Forecasting Regional to Global Plant Migration in Response to Climate Change

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The rate of future climate change is likely to exceed the migration rates of most plant species. The replacement of dominant species by locally rare species may require decades, and extinctions may occur when plant species cannot migrate fast enough to escape the consequences of climate change. Such lags may impair ecosystem services, such as carbon sequestration and clean water production. Thus, to assess global change, simulation of plant migration and local vegetation change by dynamic global vegetation models (DGVMs) is critical, yet fraught with challenges. Global vegetation models cannot simulate all species, necessitating their aggregation into plant functional types (PFTs). Yet most PFTs encompass the full spectrum of migration rates. Migration processes span scales of time and space far beyond what can be confidently simulated in DGVMs. Theories about climate change and migration are limited by inadequate data for key processes at short and long time scales and at small and large spatial scales. These theories must be enhanced to incorporate species-level migration and succession processes into a more comprehensive definition of PFTs.

Keywords: climate change, dispersal, migration, long-distance dispersal, dynamic global vegetation models

Human-induced alteration of global climate is likely to result in changes in the distribution and functioning of terrestrial ecosystems (Gitay et al. 2001). Boreal forests could shift into the tundra, while being displaced by temperate forests and grasslands. Deserts may expand in some areas and contract in others. The fate of tropical forests is uncertain, but some future climate scenarios indicate possible large losses (Neilson et al. 1998). These geographic changes imply large changes in the earth's carbon balance and hence its feedback to the climate system (King and Neilson 1992, Smith and Shugart 1993). The biosphere feedbacks to the atmosphere (e.g., changing albedo, evapotranspiration, and carbon exchange) could either ameliorate climate change or exacerbate it, depending in part on the biosphere's rate of response to climate change (Cox et al. 2000). Shifting terrestrial vegetation also has implications for water supply and quality, disturbance regimes, and possibly biological diversity (Gitay et al. 2001).

The United Nations Framework Convention on Climate Change (*http://unfccc.int/*) requires signatories to prevent "dangerous interference" with the climate system (defined broadly as exceeding the rate of change that will allow ecosystems to adapt naturally to climate change with continued food security and sustainable economic development). Future human-induced climate change may occur at a rate greater than any experienced in the past 10,000 years (Houghton et al. 2001). Although the biosphere is always changing and never in complete equilibrium with the climate, the more rapidly the climate changes, the further from equilibrium the biosphere will become, and the greater will be the potential for nonlinear or sudden changes and complex biosphere–atmosphere feedbacks (Scheffer and Carpenter 2003). This disequilibrium is due, in part, to inertia in ecosystems, which will cause lags between rapid climate change and ecosystem

responses such as biosphere carbon balance and species migrations (Johnstone and Chapin 2003).

Rapid climate change may put some species at risk of extinction, possibly reducing the functional resilience of ecosystems in the face of rapid change, which in itself could enhance the potential for positive feedbacks and have consequences for ecosystem attributes such as global carbon storage potential and biodiversity (Thomas et al. 2004). Carbon uptake by land plants clearly is dependent on the physiology and population dynamics of individual species, including migration and extinction. However, because of the large number of species, a complete coupling between global carbon cycling and species-level processes in global ecological simulation models will probably never be possible. We will explore how the interface of these two sets of processes, particularly species migration, might be accommodated in dynamic global vegetation models (DGVMs, also known as dynamic general vegetation models), and posit that this must be done in order to reduce uncertainties in assessments of both global carbon balance and global biodiversity.

Dynamic global vegetation models (figure 1) can simulate changes in vegetation distribution, regional-to-global carbon cycling and sequestration, ecosystem biophysical feedbacks to the climate system, and changes in resources such as timber, water, and other ecosystem services valued by human society (Costanza et al. 1997, Cramer et al. 2001). Among the most significant challenges involved in incorporating plant migration into DGVMs are (a) accurately estimating the importance of long-distance dispersal in the establishment and proliferation of species within new vegetation communities, (b) aggregating information from individual species into the category of plant functional types (PFTs) as simulated in DGVMs, and (c) incorporating temporal and spatial heterogeneity within large spatial grid cells into the modeling of migration.

Overview of major vegetation change issues

Changes in species composition can take two paths, via *in situ* conversion, that is, subdominant species replacing dominant ones, or via migration of species from other locales. *In situ* conversion is likely to begin before new migrants can attain a significant functional role. Yet, if the climate changes rapidly, and especially if climate change is accompanied by widespread disturbance, some species and their functions may be lost before those functions can be replaced by either dominance shifts or new migrants. Adaptability of ecosystems to rapid change appears to be related to the diversity of species traits that are available to assume old and new functions (Loreau et al. 2002). The more adaptive an ecosystem is to rapid environmental change, the less likely it is that there will be sudden changes in ecosystem function, such as carbon sequestration.

Greater diversity is often related to some redundancy of function, allowing an *in situ* conversion from one species to another (with subtly different tolerances) while retaining critical functional capability. This is often referred to as the "insurance" theory of diversity and stability of ecosystems, in

which a subdominant species may be poised to replace a dominant one under changing conditions (Loreau et al. 2002). The replacement of a regionally dominant pinyon pine (*Pinus remota*) in the southwestern United States by another species (*Pinus edulis*) during the glacial to interglacial transition may be an example of how subtle differences among species can be important in retaining ecosystem function during climatic change (Lanner and Van Devender 1998). *Pinus remota* is now relegated to a few small refugia, having once had an extensive range.

Ecosystem simulations under future climate scenarios suggest that the preferred ranges of many species could shift tens to hundreds of kilometers over only 50 to 100 years, nearly an order of magnitude faster than may have occurred since the last glaciation (Malcolm et al. 2001, Davis and Zabinski 1992). Species that cannot migrate at sufficient rates to track climate change might go extinct, possibly reducing the adaptability of those ecosystems to climate change.

Most species-level assessments of future distribution change are based on the "climate envelope" approach, which relates species boundaries to macroscale climate characteristics such as January and July temperatures and annual precipitation (Hampe 2004). The number of methods for assessing climate envelopes is quite large, including logistic regression, regression trees, and more advanced "genetic algorithms" that search for the best empirical formula to describe the species' currently observed distribution. All of the methods share the property of relating species distribution to some a priori selection of environmental variables that are intended as indices of the true underlying physiological or biophysical limits on species distributions (i.e., the fundamental niche). However, species distributions are often significantly reduced as a result of various species interactions (i.e., the realized niche; Becwar et al. 1981).

If the climate warms rapidly and the advancing competing species cannot keep pace through migration, then the southern boundary of the climate envelope may shift north, but the extant species may continue in its present range and perhaps flourish if the growing conditions improve. Thus, the realized niche will have expanded, and the species will persist outside of the originally determined climate envelope. Alternatively, if growing conditions get worse, perhaps accompanied by disturbances, such as increased wildfire or widespread drought, then local species (and their functions) may be lost, reducing the realized niche (climate envelope). Thus, the processes of migration and the physiological tolerances of species must be incorporated into global models of terrestrial biosphere dynamics to accurately assess the lags and dynamics of biosphere functional processes and biodiversity.

Most global-scale ecosystem models do not incorporate migration processes and so do not consider whether species or biomes would be able to migrate to a new locale. Kirilenko and Solomon (1998) and van Minnen and colleagues (2000) have provided notable exceptions. Kirilenko and Solomon (1998) modified a simple equilibrium global vegetation distribution model (BIOME 1; Prentice et al. 1992) by applying
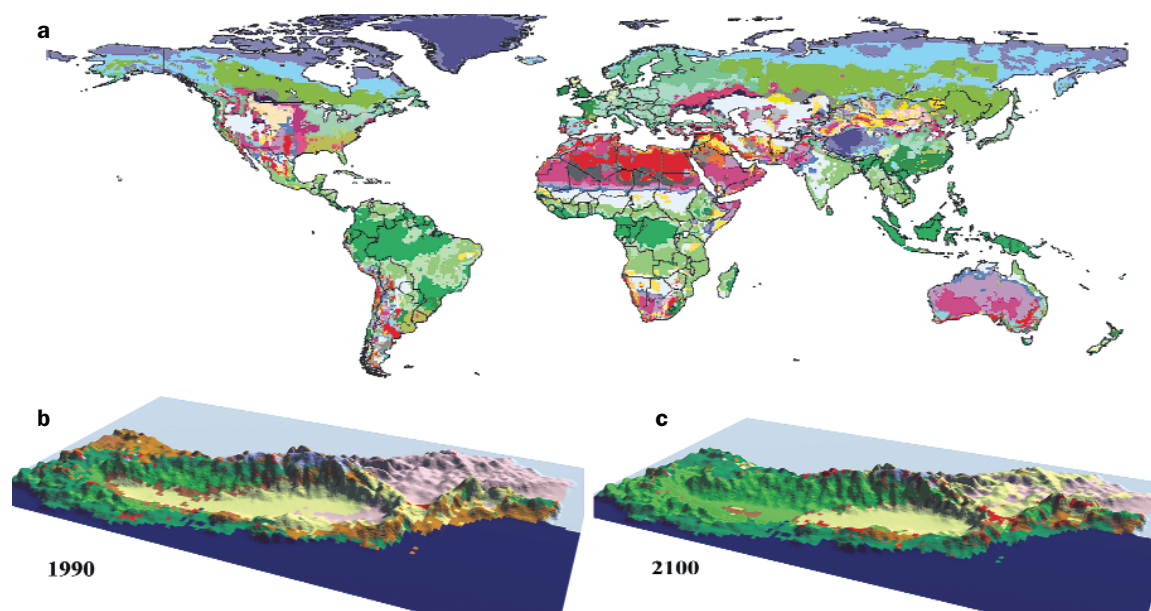
Figure 1. (a) Simulated distribution of 44 unique vegetation types using an equilibrium biogeography model, MAPSS (mapped atmosphere–plant–soil system), under current climate at 0.5° resolution (Neilson 1995). The vegetation types are derived from various mixtures of 12 plant functional types (PFTs). Currently, no dynamic global vegetation model (DGVM) is capable of simulating even this many different vegetation communities, let alone the vast number of individual plant species. Two snapshots, from the years (b) 1990 and (c) 2100, from a continuous simulation of vegetation distribution in California at 10-kilometer resolution using the MC1 DGVM, show highly aggregated vegetation communities (Lenihan et al. 2003). Greens are forest types, brown is savanna/woodland, yellow is grassland, and pink is desert. Red shows where fires were modeled in that year. The rate of PFT migration occurs at the rate of climate change in the MC1 simulation. Graphics courtesy of the MAPSS modeling team (www.fs.fed.us/pnw/corvallis/mdr/mapss/).

paleoecologically measured migration rates and modern mortality rates to determine the persistence and migration success of the PFTs (described below). In contrast, van Minnen and colleagues (2000) incorporated a simplified migration routine into a much more complex integrated assessment model (IMAGE, or integrated model to assess the global environment). On the basis of migration potential (but not mortality), whole biomes were assumed to migrate, rather than their constituent PFTs. However, the migration potential of individual PFTs determined the biome composition. If migration was insufficient, other less dominant PFTs, such as grasses, became dominant. Both Kirilenko and Solomon (1998) and van Minnen and colleagues (2000) noted that their approaches were insufficiently complex to truly explore the possibilities of sudden changes in ecosystem function related to migration and extinction processes.

Before discussing these issues, we will briefly review current understanding of plant migration. We will then propose a few research directions that might help reduce the uncertainties in assessments of future biosphere carbon balance as linked to biodiversity changes, while accommodating the necessary simplifications required for terrestrial biosphere modeling for climate change impacts. Many of the research directions will require finding solutions to three issues of scale: (1) reducing the large number of species to a few critical PFTs, (2) representing processes that occur over very short and very long time scales; and (3) representing processes that occur over very small and very large spatial scales.

Migration as a process

Migration of plant species can occur as a slow local process whereby a species migrates as a "front" in short steps, or as a rapid process mediated by long-distance dispersal events, or "jumps" (figure 2). Long-distance migration is generally a two-stage process, requiring long-distance jumps followed by the establishment and spread of local populations (figure 2). There are four basic components of local spread and long-distance migration: *fecundity* (reproductive output), *dispersal, establishment* (germination and seedling survival), and *growth* to reproductive maturity. The average age of maternal reproduction, or generation time, may range from a year to several decades, depending on the species.

For sustained long-distance migration, sufficient local spread (population growth) must usually occur after each long-distance jump in order to provide a large seed source to increase the probability of success for the next long-distance jump (Clark et al. 2001). Furthermore, the recruitment, growth, and local spread of a population may take decades,

*Figure 2. An example of long-distance dispersal with local spread. Lodgepole pine (*Pinus contorta *Douglas ex Loudon) outliers with fringe spread near Lake Ohau, South Island, New Zealand. The source of seed for the outliers is approximately 7 kilometers to the northwest. Photograph courtesy of Nick Ledgard.*

depending on the species' generation time. Seedling establishment in a mature ecosystem may be very difficult, while recently disturbed areas may produce less competitive interference, but possibly more grazing pressure (Johnstone and Chapin 2003, Lake and Leishman 2004). Rapid long-distance dispersal, colonization, and establishment in the tropics are enhanced by interactions between animal seed dispersers and plants (Fragoso 1997, Fragoso et al. 2003).

Local spread from isolated populations can occur fairly rapidly, but will be insufficient to keep up with the predicted rates of climate change. For example, if plants averaged a local dispersal distance of 50 meters (m) per year, then they would only move up to 5 kilometers (km) over a century (species with longer generation times often move at slower rates), a distance too small to spatially resolve in most global vegetation models. Thus, modeling of dispersal would not be an issue in the time frame of policy formation for addressing climate change (a few years). Long-distance dispersal with successful establishment could bring the rates of migration into a more rapid, near-term policy and modeling time frame; however, long-distance dispersal may be so rare that it is only statistically predictable over very long time frames (Clark et al. 2001). Nevertheless, it seems increasingly important for scientists to improve quantification of the possible long-term risks and benefits of near-term policy decisions.

Modes of dispersal. The two most common modes of long-distance dispersal for terrestrial plants are *anemochory,* or wind dispersal, and *zoochory,* or dispersal by animals. Many plants are wind dispersed; their "seed shadows" (density distribution of seeds with distance from the source) are typically concentrated near the parent plant (Willson and Traveset 2000). However, some seeds may also reach very long distances, especially if initially carried to high altitudes by wind updrafts (Nathan et al. 2002, Tackenberg 2003). The distance and direction of wind dispersal events are somewhat predictable: shorter distances in the direction of predominant winds under fair weather conditions and longer distances in the direction of storm tracks under foul weather conditions. With empirical information on the distribution of wind speeds and directions, at least coarse estimates of seed transport direction and distances can also be calculated.

Transport of seeds by animals is thought to be less predictable and therefore less amenable to modeling, although a few rule-based models have been developed from information on maximum distances of animal-dispersed seeds (Higgins et al. 2003). Large jumps (1 km or more) can involve selection of seeds by birds, bats, and large mammals that transport seeds several kilometers or more before defecating, regurgitating, or dropping them (Fragoso et al. 2003). Sticky seeds, or those with hooks or barbs, may remain attached to a bird or mammal for long periods of time, and small seeds may be carried in mud on the feet of animals. Recent studies indicate that long-distance dispersal is common for some animal-dispersed seeds in tropical and temperate systems (Fragoso 1997, Myers et al. 2004).

Human population growth has altered plant migration in at least two ways. First, deliberate or accidental human activity

is an increasingly important mechanism of plant dispersal, particularly in densely populated regions (Hodkinson and Thompson 1997). Major pathways of plant propagule movement include both surface and air vehicles, often with the transport of topsoil and agricultural or forestry products. Exotic invasive species complicate the prediction of future ecosystem dynamics, including the capacity of native species to migrate successfully, since many invasive species tend to be well adapted to disturbed conditions such as may accompany rapid climate change.

Humans have also highly altered and fragmented natural landscapes, affecting plant migration (figure 3). The size and spatial distribution of land-cover patches directly affect migration rates. Land-cover changes can influence migration rates by affecting local population sizes and seed production and by altering the amount of suitable habitat for new populations. Increasingly fragmented landscapes may present thresholds of fragmentation whereby dispersal is nearly truncated and the risk of local extinction is significantly increased (Fahrig 2002). Yet, by increasing the number of border zones where different types of land cover meet, fragmentation can also enhance seed transport by animal species that travel along and cache seeds near edges (Fragoso 1997).

A fourth means of seed transport is by streams and rivers (*hydrochory*), particularly above 55° or 60° N latitude (van der Pijl 1982). The direction of hydrochorous seed transport is highly predictable, although the establishment of upland species is much less predictable, since their survival in water and subsequent transport to upland habitat may be relatively rare. Thus, water dispersal is predictable primarily for riparian and wetland species.

Observations of migration. The scarcity of data describing the migration process severely limits the development of migration models. Paleoecological data from buried pollen and macrofossils document plant migrations over great distances (Muller and Richard 2001). However, pollen and macrofossil data are abundant only in some regions and for only a small fraction of the earth's biota. Quantitative observations of short-distance seed transport have been generated in many forest management studies (Willson and Traveset 2000), and seed trap experiments have captured seeds for analysis of downwind deposition patterns or seed shadows (Nathan et al. 2002).

Observations of long-distance transport and establishment are occasionally available from chance events (Fragoso et al. 2003, Myers et al. 2004). Regional abandonment of managed lands also has provided observational data on plant invasion and local population expansion. The rapid spread of imported tree species across parts of New Zealand during the past 40 years (Hunter and Douglas 1984) exemplifies the kind of migration and establishment data that can be used to test migration models. Finally, recent analyses of changes in distributional limits provide evidence of plant migration in response to contemporary climate change (Parmesan and Yohe 2003). Lodgepole pine, for example, appears to be expanding

at its northern limits, with establishment being facilitated by fire (Johnstone and Chapin 2003). Long-distance dispersal and the regeneration niche appear to be the primary constraints on the rate of migration, with the pine's expansion lagging behind the rate of climate change (Johnstone and Chapin 2003).

Challenges of implementing migration in DGVMs

DGVMs are a relatively new class of model conceived to merge vegetation distribution (biogeography of species, PFTs, and biomes) and ecosystem process models (biogeochemical processing of carbon, water, and nutrients) (Cramer et al. 2001). These combined models also require new processes for the simulation of fire occurrence and impacts, and of the rate and direction of postfire vegetation succession (Bachelet et al. 2003, Thonicke et al. 2001). Other approaches are being taken in DGVM construction (Smith et al. 2001), but all of these approaches should be capable of simulating the processes of water, carbon, and nutrient cycling and the processes controlling vegetation redistribution. Recent advances in the capabilities of DGVMs have been impressive and include dynamic simulations of vegetation distribution, carbon sequestration, fire, and coupled biosphere–atmosphere feedbacks for national and global assessments of climate change (Cox et al. 2000, Cramer et al. 2001, Bachelet et al. 2003).

Modeling approaches: Balancing realistic process simulation with spatial and temporal scale. Vegetation and dispersal processes span many orders of magnitude in both space and time. In fact most processes occur at scales far smaller in space and shorter in time than typically can be simulated in global models. Current DGVMs often operate with a grid-cell size of approximately 50 km on a side, three orders of magnitude larger than local dispersal distances, and even pushing the resolution for long-distance dispersal. Inevitably, many of the most important processes (e.g., photosynthesis, flowering, and seed set) are also faster than the model time step, which is typically daily to monthly, and must therefore be scaled up or empirically parameterized. That is, simplified equations, which roughly represent the processes, are used instead of detailed mechanistic simulations (Lischke 2001). Even with advanced computer technology, there will always be a threshold beyond which certain processes occur over shorter distances or at faster rates than can be mechanistically simulated. At the other extreme, most long-distance dispersal events may be so rare as to be nearly unpredictable.

Mechanistic simulation of seed transport has been modeled in a similar way to the modeling of transport of particulate pollutants from power plants and urban areas via strong winds (Nathan et al. 2002). In contrast, empirical parameterization of the same processes may use seed dispersal curves that estimate the seed rain, defined statistically from spatial distributions of seeds and seedlings (Clark et al. 2001). The empirical approach can lead to good descriptions of the short-range dispersal of seeds, and new methods can even estimate long-distance events (Clark et al. 2001). Mechanistic models, however, may be better if there are changes in driving

Figure 3. Northwest corner of the H. J. Andrews Experimental Forest in the Oregon Cascade Mountains. Human disturbance of the landscape can cause patterns of fragmentation that may inhibit the dispersal of some species, while enhancing the dispersal of others. Such fragmentation alters wind patterns affecting wind-dispersed seed and alters both avian and terrestrial animal habitat, affecting animal movements and seed dispersal patterns. Photograph courtesy of Al Levno.

conditions, such as the frequency of strong wind events or the extinction of large mammals, whereas empirical models usually assume statistical stationarity of such processes.

Thus, to simulate migration in DGVMs, the scales of processes need to be considered in relation to the scales over which the DGVM is operating. The coarser a spatial grid, the more simplified or abstract will be the migration simulation, since most of the migration processes would occur inside the grid cells. Even long-distance jumps of 1 to 5 km would fall within a typical DGVM grid cell. Long-distance dispersal could be more mechanistically simulated across the grid, providing the dispersal distances are long compared to the grid resolution. However, many more processes would need to be considered, such as wind dispersal processes or animal population and migration dynamics. The application of mesoscale atmospheric models for simulating long-distance wind dispersal of seeds over complex terrain and heterogeneous landscapes (Nathan et al. 2005) is expected to provide a powerful tool for incorporating dispersal in DGVMs. These computer-intensive mechanistic models can generate data to build simple statistical models for use by DGVMs.

Incorporating spatial heterogeneity and associated processes.
Migration processes occur on structurally and dynamically heterogeneous landscapes, both above and below typical grid-cell resolutions. Structural or topographic heterogeneity occurs at all scales, from continental to local, and is generally static over periods of a few decades. Structural heterogeneity results from variations in topography, soils, and persistent land use. Dynamic landscape heterogeneity also occurs over all scales, local to regional. It occurs when human or natural disturbances or migrating plants create new age cohorts or transient land-cover types in what would otherwise be a homogeneous vegetation type. At the sub–grid-cell level, both types of heterogeneity are important, but are typically not explicitly simulated, and their effects must therefore be simulated using empirical dispersal rules. However, at scales exceeding the model grid dimensions, multiscale mechanistic modeling of dispersal processes is being developed (Nathan et al. 2005).

Spatial heterogeneity may provide stepping-stones for migration or, conversely, may act to inhibit dispersal. Percolation theory, according to which entities can move, but only limited distances to favorable grid cells, and are blocked by unfavorable ones (as in a sieve), has been used to examine rates and thresholds of spread through fragmented landscapes (Plotnick and Gardner 2002). For example, a cellular automata approach, in which each grid cell contains an autonomous ecosystem model that can produce propagules for horizontal spread, was used to simulate long-distance

dispersal over a relatively coarse grid with current land use (Schwartz et al. 2001).

Long-distance dispersal of seeds to a new site does not guarantee a successful establishment. The site must be suitably receptive. Biotic receptivity may require an opening in the existing vegetation, produced by a tree fall or some other disturbance, such as logging, fire, drought, pathogen infestation, or blowdown (Johnstone and Chapin 2003). Once a seed has landed, it must be greeted by proper conditions for germination and competitive growth to reproductive status (Lake and Leishman 2004). Vegetation gap model studies indicate that the higher the disturbance rate (gap formation rate), the more rapid is the simulated tree migration (Sykes and Prentice 1996). However, this level of temporal and spatial detail (rate of small gap formation) is typically below the grid-cell resolution of DGVMs, thus challenging their capability to accurately represent the local dispersal and establishment processes. The more sophisticated, emerging DGVMs will simulate local site conditions in the context of subgrid heterogeneity, both structural and dynamic, and may include competitive and other biotic influences on seedling establishment and growth.

Several approaches are being explored to incorporate the sub–grid-cell processes of plant migration in DGVMs (e.g., Dolman and Blyth 1997, Löffler and Lischke 2001). The options fall into two broad categories, with trade-offs between areal extent and spatial resolution: (1) using high-resolution grids (e.g., 100 m) or variable grids, coarse in some areas and fine in others (generally impractical for global simulation models, even with the fastest supercomputers); or (2) simulating sub–grid-cell structural and dynamic features as aggregated statistical features, rather than specific spatial locations within the grid cell (Dolman and Blyth 1997).

Current attempts appear to be converging on the second approach, but not without difficulties. In the second approach, the area, nature, and dynamics of subgrid patches are simulated, but not their spatial location or their degree of fragmentation (e.g., Löffler and Lischke 2001). The lack of spatial information in this approach to subgrid heterogeneity imposes the need for assumptions about it. The form of simple submodels of local population spread and migration across the cell carries implicit assumptions about whether patches within a grid cell are uniformly, randomly, or fractally distributed; about the degree of fragmentation and spatial pattern; and about how these patterns affect the movement of propagules (Fahrig 2002).

Using plant functional types in place of species. Plant functional types are an essential simplification, since global models cannot simulate all plant species. PFTs capture key aspects of plant functioning, and allow grouping of diverse species under a single functional umbrella when they share critical traits (Diaz and Cabido 1997). Differences in natural-history traits are omitted when species are aggregated into only a few PFTs, making it more difficult to test models against species data. As currently implemented in DGVMs, PFTs do not in-

corporate dispersal and migration life-history traits. Rather, most PFTs encompass species with a large variety of dispersal and other migratory traits, and so need to be subdivided into finer categories in order to incorporate these traits.

Some relationships between PFT characteristics have been demonstrated, such as the relationship between growth form and plant size, or between seed size and dispersal mode (Leishman et al. 2000). In temperate floras, plant height accounts for about 20% of the variation in seed size, while dispersal mode accounts for 29% of the variation among species in seed weight (Leishman et al. 2000). However, even though big seeds (> 100 milligrams [mg]) tend to be dispersed by vertebrates, and small seeds (< 0.1 mg) by wind, any dispersal mode could be expected between these extremes (Higgins et al. 2003). Human-dispersed plants tend to have predictable suites of traits: for example, short life histories, small seeds, and persistent seed banks in the case of species dispersed by vehicles and transported soil (Hodkinson and Thompson 1997). Many different life-history traits often covary and collectively produce a set of capabilities that enhance a given dispersal mode, establishment requirements, early competitive capabilities, and so forth (Grime 1993). We refer to this overall collection of interactive traits as a syndrome.

Regenerative traits may be only weakly constrained by vegetative traits (Leishman et al. 2000). However, a study of pines suggests that within a single PFT, evergreen–needleleaf trees, a large spectrum of "invasive" traits is expressed and is closely related to relative growth rate, seed mass, and generation time (Grotkopp et al. 2002). Relative growth rate, in turn, was closely associated with specific leaf area, the ratio of leaf area to leaf mass. These results suggest the possibility of defining life-history syndromes within PFTs, such as "invasive, early successional" to "noninvasive, late successional," with each defined by sets of covarying life-history traits.

DGVM simulations could filter PFT subclasses (syndromes) by migration potential over space and time. Areas with high rates of climate change would initially be colonized by fast-migrating PFT subclasses. Indeed, Dynesius and Jansson (2000) show that Pleistocene climate change filtered biota in this way, with highly mobile species more likely to be found at high latitudes that experienced high rates of climate change, and less mobile species in regions with low rates and amplitude of past climate change. This filtering might also provide an assessment of potential biodiversity loss under climate change scenarios, as related to the changing richness of PFT subclasses. Also, although the data are sparse, it may be possible to define unique PFT dispersal spectra associated with different biogeographic zones. For example, more than 80% of wet tropical tree and shrub species are animal dispersed, while in the higher latitudes both wind and animal dispersal are important (Levey et al. 1994, Willson and Traveset 2000).

Simulating vegetation change in DGVMs. DGVMs have been used to simulate succession or change in vegetation structure, as defined by shifts in dominance among PFTs (e.g., Smith et al. 2001, Bachelet et al. 2003). These changes occur in nature

through a shift in dominance of PFTs already present in an area, and through the immigration of novel PFTs by way of dispersal and establishment. To the extent that the DGVM simulates only a single climate within a grid cell, the available PFTs will be fewer than are possible in the real world, where diverse microclimates can harbor a greater diversity of species and PFTs. A sub–grid-cell scheme that accounts for heterogeneity will allow some representation of the diversity of microclimates within a cell, but will inevitably fall short of representing all possible microclimates and subdominant PFTs (e.g., figure 4).

A classic example of this problem is the almost instantaneous appearance of eastern hemlock in pollen records throughout the northern half of the lower peninsula of Michigan between 5000 and 6000 years ago (Davis et al. 1986). Either it spread incredibly fast from its initial colonies near the Straits of Mackinac, or it expanded from numerous local refugia, hidden in complex terrain and thus not recorded in pollen records. The fossil record is too sparse to permit resolution of this question, analogous to the problem of coarse-grid resolution in DGVMs. Similarly, rapid shifts in regional dominance could occur under rapid climate change without any long-distance dispersal. Nevertheless, migration will still be a major issue, especially between largely distinct floristic zones. Major biome boundaries are zones where vegetation structure and dominant PFTs change, but are also usually locations of significant species change, and should be the locations where migration lags become most obvious.

Rapid climate change will cause a sorting of migration syndromes into bands along a migrational front, led by the fastest (most invasive) dispersers and trailed by the slowest (least invasive), which are perhaps at the most risk of local extinction. Thus, rapidly migrating native species will increasingly "invade" more sedentary, late-successional, or endemic species, enhancing risks of local or total extinction of some species. This spatial sorting of PFT dispersal syndromes (and real species) under rapid climate change, and the ensuing successional interactions among relatively sedentary local species and aggressive native "invaders," could be one of the most crucial attributes of ecosystem change to capture in DGVM simulations.

Research directions

This has been a brief review of the needs and challenges involved in global-scale modeling of plant migration as a response to global change. Output from DGVMs should be a primary tool for decisionmakers to evaluate the question of safe rates of climate change, and associated impacts on carbon and other biosphere feedbacks to the atmosphere, water resources, protection of species, and other resource issues and their management. However, the value of these powerful tools will be seriously curtailed if migration is not incorporated into the models.

The entire process of migration is lacking in observational data to inform general theories for use in models of the natural world. Required data span the processes from flowering and seed set to short- and long-distance dispersal, followed by establishment and growth to completion of the cycle. The extinction of megafaunal dispersing agents is also of concern. Quantification of these processes is a major problem (Clark et al. 2001, Nathan et al. 2003); however, new methods are being developed for obtaining some of the critical data and estimating long-distance dispersal (Fragoso et al. 2003, Nathan et al. 2003).

There is a shortage of useful trait data for the majority of species (Knevel et al. 2003). Even so, to generalize this information into PFTs, researchers must also document correlated plant traits that affect dispersal, rate of growth, competitive ability, and generation time (Leishman et al. 2000). It remains to be seen whether dispersal, invasive, and successional characteristics are sufficiently correlated to define a small number of plant migration syndromes within each PFT, as well as their frequency distributions (Grime 1993, Leishman et al. 2000).

Data needs include quantification of initial establishment and early growth in the face of competition and other biotic interactions. Disturbances and other processes that create suitable establishment sites are poorly quantified in relation to climate variability and change. Documentation of rare PFTs that could shift into dominance with a change in climate is also needed. In addition, data on the risks of local extinction from climate change and the loss of critical PFTs are almost nonexistent. However, there will always be fewer data than desired. Thus, theories of migration and succession must be developed in the face of uncertain knowledge and tested for sensitivity to assumptions of initial conditions and changing boundary conditions.

Theory development for rapid, climate-induced vegetation change involves time and space scaling of vegetation succession and plant dispersal processes relative to model scales of time and space, as well as simplification of species into PFTs. The aggregation of species into PFTs and the simulation of the successful invasion of migrants into different communities pose particular challenges. The processes are generally fast, even if infrequent over long time scales. The spatial scales span both subgrid scales and across-grid scales. Grid-cell size will probably never be small enough to explicitly simulate all mechanisms of plant dispersal over the globe. Thus, a persistent theoretical challenge is the simplification of complex, mechanistic models, such as multiscale wind dispersal simulators, into more compact, empirical formulations, which are robust in the face of rapidly changing environmental conditions. A combination of empirical and mechanistic approaches is likely to prove optimal, but must be validated to the extent possible against finer-scale models and observations. For example, over smaller domains, more mechanistic models of migration, succession, and shifting dominance could operate at a species level with very high grid resolutions and short time steps and could be used to train DGVMs in more empirical simulations of PFT dynamics.

It is always speculative to suggest directions that future modeling might take, but a few thoughts are worth noting. Some

Figure 4. A northern Utah landscape, supporting numerous unique plant functional types (PFTs) that would normally be simulated over large geographical distances in a dynamic global vegetation model (DGVM). These PFTs include boreal needleleaf (spruce, fir), boreal broadleaf winter deciduous (aspen), temperate needleleaf (pine), temperate broadleaf winter deciduous (oak, maple), and both microphyllous evergreen and broadleaf winter deciduous shrubs. Shifting dominance requires the presence of several different PFTs in a landscape, perhaps separated by unique microclimates or successional stages. Regional climate change can expand or contract those microclimates, causing a shift in PFT dominance without requiring long-distance dispersal. However, most DGVMs do not simulate local-scale microclimates and thus may not be able to support many different PFTs in a single grid cell, even with complicated sub–grid-cell schemes. Photograph courtesy of Ron Neilson.

processes, such as the rate of local spread within a grid cell, could be empirically indexed to fragmentation or animal extinction events, which could further be indexed to both structural and dynamic heterogeneity. Even long-distance events within grid cells could be empirically modeled as informed by very high-resolution, increasingly mechanistic simulations using locally tailored models.

Direct, dynamic nesting of models may be one means of insuring more consistency between global simulations on coarse grids with highly aggregated PFTs and regional, species-based models on finer grids. The nested model could be directly constrained by the boundary conditions and temporal dynamics provided by the global model. The coarse PFTs in the global model could be subdivided into more categories or individual species in the local or regional model. Such model nesting could be strategically located in hotspots of species diversity or in areas where ecological function may be most at risk of collapse under rapid change. For example, a mesoscale dispersal modeling approach is already capable of incorporating landscape heterogeneity and winds over scales of meters to thousands of kilometers (Nathan et al. 2005).

Questions remain regarding the potential loss of crucial PFTs and biodiversity for the maintenance of critical ecosystem functions, such as carbon sequestration. New mechanistic models are being developed that simulate the spatial pattern of PFT diversity relative to climate and topography (Kleidon and Mooney 2000). If nested within a DGVM, such a model could provide inferences regarding the risk of extinction of critical PFTs and feed back to the DGVM, thus affecting the functional response of the DGVM to climate change.

Conclusions

The fundamental question "What is a safe rate of climate change?" involves understanding the entire biosphere and its potential responses to rapid climate change, with the caveat that different regions or elements of the biosphere could respond much more rapidly or catastrophically than others. It may be possible to identify some of the particularly sensitive regions and focus research on them. The processes of biosphere response to climate change involve *in situ* changes both in ecosystem function and in the relative abundance of species, as well as the migration of biota across the global land-

scape. There are always trade-offs in ecosystem modeling, regardless of the scale, but most certainly at the global scale. The greater precision that is desired in one domain, such as spatial realism, will require a reduction in precision somewhere else, such as in modeling temporally dependent processes. However, the goal should be to at least retain overall accuracy, if not precision, in the simulated outcome.

It is often assumed, for example, that one can accurately simulate the future dynamics of global carbon balance with a relatively small number of PFTs (van Minnen et al. 2000), and this may be true. However, every new simulation using PFTs under future climate scenarios requires consideration of a different and always changing set of biophysical domains, shared by different combinations of species. The risk of sudden changes in biosphere function (e.g., rapid, disturbance-induced losses of ecosystem carbon) may hinge on the persistence or loss of key PFT attributes, or even attributes of individual species. Migration processes may be among the most important in determining possible threshold responses of the biosphere, or in estimating the continued sustainability of ecosystem integrity, goods, and services.

The biosphere is losing species at an extremely rapid rate, gradually eroding redundancy within functional types, and thus risking extinction of key functions and possibly reducing the planet's resilience to rapid change (Millennium Ecosystem Assessment 2005). A variety of ecosystem goods and services, such as clean and abundant water, carbon sequestration, recreation, and wood and forage production, may be placed at risk if species represented by various PFTs cannot migrate sufficiently fast to track climate change. Perhaps some of these functions will be maintained by subdominant species replacing dominant ones before migrants can arrive, but this cannot be universally assumed. Thus, incorporating an expanded concept of PFTs in DGVMs, including the processes of migration and *in situ* conversion, will be necessary to address the true importance of changes in biological diversity to sustained ecological function in a rapidly changing world.

Acknowledgments

References cited

Bachelet D, Neilson RP, Hickler T, Drapek RJ, Lenihan J, Sykes M, Smith B, Sitch S, Thonicke K. 2003. Simulating past and future dynamics of natural ecosystems in the conterminous United States. Global Biogeochemical Cycles 17: 14-1–14-16.

Becwar MR, Rajashekar C, Hansen-Bristow KJ, Burke MJ. 1981. Deep undercooling of tissue water and winter hardiness limitations in timberline flora. Plant Physiology 68: 111–114.

Clark JS, Lewis M, Horvath L. 2001. Invasion by extremes: Population spread with variation in dispersal and reproduction. American Naturalist 157: 537–554.

Costanza R, et al. 1997. The value of the world's ecosystem services and natural capital. Nature 387: 253–260.

Cox PM, Betts RA, Jones CD, Spall SA, Totterdell IJ. 2000. Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. Nature 408: 184–187.

Cramer W, et al. 2001. Global response of terrestrial ecosystem structure and function to CO_2 and climate change: Results from six global dynamic vegetation models. Global Change Biology 7: 357–373.

Davis MB, Zabinski C. 1992. Changes in geographical range resulting from greenhouse warming: Effects on biodiversity in forests. Pages 297–308 in Peters RL, Lovejoy TE, eds. Global Warming and Biological Diversity. New Haven (CT): Yale University Press.

Davis MB, Woods KD, Webb SL, Futyma RP. 1986. Dispersal versus climate: Expansion of *Fagus* and *Tsuga* into the Upper Great Lakes region. Vegetatio 67: 93–103.

Diaz S, Cabido M. 1997. Plant functional types and ecosystem function in relation to global change. Journal of Vegetation Science 8: 463–474.

Dolman AJ, Blyth EM. 1997. Patch scale aggregation of heterogeneous land surface cover for mesoscale meteorological models. Journal of Hydrology 190: 252–268.

Dynesius M, Jansson R. 2000. Evolutionary consequences of changes in species' geographical distributions driven by Milankovitch climate oscillations. Proceedings of the National Academy of Sciences 97: 9115–9120.

Fahrig L. 2002. Effect of habitat fragmentation on the extinction threshold: A synthesis. Ecological Applications 12: 346–353.

Fragoso JMV. 1997. Tapir-generated seed shadows: Scale-dependent patchiness in the Amazon rain forest. Journal of Ecology 85: 519–529.

Fragoso JMV, Silvius KM, Correa JA. 2003. Long-distance seed dispersal by tapirs increases seed survival and aggregates tropical trees. Ecology 84: 1998–2006.

Gitay H, Brown S, Easterling W, Jallow B. 2001. Ecosystems and their goods and services. Pages 235–342 in McCarthy JJ, Canziani OF, Leary NA, Dokken DJ, White KS, eds. Climate Change 2001: Impacts, Adaptation, and Vulnerability. Contribution of Working Group II to the Third Assessment Report of the Intergovernmental Panel on Climate Change. New York: Cambridge University Press.

Grime JP. 1993. Vegetation functional classification systems as approaches to predicting and quantifying global vegetation change. Pages 293–305 in Solomon AM, Shugart HH, eds. Vegetation Dynamics and Global Change. London: Chapman and Hall.

Grotkopp E, Rejmanek M, Rost TL. 2002. Toward a causal explanation of plant invasiveness: Seedling growth and life-history strategies of 29 pine (*Pinus*) species. American Naturalist 159: 396–419.

Hampe A. 2004. Bioclimate envelope models: What they detect and what they hide. Global Ecology and Biogeography 13: 469–471.

Higgins SI, Nathan R, Cain ML. 2003. Are long-distance dispersal events in plants usually caused by nonstandard means of dispersal? Ecology 84: 1945–1956.

Hodkinson DJ, Thompson K. 1997. Plant dispersal: The role of man. Journal of Applied Ecology 34: 1484–1496.

Houghton JT, Ding Y, Griggs DJ, Noguer M, van der Linden PJ, Dai X, Maskell K, Johnson CA, eds. 2001. Climate Change 2001: The Scientific Basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change. New York: Cambridge University Press.

Hunter GG, Douglas MH. 1984. Spread of exotic conifers in South Island rangelands. Journal of Forestry 29: 78–96.

Johnstone JF, Chapin FS. 2003. Non-equilibrium succession dynamics indicate continued northern migration of lodgepole pine. Global Change Biology 9: 1401–1409.

King GA, Neilson RP. 1992. The transient response of vegetation to climate change: A potential source of CO_2 to the atmosphere. Water, Air, and Soil Pollution 64: 365–383.

Kirilenko AP, Solomon AM. 1998. Modeling dynamic vegetation response to rapid climate change using bioclimatic classification. Climatic Change 38: 15–49.

Kleidon A, Mooney HA. 2000. A global distribution of biodiversity inferred from climatic constraints: Results from a process-based modelling study. Global Change Biology 6: 507–523.

Knevel IC, Bekker RM, Bakker JP, Kleyer M. 2003. Life-history traits of the Northwest European flora: The LEDA database. Journal of Vegetation Science 14: 611–614.

Lake JC, Leishman MR. 2004. Invasion success of exotic plants in natural ecosystems: The role of disturbance, plant attributes and freedom from herbivores. Biological Conservation 117: 215–226.

Lanner RM, Van Devender TR. 1998. The recent history of pines in the American Southwest. Pages 171–182 in Richardson DM, ed. The Ecology and Biogeography of *Pinus.* New York: Cambridge University Press.

Leishman MR, Wright IJ, Moles AT, Westoby M. 2000. The evolutionary ecology of seed size. Pages 31–57 in Fenner M, ed. Seeds: The Ecology of Regeneration in Plant Communities. Wallingford (United Kingdom): CABI.

Lenihan JM, Drapek RJ, Bachelet D, Neilson RP. 2003. Climate change effects on vegetation distribution, carbon and fire in California. Ecological Applications 13: 1667–1681.

Levey DJ, Moermand TC, Denslow JS. 1994. Frugivory: An overview. Pages 282–294 in McDade LA, Bawa KS, Hespenheide HA, Hartshorn GS, eds. La Selva: Ecology and Natural History of a Neotropical Forest. Chicago: University of Chicago Press.

Lischke H. 2001. New developments in forest modeling: Convergence between applied and theoretical approaches. Natural Resource Modeling 14: 71–102.

Löffler TJ, Lischke H. 2001. Incorporation and influence of variability in an aggregated forest model. Natural Resource Modeling 14: 103–137.

Loreau M, Downing A, Emmerson A, Gonzalez A, Hughes J, Inchausti P, Joshi J, Norberg J, Sala O. 2002. A new look at the relationship between diversity and stability. Pages 79–91 in Loreau M, Naeem S, Inchausti P, eds. Biodiversity and Ecosystem Functioning: Synthesis and Perspectives. Oxford (United Kingdom): Oxford University Press.

Malcolm JR, Markham A, Neilson R. 2001. Can species keep up with climate change? Conservation Biology in Practice 2: 24–25.

Millennium Ecosystem Assessment. 2005. Ecosystems and Human Well-Being: Synthesis. Washington (DC): Island Press.

Muller SD, Richard PJH. 2001. Post-glacial vegetation migration in conterminous Montreal Lowlands, southern Quebec. Journal of Biogeography 28: 1169–1193.

Myers JA, Vellend M, Gardescu S, Marks PL. 2004. Seed dispersal by white-tailed deer: Implications for long-distance dispersal, invasion, and migration of plants in eastern North America. Oecologia 139: 35–44.

Nathan R, Katul G, Horn HS, Thomas SM, Oren R, Avissar R, Pacala SW, Levin SA. 2002. Mechanisms of long-distance dispersal of seeds by wind. Nature 418: 409–413.

Nathan R, Perry G, Cronin JT, Strand AE, Cain ML. 2003. Methods for estimating long-distance dispersal. Oikos 103: 261–273.

Nathan R, et al. 2005. Long-distance biological transport processes through the air: Can nature's complexity be unfolded *in silico?* Diversity and Distributions 11: 131–137.

Neilson RP. 1995. A model for predicting continental-scale vegetation distribution and water balance. Ecological Applications 5: 362–395.

Neilson RP, Prentice IC, Smith B, Kittel TGF, Viner D. 1998. Simulated changes in vegetation distribution under global warming. Pages 439–456 in Watson RT, Zinyowera MC, Moss RH, Dokken DJ, eds. The Regional Impacts of Climate Change: An Assessment of Vulnerability. New York: Cambridge University Press.

Parmesan C, Yohe G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421: 37–42.

Plotnick RE, Gardner RH. 2002. A general model for simulating the effects of landscape heterogeneity and disturbance on community patterns. Ecological Modelling 147: 171–197.

Prentice IC, Cramer W, Harrison SP, Leemans R, Monserud RA, Solomon AM. 1992. A global biome model based on plant physiology and dominance, soil properties and climate. Journal of Biogeography 19: 117–134.

Scheffer M, Carpenter SR. 2003. Catastrophic regime shifts in ecosystems: Linking theory to observation. Trends in Ecology and Evolution 18: 648–656.

Schwartz MW, Iverson LR, Prasad AM. 2001. Predicting the potential future distribution of four tree species in Ohio using current habitat availability and climatic forcing. Ecosystems 4: 568–581.

Smith B, Prentice IC, Sykes MT. 2001. Representation of vegetation dynamics in the modeling of terrestrial ecosystems: Comparing two contrasting approaches within European climate space. Global Ecology and Biogeography 10: 621–637.

Smith TM, Shugart HH. 1993. The transient response of terrestrial carbon storage to a perturbed climate. Nature 361: 523–526.

Sykes MT, Prentice IC. 1996. Climate change, tree species, distributions and forest dynamics: A case study in the mixed conifer/northern hardwoods zone of northern Europe. Climatic Change 34: 161–177.

Tackenberg O. 2003. Modeling long distance dispersal of plant diaspores by wind. Ecological Monographs 73: 173–189.

Thomas CD, et al. 2004. Extinction risk from climate change. Nature 427: 145–148.

Thonicke K, Venevsky S, Sitch S, Cramer W. 2001. The role of fire disturbance for global vegetation dynamics: Coupling fire into a Dynamic Global Vegetation Model. Global Ecology and Biogeography 10: 661–677.

van der Pijl L. 1982. Principles of Dispersal in Higher Plants. Berlin: Springer Verlag.

van Minnen JG, Leemans R, Ihle F. 2000. Defining the importance of including transient ecosystem responses to simulate C-cycle dynamics in a global change model. Global Change Biology 6: 595–612.

Willson MF, Traveset A. 2000. The ecology of seed dispersal. Pages 85–110 in Fenner M, ed. Seeds: The Ecology of Regeneration in Plant Communities. 2nd ed. Wallingford (United Kingdom): CABI.