexities of predicting whether a species that appears to be physiologically suited to a site will indeed invade that site. This subject has both entertained and frustrated invasion biologists for decades, and although significant progress has been made, experience from invasions suggests that our predictive power remains modest (Rejmanek et al. 2004). Studies of spreading invasives also inform us that alien species will migrate rapidly; simple calculations based on the differences in demographic rates between native and alien species with similar life histories suggest that aliens will indeed migrate orders of magnitude faster than native species (Richardson et al. 2000).

A great difference for plants between past episodes of climate change and the current anthropogenic warming is the human alteration of landscapes, involving fragmentation of pristine habitat into patches of varying sizes and connectivity, and the creation of barriers to dispersal. Theoretical models of spread in landscapes influenced by fragmentation and habitat loss show that there may be critical thresholds in landscape connectivity beyond which migration processes cease (Higgins et al. 2003), but the data needed to test these models are far from complete, and will be very challenging to collect. More detailed models of spread that include occasional long distance dispersal have demonstrated that although thresholds may not exist, linear decreases in spread rate with increasing fragmentation and habitat loss are to be expected (Collingham and Huntley 2000; Higgins and Richardson 1999; Lavorel et al. 1995; Malanson 2003). These studies emphasize that additional dispersal traits that define how dispersal will interact with human-transformed landscapes, are needed to predict spread rates in contemporary landscapes (Higgins et al. 2003).

11.4 Linking Migration and Niche Based Models

The previous section has reviewed how an incomplete knowledge of the potential migration rate of species limits our current capacity to predict the impacts of global climate change on the future geographic distribution of species, their range sizes and even potential vulnerability to extinction. Yet very few studies have combined mechanistic models of migration with spatially-explicit models of geographic range shifts. Niche-based models offer a potentially useful tool to predict species range shifts for indigenous species, and even areas susceptible to invasion by alien species (albeit these correlation approaches can only interpolate, not extrapolate into the future). Recent studies (Hoffman 2001; Peterson 2003; Peterson et al. 2003; Peterson and Vieglais 2001; Welk et al. 2002) have shown that this approach could provide a robust alternative to more complex, process-based models (Sutherst et al. 2000). However, despite the usefulness of such niche-based models in drawing potential maps of risk, species migration is not routinely incorporated in this approach.

Some preliminary attempts to integrate niche-based models and mechanistic dispersal models have been carried out. For instance, Iverson, Schwartz and colleagues (Iverson et al. 2004; Schwartz et al. 2001) have recently developed interesting analyses to predict the shift of trees due to climate changing in eastern US, based on the coupling between a niche-based model simulating the future potential suitable area for a species, and a cellular automaton simulating seed dispersal into a fragmented landscape. Such "hybrid" approaches combining different models are promising because they allow inclusion of transient responses of species to changing environments (see also Collingham (2000) and Malanson (2003)). These approaches are also useful in that they encompass a spatial scale within which migration can be simulated realistically, especially by differentiating between long- and short-distance dispersal of propagules, and assessing the relative importance of uncertainty inherent in their estimation. More studies of this kind are needed in order to develop better forecasts of future species range size, distribution and vulnerability to extinction under a wide range of migration rate assumptions (Higgins et al. 2003).

11.5 Summary and Conclusions

As we show above, a failure to incorporate migration limitations into models of vegetation response to climate change greatly compromises their predictive capability, and the uncertainty due to migration is therefore substantial. Species range shifts have been a ubiquitous response by plant species during Pleistocene climate change, and early signs of this response are evident in modern assemblages. Recent work has increased our understanding of the dispersal limitations to migration rate, but there has been far less focus on the issues which govern population establishment and growth rate, especially at the edge of species' ranges.

An overall understanding of community responses to climate change would also benefit from better understanding of *in situ* adaptive responses, as these appear to be significant in some species. Much has been learned from reconstructions of past migration patterns in the paleo-record, and from studies of alien invasive plants, but these "natural experiments" are limited in that they represent special cases where species migration occurs over landscapes unfragmented by human activities (paleo-record), or are experiencing release from predators and pathogens (alien species).

Finally, promising approaches are being developed that address the issue of how human transformation of landscapes will modify migration rates, and that combine mechanistic migration models with spatially explicit models of species geographic ranges at spatial scales relevant to simulating plant propagule dispersal and demographic behavior. These approaches will provide useful insights into biodiversity change under climate and land-use change scenarios. However, the potential increase in spatial resolution of DGVM simulations, and their increasing capacity to simulate more finely defined plant functional types, will allow them to provide an independent alternative assessment of the role of migration in determining the future structure and function of the ecosystems of the Earth.

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