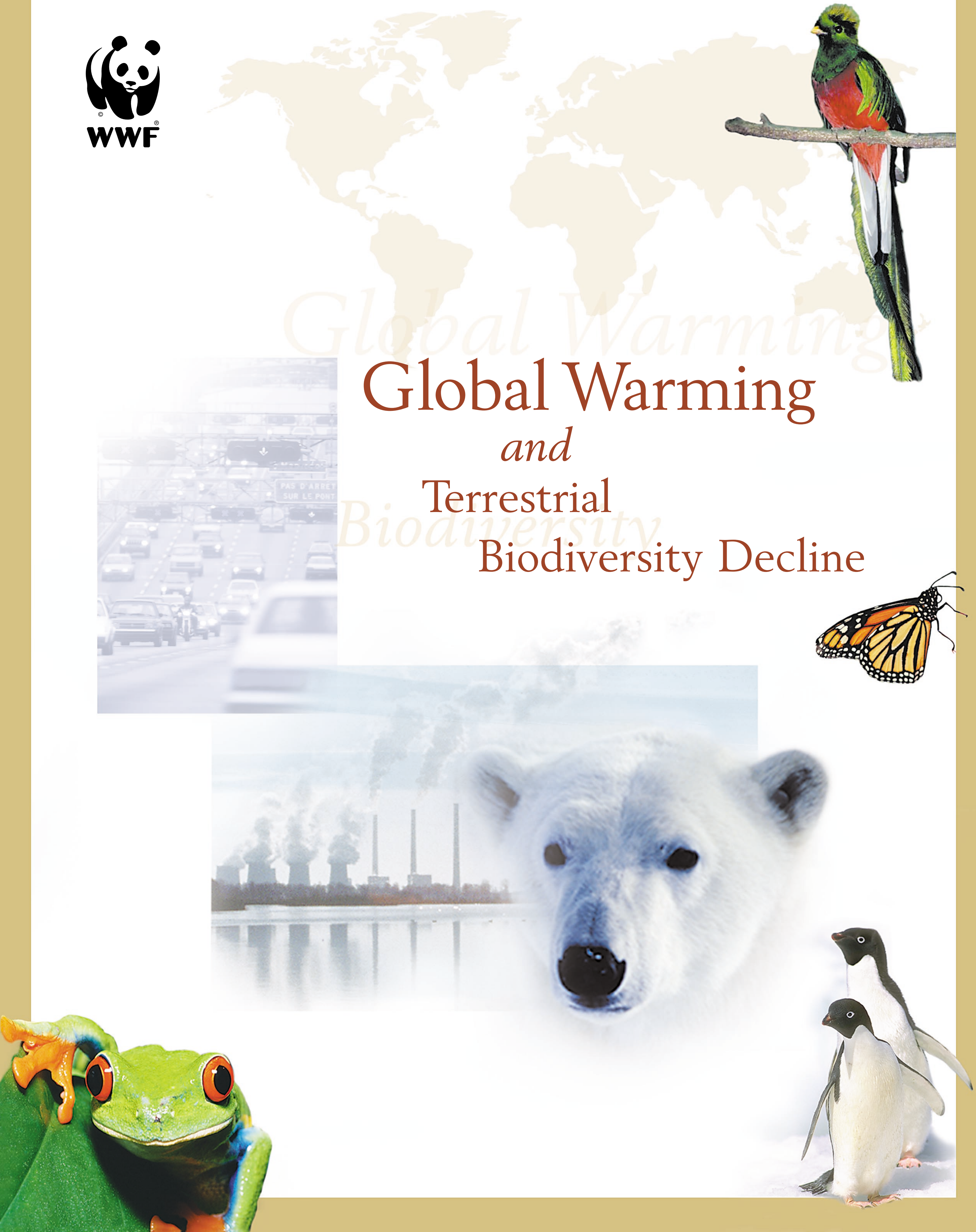

Global Warming
Biodiversity

Global Warming
and
Terrestrial
Biodiversity Decline

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Global Warming and Terrestrial Biodiversity Decline

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Executive Summary

Past efforts to model the potential effects of greenhouse warming on global ecosystems have focussed on flows of energy and matter through ecosystems rather than on the species that make up ecosystems. For this study, we used models that simulate global climate and vegetation change to investigate three important threats to global terrestrial biodiversity:

1) Rates of global warming that may exceed the migration capabilities of species
2) Losses of existing habitat during progressive shifts of climatic conditions
3) Reductions in species diversity as a result of reductions in habitat patch size.

We also analyzed the effects that major natural barriers such as oceans and lakes, and human-caused impediments to migration, including agricultural land and urban development, might have on the ability of species to move in response to global warming.

Seven climate models (general circulation models or GCMs) and two biogeographic models were used to produce 14 impact scenarios.[1] The models do not provide information on biodiversity *per se*, but instead simulate future distributions of major vegetation types (biomes) such as boreal coniferous forest and grassland. We were able to use the models to indirectly investigate potential biodiversity change in several ways:

- To measure the rates of migration that greenhouse warming might impose on species, we calculated the rates at which major vegetation types would need to move if they were to be able to successfully keep up with climate change. The shifts of biome boundaries under the different climate scenarios were used as proxies for shifts in the distributional boundaries of plant species.
- To measure the potential loss of existing habitat, we compared current vegetation distributions with those projected for the future under the various scenarios, and quantified the areas of change.
- Finally, by making use of well-established relationships between habitat patch size and species richness, we investigated the potential for species loss due to predicted reductions in the area of habitat patches remaining after warming.

The fate of many species in a rapidly warming world will likely depend on their ability to permanently migrate away from increasingly less favorable climatic conditions to new areas that meet their physical, biological and climatic needs. Unfortunately, the ability of species to migrate is generally poorly understood so it is difficult to determine just how serious the impacts of climate change might be on biodiversity. Much of our knowledge about potential for rapid migration of species comes from fossil evidence of how forests re-colonized previously glaciated areas after the last ice age. However, scientists are not in agreement as to whether the rates attained at that time are the maximum attainable rates, or whether at least some species could move faster if necessary. Therefore, instead of attempting to predict how fast species and biomes might be able to move, we analyzed how fast they might be *required* to move in order to keep up with projected warming.

We calculated “required migration rates” (RMRs) for all terrestrial areas of the globe. RMRs of greater than 1,000 m / yr were judged to be “very high” because they are very rare in the fossil or historical records. We compared RMRs under scenarios where CO_2 doubling equivalent was reached after 100 years, and after 200 years, in order to assess the influence of the rate of global warming on the vulnerability of species. In fact, even relatively optimistic emissions scenarios suggest that CO_2 concentrations in the atmosphere are likely to have doubled from pre-industrial levels around the middle of this century and will almost triple by 2100. This means that the RMRs reported here are likely to be on the conservative side and that species may need to move even faster than reported here. Our results indicate that climate change has the potential to radically increase species loss and reduce biodiversity, particularly in the higher latitudes of the Northern Hemisphere.

Summary of key findings

Specific conclusions:

- All model combinations agreed that “very high” required migration rates or RMRs (≥1,000 m / yr) were common, comprising on average 17 and 21% of the world's surface for the two vegetation models.
- RMRs for plant species due to global warming appear to be 10 times greater than those recorded from the last glacial retreat. Rates of change of this magnitude will likely result in extensive species extinction and local extirpations of both plant and animal species.
- High migration rates were particularly concentrated in the Northern Hemisphere, especially in Canada, Russia, and Fennoscandia. Despite their large land areas, an average of 38.3 and 33.1% of the land surface of Russia and Canada, respectively, exhibited high RMRs.
- The highest RMRs are predicted to be in the taiga / tundra, temperate evergreen forest, temperate mixed forest and boreal coniferous forest, indicating that species dependent on these systems may be amongst the most vulnerable to global change.
- Even halving the rate of global warming in the models did little to reduce the areas with high RMRs.
- Water bodies, such as oceans and large lakes, that can act as barriers to migration were shown to be significant factors in influencing RMRs in some regions, especially on islands such as Newfoundland, and peninsulas such as western Finland.
- The barriers to migration represented by human population density and agriculture were also regionally influential, particularly along the northern edges of developed zones in northwestern Russia, Finland, central Russia and Central Canada.
- In addition to imposing high RMRs on species, global warming is likely to result in extensive habitat loss, thereby increasing the likelihood of species extinction. Global warming under CO_2 doubling has the potential to eventually destroy 35% of the world’s existing terrestrial habitats, with no certainty that they will be replaced by equally diverse systems or that similar ecosystems will establish themselves elsewhere.
- Russia, Sweden, Finland, Estonia, Latvia, Iceland, Kyrgyzstan, Tajikistan, and Georgia all have more than half of their existing habitat at risk from global warming, either through outright loss or through change into another habitat type.
- Seven Canadian provinces / territories – Yukon, Newfoundland and Labrador, Ontario, British Columbia, Quebec, Alberta and Manitoba - have more than half their territory at risk.
- In the USA, more than a third of existing habitat in Maine, New Hampshire, Oregon, Colorado, Wyoming, Idaho, Utah, Arizona, Kansas, Oklahoma, and Texas could change from what it is today.
- Local species loss under CO_2 doubling may be as high as 20% in the most vulnerable arctic and montane habitats as a result of climate change reducing the size of habitat patches and fragments. Highly sensitive regions include Russia’s Taymyr Peninsula, parts of eastern Siberia, northern Alaska, Canadian boreal / taiga ecosystems and the southern Canadian Arctic islands, northern Fennoscandia, western Greenland, eastern Argentina, Lesotho, the Tibetan plateau, and southeast Australia. These losses would be in addition to those occurring as a result of overall habitat reduction.

General conclusions:

- It is safe to conclude that although some plants and animals will be able to keep up with the rates reported here, many others will not.
- Invasive species and others with high dispersal capabilities can be predicted to suffer few problems and so pests and weedy species are likely to become more dominant in many landscapes.
- However, in the absence of significant disturbance, many ecosystems are quite resistant to invasion and community changes may be delayed for decades.

- Global warming is likely to have a winnowing effect on ecosystems, filtering out those that are not highly mobile and favoring a less diverse, more “weedy” vegetation or systems dominated by pioneer species.
- Non-glaciated regions where previous selection for high mobility has not occurred among species may suffer disproportionately. Therefore, even though high RMRs are not as common in the tropics, there may still be a strong impact in terms of species loss.
- Some species have evolved *in situ* and may fail to migrate at all.
- Future migration rates may need to be unprecedented if species are to keep up with climate change.
- Human population growth, land-use change, habitat destruction, and pollution stresses will exacerbate climate impacts, especially at the pole-ward edges of biomes.
- Increased connectivity among natural habitats within developed landscapes may help organisms to attain their maximum intrinsic rates of migration and help reduce species loss.
- However, if past fastest rates of migration are a good proxy for what can be attained in a warming world, then radical reductions in greenhouse gas emissions are urgently required in order to reduce the threat of biodiversity loss.

In conclusion, this study demonstrates that rapid rates of global warming are likely to increase rates of habitat loss and species extinction, most markedly in the higher latitudes of the Northern Hemisphere. Extensive areas of habitat may be lost to global warming and many species may be unable to shift their ranges fast enough to keep up with global warming. Rare and isolated populations of species in fragmented habitats or those bounded by large water bodies, human habitation and agriculture are particularly at risk, as are montane and arctic species.

Introduction

Climate plays a primary role in determining both the geographic distributions of organisms and the distributions of the habitats upon which they depend. In the past, directional climate change has resulted in significant shifts in the distributions of species (Davis 1986). Temperate tree species, for example, migrated at rates of tens of metres per year or more to keep up with retreating glaciers during the Holocene (Huntley and Birks 1983). If allowed to continue, greenhouse warming is similarly expected to result in significant shifts in vegetation types. To illustrate, a recent effort to model the effect of a doubling of greenhouse gas concentrations on vegetation projected shifts in major vegetation types in 16-65% of the land area of the lower 48 U.S. states, depending on the exact combination of models used (VEMAP Members 1995). While climatic shifts of this sort have been observed in the past, and can be expected in the future even in the absence of human activities, the rate of greenhouse warming appears likely to be unprecedented in at least the last 100,000 years, with a doubling of greenhouse gases concentrations and associated warming expected to occur within a mere 100 years. Although poorly understood, the rapidity of the change could have important implications for terrestrial biodiversity, with the possibility of significant species loss (Malcolm and Markham 1996, 1997).

With improved abilities to model future global climate and vegetation change comes the possibility to investigate in more detail this threat to global biodiversity. Unfortunately, this important task as yet has received little attention. Instead, research has tended to focus on functional properties of ecosystems, such as the ways in which they process energy and matter (e.g. VEMAP Members 1995). The few attempts to model processes acting at the species level have been restricted to one or a few localities and a small subset of the flora and fauna. In this report, we examine the question of global biodiversity decline. In particular, we use global climate and vegetation models to investigate three possible threats to global biodiversity:

1) Warming that exceeds the migrational capabilities of species
2) Losses of habitat during progressive shifts of climatic conditions
3) Reductions in species diversity through reductions in habitat patch size.

Although the models do not provide direct information on changes in species diversity (rather, they map distributions of vegetation types), we can nevertheless use them in a heuristic fashion to indirectly examine these threats. For example, to assess the migration speeds that species might have to achieve in order to keep up with shifting climatic conditions, we can measure the speed of shifting vegetation types. Similarly, habitat losses and reductions in the areas of habitat patches can be quantified by comparing current and future vegetation maps and quantifying areas of change. Although indirect, these methods provide powerful tools to investigate possible threats to biodiversity.

Rapid Climate Shifts

Although species have inherent abilities to respond to climatic shifts through population processes such as birth, death, and dispersal, the speed at which they can respond is limited. If climatic conditions shift quickly enough, slower moving species may be left behind, especially if human activities have destroyed and fragmented existing habitat. As shown schematically in Figure 1A, as climatic conditions shift, so will the conditions for successful growth and reproduction of many species. In order to occupy newly-suitable areas, species must migrate from existing source populations. Although many species have migrated in the past in response to changing climates, the shifts imposed by global warming may exceed the capabilities of many species. For example, Dyer (1995) modeled migrations of trees dependent on wind or bird dispersal and concluded that even in relatively undisturbed landscapes, migration rates fell short of projected global warming range shifts by at least an order of magnitude. Other studies have similarly concluded that future plant migration could lag behind climatic warming, resulting in altered relationships between climatic conditions and species distributions, enhanced susceptibility of plant communities to natural and anthropogenic disturbances, and eventual reductions in species diversity (Davis 1989, Overpeck et al. 1991). Added to the problem of rapidly shifting climatic zones are habitat losses in human-dominated landscapes, with current landscapes providing fewer possibilities for migration than historic ones.

The possibility that global warming might require relatively high migration rates has serious implications, especially if the mismatch between climatic warming and migration rates affects species such as trees that disproportionately affect ecosystem properties. One potential consequence of high migration rates, for example, is a decrease in the ability of forests to store carbon from the atmosphere and hence a decrease in their ability to ameliorate greenhouse warming. In a scenario in which trees were perfectly able to keep up with global warming, Solomon and Kirilenko (1997) observed that the warming associated with a doubling of atmospheric CO_2 resulted in a 7-11% increase in global forest carbon. In a contrasting scenario in which they assumed zero migration, a 3-4% decline in global forest carbon was observed. Kirilenko and Solomon (1998) obtained a similar result when they used past tree migration rates as estimates of potential future migration rates and found that a large portion of the earth became occupied by plant assemblages that were less diverse. Sykes and Prentice (1996) also investigated an all-or-none migration scenario at a site in southern Sweden. Compared to perfect migration, zero migration resulted in fewer tree species, lower forest biomass, and increased abundance of early successional species.

Although several studies have investigated the capabilities of species to migrate in response to global warming, none has investigated in detail the overall rates of migration that global warming might impose. How do these possible future rates compare with past rates? Are migration rates uniform across the surface of the planet or are they particularly high in some regions? Perhaps most importantly, how will human behaviour influence these future rates? Are the rates substantially elevated in areas where habitat has been lost through development? What is the relationship between the rate of greenhouse warming and future migration rates?

Habitat Loss

Worldwide, habitat loss has been identified as a primary cause of species extinction and endangerment. Climate change can be expected to result in shifts in habitat conditions, with the eventual loss of existing habitats in many areas (Figure 2B). New habitats may reappear elsewhere, but in many cases only if the requisite biotic (living) elements are able to track the abiotic (physical) change. Appropriate habitat usually depends on both abiotic and biotic elements, although the importance of the two varies from one species to another. If climatic conditions shift, but suitable biotic elements fails to migrate, then new habitat areas may be of lower quality for many species. An example would be the failure of trees to migrate pole-ward despite the fact that suitable conditions for forest cover have shifted towards higher latitudes. Species dependent on forest conditions for food, nesting, or cover would be unable to utilize the new area.

Several studies have used global vegetation models to map areas of possible vegetation change. Here, we expand on previous efforts by simultaneously investigating vegetation change for a large suite of global climate and vegetation models. We were interested in the consistency of the patterns of change among models and in whether or not patterns of habitat loss were concentrated in particular regions of the globe.

Declines in Patch Area and Associated Species Loss

The rate of climate change is expected to vary from one region to another, with some regions undergoing less rapid change than others. However, even if the climate (and habitat) in an area remains relatively unchanged, changes in the surrounding landscape may have indirect effects. In particular, if the extent of a habitat patch declines over time, then declines in species diversity within the patch can be expected. This species loss will arise from a combination of factors, including reduced population sizes of the various species that inhabit the patch and reduced diversity of micro-habitat types within the patch. A considerable body of research over the past decades has identified a strong relationship between habitat area and species richness. Following MacArthur and Wilson's (1967) development of the Theory of Island Biogeography, which predicted that species diversity would decrease with island size, ecologists began applying similar concepts to “habitat islands,” such as forest patches, lakes, and mountain tops. Empirical evidence has shown that if species richness and patch area are plotted against each other, species richness strongly increases with area.[2] A classic application of this observation to the problem of global warming was provided by McDonald and Brown (1992). These authors used temperature gradients to investigate the future distributions of high altitude habitats in isolated mountain ranges of the Great Basin of the U.S. Southwest. This area of sagebrush desert is interrupted at irregular intervals by isolated mountain ranges that provide the cool moist conditions required to support a relictual boreal mammal fauna. The limits of this cooler habitat can be mapped quite accurately by using temperature, hence the authors could compare current and projected future distributions of the habitat by comparing current and future temperature maps. Possible changes in species richness could then be investigated based on the relationship between habitat area and species richness. Under mean warming of 3 ^{O}C, McDonald and Brown (1992) observed that montane ecosystems decreased in size due to upslope migration, with individual ranges losing anywhere between 35 and 96% of their original boreal habitat. Based on the species-area relationship, different mountain ranges lost between 9 and 62% of their boreal mammal species. Three of fourteen mammal species were predicted to go extinct across the entire Great Basin.

Surprisingly, this approach has not been undertaken over larger areas. Here, we use their approach, albeit at a coarser scale of resolution, and apply it at the global scale. We were particularly interested in the possibility of biodiversity loss in alpine and arctic habitats. As temperatures rise and the cool conditions required by these habitats shift upward and pole-ward, reductions in area are expected. Are these decreases likely to be accompanied by significant species loss?

Methods

Quantifying Threats to Biodiversity

To investigate these threats to biodiversity, we employed linked global climate and vegetation models. In combination, these models can be used to map the potential future distributions of major vegetation types (biomes). Given any atmospheric CO_2 concentration, the climate models simulate climatic conditions, and given this simulated climate, the vegetation models determine potential vegetation types. Two sets of models were run: a “control” set in which atmospheric CO_2 concentrations approximated recent historical conditions (e.g. 1961-1990) and a “future” set in which atmospheric CO_2 concentrations were twice as high. The global climate models, known as General Circulation Models (GCMs), are detailed computer simulations that model three-dimensional representations of the earth's surface and solve the systems of equations that govern mass and energy dynamics. They suffer from coarse grid sizes and numerous simplifying assumptions; however, they have met with considerable success in modeling global climatic patterns (e.g. Hasselmann 1997, Houghton et al. 1996, Kerr 1996). The vegetation models make use of ecological and hydrological processes and plant physiological properties to predict potential vegetation on upland, well-drained sites under average seasonal climate conditions. A simulated mixture of generalized life forms such as trees, shrubs, and grasses that can coexist at a site is assembled into a major vegetation type (or biome) classification (Neilson et al. 1998). These models are termed “equilibrium” models because they model the vegetation that would be expected to occur at a site once both climate and vegetation change at the site have stabilized. A standardized series of climate and vegetation models such as that used in the VEMAP project (VEMAP Members 1995) was not available at the global scale; however, 14 combinations of models were available to us. These included seven global climate models, including both “older” and “newer” generation models[3], and two global vegetation models (MAPSS [Neilson 1995] and BIOME3 [Haxeltine and Prentice 1996])[4]. The state of climate and vegetation modeling is not such that the model outcomes can be viewed as predictions (VEMAP Members 1995). Rather, the models represent a range of possible future outcomes as envisioned by different groups of scientists. Uncertainties concerning the best ways in which to model climate and vegetation are considerable, hence our use of this range of possibilities. However, it is important to note that the uncertainty concerning the effects of increasing greenhouse gas concentrations should not be confused with an increased possibility of the “no change” option. More extreme change than predicted is as likely as less extreme change.

A Heuristic Approach to Modeling Biodiversity Change

Any attempt to model the effect of climate change on all of the myriad species in an ecosystem would be a very detailed and difficult undertaking. Basic information is often lacking, for example, where species occur and how quickly they might respond to change. At the global level, information gaps become even more serious; for example, it is not yet possible to accurately map species ranges across the entire planet for any group of organisms, with the possible exception of birds. Equally problematic are the complex sets of interactions among species, which often determine how they respond to change. An illustrative example is the distinction between the “fundamental” and “realized” niches of a species. The former represents the possible range of physical conditions which the species can occupy, whereas the latter represents the observed set of conditions that it actually occupies under the influence of additional factors such as predation, competition, etc. Predicting the effect of global warming on physical conditions is relatively straightforward, but disentangling the interaction of both physical and biotic changes is enormously difficult.

Nevertheless we can apply general ecological principles to investigate possible biodiversity change. In this paper, rather than attempting to model each species, we apply a broader brush and, as detailed below, take a more heuristic approach. A good example of this sort of approach is provided by McDonald and Brown (1992) who used empirical species-area relationships to study biodiversity loss as described above.

Migration rates

The factors affecting the ability of organisms to migrate in response to climate changes are not well understood even for relatively well-known organisms such as trees. Some studies have assumed that trees can migrate at most at observed post-glacial rates; however, the validity of this assumption has been questioned (Clark 1998, Clark et al. 1998). Therefore, instead of attempting to predict how fast species and biomes might be able to move, we instead asked how fast might species and biomes be *required* to move in order to keep up with the projected warming.

As noted above, the climate/vegetation models provided information on the current and future distributions of major vegetation types. Therefore, we could use the models to calculate the speeds that biomes might have to achieve in order to keep up with the warming. However, our primary interest was not in the biomes themselves (a biome is, after all, an abstract entity), but rather in the species within them. Note however that at least in a heuristic sense, the movement of the biomes provides indirect information on the movements of species. The same sorts of physiological variables that the vegetation models use to map biome distributions are also relevant in mapping the distributions of individual species (especially plant species) (e.g. Sykes and Prentice 1996). In this sense, the “biome climate envelopes” that the vegetation models simulate can be thought of as proxies for “species climate envelopes.” Additionally, species distributions in many cases are strongly associated with particular biome types; for example, the many plants and animals that can only survive in arctic conditions.

As detailed below, in a series of core calculations we measured required biome migration rates under a single set of assumptions. To investigate the importance of these assumptions, we also undertook sensitivity analyses in which they were systematically varied.

Core Calculations

To calculate a migration rate, one divides the migration distance by the time period over which the migration occurs. To measure distances, we reasoned that the nearest possible immigration source for a locality with future biome type *x* would be the nearest locality of the same biome type under the current climate. Thus, the migration distance was calculated as the distance between a future locality and the nearest same-biome-type locality in the current climate. For example, the tree shown in Figure 1A in the new habitat patch must have come from an area where the species already occurred. The simplest assumption is that it came from the nearest possible locality in the species former range. Note that where current and future vegetation types stay the same (the region labeled “a” in Figure 1A), the species would not have to migrate at all, and the required migration rate would be zero. An average required rate for a species thus includes these areas of zero migration.

Based on IPCC estimates (Houghton et al. 1996), we assumed that the doubled CO_2 climate would occur in 100 years. This assumption is based on an IPCC midrange emission scenario, “medium” climate sensitivity (2.5 ^{O}C), and sulphate aerosol cooling. Some transient model runs suggest that 2 x CO_2 forcing may be reached over a considerably shorter time period (see references in Solomon and Kirilenko 1997); hence, our migration rates may be conservative.

A final important factor to consider is the breadth of the biome definitions. The two vegetation models used somewhat different definitions of a “biome” and also divided up major biome types in different ways. Specifically, BIOME3 modeled 18 biome types, whereas MAPSS modeled 45. In general, the use of fewer, more broadly-defined climate envelopes (as in BIOME3) can be expected to result in lower average migration rates, because existing and future distributions of a biome will show larger areas of overlap and hence larger areas of zero migration. The use of fewer biome types is equivalent to assuming that species have relatively large geographic ranges (and broad habitat requirements). We used a conservative figure, and following Neilson et al. (1998), in the core calculations used 10 biome types for both models (see Table 1).

Sensitivity Analyses

The variables that we considered in our sensitivity analyses were:

1) Impediments to migration (large water bodies and human land-use change)
2) The time period to attain the doubled CO_2 climate
3) The breadth of the biome definitions

The distances that we measured in the core calculations were “crow-fly” distances, i.e., the shortest straight-line distance between two localities (map grid cell centres). Such distances ignored potential barriers to migration, such as bodies of water and anthropogenic development. To incorporate water barriers, we contrasted the crow-fly distances with distances calculated using “shortest terrestrial paths.” These consisted of the shortest distances linking centres of neighbouring terrestrial map cells (including diagonally linked cells). Thus, the calculated paths were the shortest distances around water bodies[5]. We also investigated the potential impact of anthropogenic habitat loss and attendant decreases in migration possibilities by removing from the shortest path calculations cells that were “highly impacted” by human activities. These highly impacted cells were assumed to be completely impermeable to migration; that is, in the shortest path calculations they behaved as though they were water bodies. Our definition of “highly impacted” was based on model results by Turner (reported in Pitelka et al. 1997), which suggested that thresholds of movement though fragmented landscapes occurred when approximately 55% or 85% of habitat was destroyed (respectively, depending on whether fragmentation was random or aggregated). Simulations by Schwartz (1992) also indicated shifts in migration rates at close to these values (respectively, depending on whether dispersal followed negative exponential or inverse power functions). To quantify habitat destruction, we made use of the global 1-km unsupervised classification of AVHRR satellite data undertaken by the United States Geological Service[6].

For comparison to the core scenario in which climate change was assumed to occur in 100 years, we assumed a more conservative time period, namely 200 years. Additionally, we took advantage of research on post-glacial rates of spruce (*Picea*) migration (see Pitelka et al. 1997) and compared *Picea* migration rates against required migration rates calculated for the boreal biome. We used the boreal biome because the current geographic distribution of *Picea* in North America is fairly well approximated by the boreal biome. In the comparisons, we varied the time period of climate forcing until we achieved maximum agreement between *Picea* and boreal rates.

Finally, we investigated the relationship between migration rate and biome area by plotting mean migration rate against biome area for biomes in North America and Africa[7]. Because biomes in Africa tended to be distributed into northerly and southerly portions, we calculated areas and rates separately for the northern and southern portions. This made the African biomes more contiguous and hence more comparable with the North American biomes.

Current Habitat Loss

As shown in Figure 1B, we defined current habitat loss based on areas where current and future biome types differed. If a grid cell was biome *x* in the current climate, but became biome type *y* in the future climate, then that habitat was assumed to have been lost. As in the core migration calculations, we used 10 biome types (see Table 1).

Declines in Habitat Patch Area and Associated Species Loss

If species richness is plotted against area on a log-log scale, a more-or-less linear relationship is typically observed between the two. The slope of the relationship has been observed to vary systematically under the influence of a variety of factors – for example, slopes in island systems typically range from 0.24 to 0.33, whereas in continental situations they range from about 0.12 to 0.17 (Pianka 1978). We took a relatively conservative approach and used a value of 0.15. It is not difficult to show that given some proportion *p* of habitat remaining, the expected proportion of species remaining is *p* raised to the power of the slope (0.15 in this case). For example, an 85% reduction in the area can be expected to result in a 25% reduction in species richness (see Figure 1C for examples).

To calculate decreases in patch size, first we calculated the areas of patches of contiguous grid cells of the same biome type under the current climate (these patches included diagonally linked cells). Second, we calculated the area of the patch that was lost (if any) by determining which of the original patch cells had changed to a new biome type under the new climate. Notice that migrations of species into newly-suitable areas may act to partly offset habitat and species loss (should habitats in the new areas materialize); however, in our calculations we considered only the effect of the reduction in area.

Results

Migration Rates

Core calculations

Several of the differences among the climate and vegetation models influenced biome migration rates, including the type of vegetation model[8], the age of the GCM (older vs. newer generation models)[9], the presence or absence of sulphate cooling[10], and the possibility of direct CO_2 effects on plant water use efficiency[11]. However, all models agreed in that “very high” migration rates (≥1,000 m/yr) were relatively common, comprising on average 17 and 21% of the world's surface for the two vegetation models (Figure 2). Migration rates of ≥10,000 m/yr were rare (<1% of the world's surface).

To visually examine the required migration rates, for each grid cell in the world map we plotted the percent of models that exhibited “unusually” high (≥1,000 m/yr) migration rates. We used 1,000 m/yr as a cut-off point because higher tree migration rates rarely have been observed in the past (see Clark 1998). High migration rates were consistently observed in the Northern Hemisphere and included large areas in Canada, Alaska, Russia, Finland, and Sweden (Map 1). Finland was the hardest hit country overall, with an average of nearly 60% of the country exhibiting unusually high rates (Table 2). The high percentages observed for Russia and Canada (respectively 38.3 and 33.1%) are especially notable because of the large sizes of these countries. Unusually high migration rates were indicated for many large areas in Canada, with over 40% of their territory with high rates for Ontario, Newfoundland/Labrador, Quebec, and Manitoba (Table 2). Areas affected in the United States were also substantial, ranging from 35.7 to 14.7% among the top 20 hardest hit states. Other areas with consistently high rates included parts of eastern Brazil; Uruguay; eastern Argentina; the savanna/rainforest border in Africa; southern England; Saudi Arabia; Iraq; India; northeastern China; Thailand; Cambodia; and southwestern Australia (Map 1). Distinct banding parallelling the orientation of biome boundaries was evident in several areas, including Canada, Africa, and northern Asia. These bands reflected the high migration rates required to track the leading edges of poleward-shifting biomes. The high migration rates in the Northern Hemisphere were also evident when future migration rates were compared among latitudinal classes and vegetation types. Lowest migrations rates were observed within 20 degrees of the equator, where 6-8% (BIOME3 vegetation model) or 11-13% (MAPSS vegetation model) of map grid cells had migration rates that exceeded 1,000 m/yr (Figure 3). Average migration rates were nearly constant up to 40 degrees of latitude for BIOME3, but thereafter jumped markedly. The highest migration average for BIOME3 was in the northernmost latitudinal class (>60 degrees), where 35% of cells averaged rates ≥1,000 m/yr. The relationship between latitudinal class and average migration rate was more monotonic for MAPSS than for BIOME3. Maximum migration rates were again observed in the northernmost latitudinal class for MAPSS and were similar in magnitude to those observed for BIOME3. Average migration rates for both vegetation models were markedly higher in temperate vegetation types (Taiga/Tundra, Temperate Evergreen Forest, Temperate Mixed Forest, and Boreal Coniferous Forest) than elsewhere (Figure 4). In these temperate vegetation types, on average approximately 35% of pixels had rates >1,000 m/yr, with a maximum of 44% in Temperate Mixed Forest (MAPSS) and a minimum of 27% for Temperate Evergreen Forest (MAPSS). Average migration rates in the other vegetation (excluding Tundra) tended to be higher for MAPSS than BIOME3. Respectively, an average of 13% and 9% of cells in these remaining vegetation types had rates above 1,000 m/yr. Because Tundra rarely shifted to new areas, but instead was encroached upon, it had migration rates of close to zero in both vegetation models.

Sensitivity Analyses

Barriers to migration. – Averaged over the whole globe, the migration rates calculated ignoring water barriers (that is, using "crow-fly" distances) were usually similar to those calculated taking water barriers in to account (that is, using "shortest-terrestrial-path" distances). Averaged across all models, 99% of grid cells had shortest-path rates that were within 316 m/yr of their crow-fly rates (99.1 and 98.9 for BIOME3 and MAPSS respectively; see Table 3). However, the effect of water as a barrier to migration was often regionally important, especially on islands (such as Newfoundland) and peninsulas (such as western Finland) (Map 2).

When "human modified" cells were assumed to be off limits to migration, shortest-path migration rates also changed relatively slightly at the global scale. Compared to shortest-terrestrial-path distances, the percent of cells that changed their migration rates by 316 m/yr or less averaged between 97 and 99% for the two vegetation models (Table 3). However, the incorporation of human barriers was sometimes regionally important. Grid cells with large increases in migration rates (≥1,000 m/yr) tended to be concentrated along the northern edges of developed areas in the northern temperate zone, especially in northwestern Russia, Finland, central Russia and central Canada (Map 3).

The time period of climate change. – Doubling the period of warming from 100 to 200 years decreased the percentage of cells with very high migration rates (≥1,000 m/yr) by about one third for BIOME3 (17.4 to 11.8%) and by nearly one half for MAPSS (21.3 to 11.9%) (Table 4). However, this doubling of the warming period did little to bring required Boreal migration rates into agreement with rates of spruce (*Picea*) migration observed during the glacial retreat. The best fit between Boreal and spruce rates was obtained when the period of warming was instead increased by approximately an order of magnitude, to 1070 years for BIOME3 and to 1150 years for MAPSS (Figure 5A). At these slower rates of warming, an average of only 1.3% of nonzero Boreal cells had rates exceeding 1,000 m/yr (Figure 5C). For 100-year warming on the other hand, percentages of non-zero Boreal cells exceeding 1,000 m/yr averaged 61% for both BIOME3 and MAPSS (Figure 5B). Therefore, an approximate order of magnitude decrease in the rate of 2 x CO_2 climate change was required in order to bring the two sets of migration rates into agreement. On a more positive note, however, improvement in the rate of fit between the two sets was most rapid for slight increases in the time period. Thus, slight decreases in the rate of warming had a disproportionate effect in reducing required migration rates.

Number of biome types. – As expected, use of more biomes types (18 for BIOME3 and 45 for MAPSS) yielded higher average migration rates than when only 10 types were used, indicating that species with smaller ranges may be more strongly impacted. In comparison to core calculations, 10% more pixels for BIOME3 and 14% for MAPSS had rates above 316 m/yr. This increase in migration rates was confirmed when average migration rates was plotted against biome types for biomes in North America and Africa (Figure 6). As biome area decreased by an order of magnitude, average BIOME3 migration rates increased by approximately 0.5 orders of magnitude and average MAPSS rates by an order of magnitude. The importance of latitude in influencing migration rates was evident in that for a given biome area, North American migration rates were above African ones[12].

Habitat Loss

A global map of percentage habitat loss showed a pattern similar to the map of high required migration rates. Loss of existing habitats was markedly concentrated in the Northern Hemisphere, especially in Canada, Alaska, Russia, and Fennoscandia (Map 4, Table 5). Other areas with consistently high loss included parts of the western and south-central United States, northeastern Saudi Arabia, and parts of Argentina, Australia, China, and Mongolia. Among the top 20 hardest hit countries, habitat loss was always above 40% (Table 5). Again, because of their large size, habitat loss was especially notable in Canada and Russia (respectively, 55.8 and 46.3%). More than half of Canadian provinces/territories had greater than 50% habitat loss and it was especially concentrated along the southern and northern margins of the boreal zone. Within the United States, the most heavily influenced states were usually in the western and south-central sections of the country. Among the top 20 states, habitat loss always averaged greater than 24%.

Averaged over the whole world, habitat loss averaged 35.7% of the land area. For comparison, habitat already seriously impacted by human activities (as judged by USGS-calculated conversion of 55% of the underlying 1-km pixels) was some 20.1% of the total land area.

Declines in Habitat Patch Area and Associated Species Loss

Species loss associated with decreases in the sizes of habitat patches showed quite a different spatial pattern (Map 5). Although threats to biodiversity were again concentrated in the Northern Hemisphere; they tended to occur even further north, into the southern Canadian Arctic islands and the Taymyr Peninsula of Russia for example. Other concentrations of species loss included northern Alaska, western Greenland, the northern boreal/taiga zone of Canada, eastern Argentina, northern Fennoscandia, the Tibetan Plateau of China, and parts of eastern Siberia (Map 5, Table 6).

Discussion and Conclusions

These results indicate that global warming has the potential to radically affect the long-term persistence of terrestrial species. Both vegetation models indicated that required migration rates under global warming were ten times higher than the rapid rates observed during the most recent glacial retreat. In large areas of the Northern Hemisphere, especially in Canada, Russia, and Fennoscandia, high-required migration rates (≥1,000 metres per year) were common. For example, these high rates were recorded for some 60% of Finland, 38% of Russia, and 33% of Canada. Barriers to migration had regional important effects in exacerbating these high rates. A notable example was Finland, where its peninsular nature and the existence of large areas of human development to the south both contributed to substantially higher migration rates (often >3,000 m per year). Even when it was assumed that 2 x CO_2 warming would occur over a much longer time period (i.e., during 200 rather than 100 years), areas of high-required migration rates remained widespread. Increasing the period of warming from 100 to 200 years did little to bring the potential future rates into line with post-glacial rates. If past rates are used as a metric of what species are able to achieve, then a radical decrease in the rate of greenhouse gas accumulation is indicated.

The global warming scenarios also had very strong impacts on habitat loss, indicating that global warming could significantly increase extinction rates. Again, habitat loss was most extreme in northern areas, usually more than 50% of the land base. It was regionally important elsewhere, however, such in parts of the western United States. The areas potentially affected were extensive. Among the top 20 countries, average percent loss ranged from 43% for Iraq to 82% for Iceland. Russia and Canada were notable because of their combination of large land area and high habitat loss. Within the top 20 U.S. states, losses ranged from 25% in Georgia to 44% in Maine. Within Canada, six provinces and one territory showed losses in excess of 50%.

The indirect effect of global warming on habitat patches was also of concern. Species loss in the top 20 hardest hit countries ranged from 2.3 to 5.4% (averaged over the total land area). Species loss was especially high in arctic and mountain areas, where losses typically ranged from 6 to 20% of the total. Note that this loss is for habitats that persisted into the future, and thus comes in addition to species loss that might occur due to habitat loss.

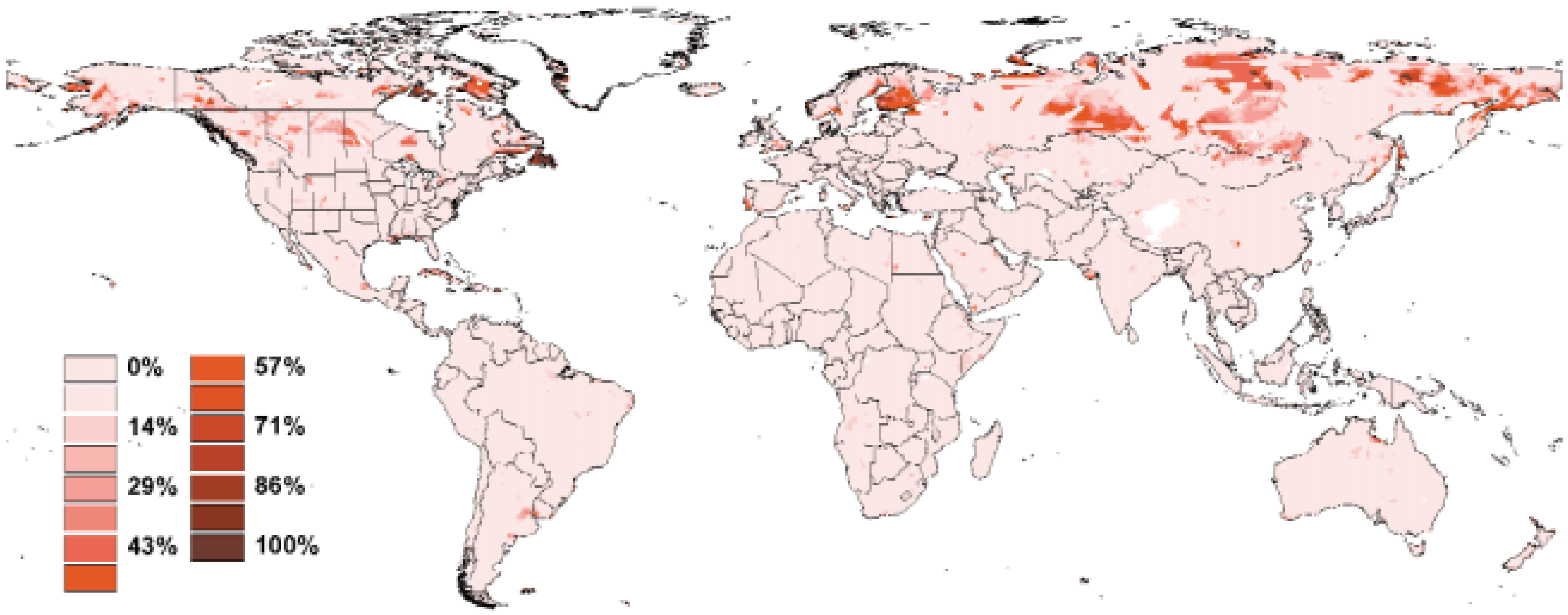
“At the same time, various caveats should be kept in mind. Our global approach necessitated that we take a broad-brush, heuristic approach. At present, uncertainties exist in the ability of the scientific community to model future conditions. As with most scientific studies, this required that we make certain assumptions: some pessimistic, others optimistic. Our results should be taken as indicative, but not conclusive. Several of the main assumptions and uncertainties are addressed below:”

Map 1

A map showing areas where species might have to achieve unusually high migration rates (≥1,000 metres per year) in order to keep up with 2 x CO_2 global warming in 100 years. Shades of red indicate the percent of 14 models that exhibited unusually high rates.

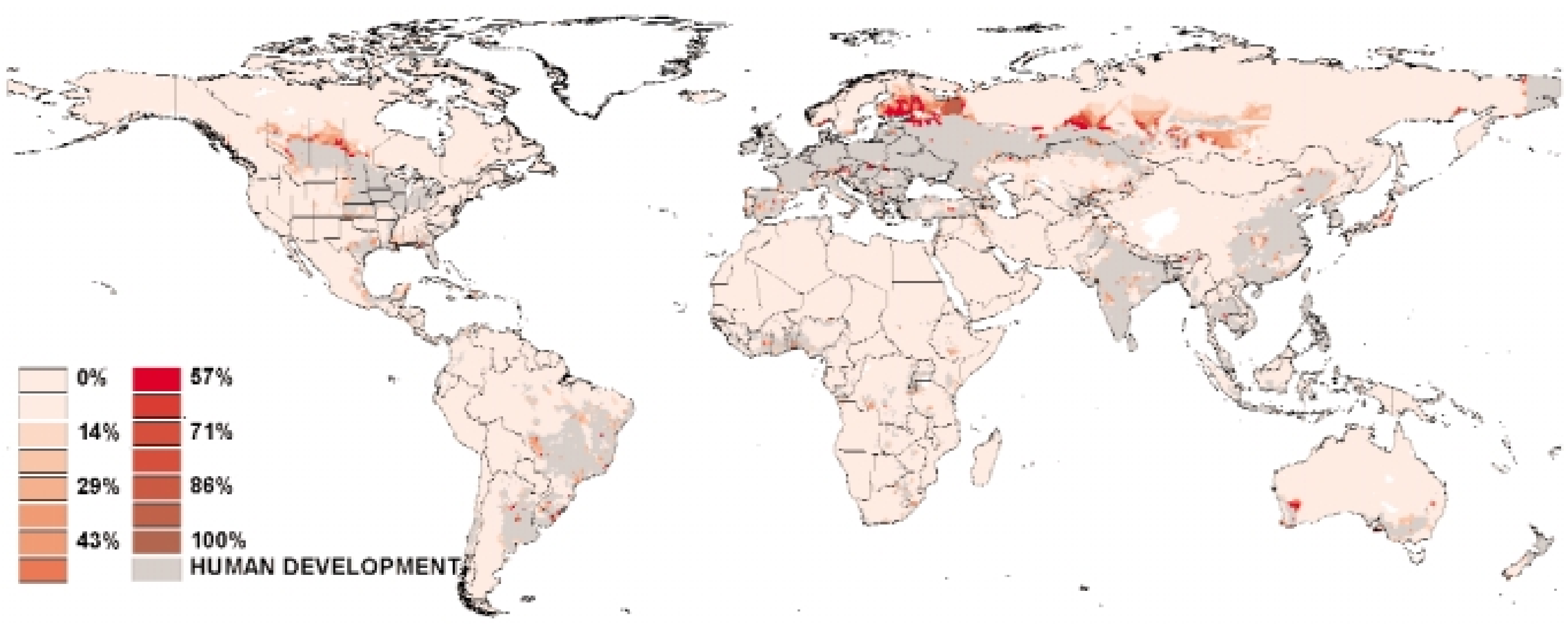
Map 2

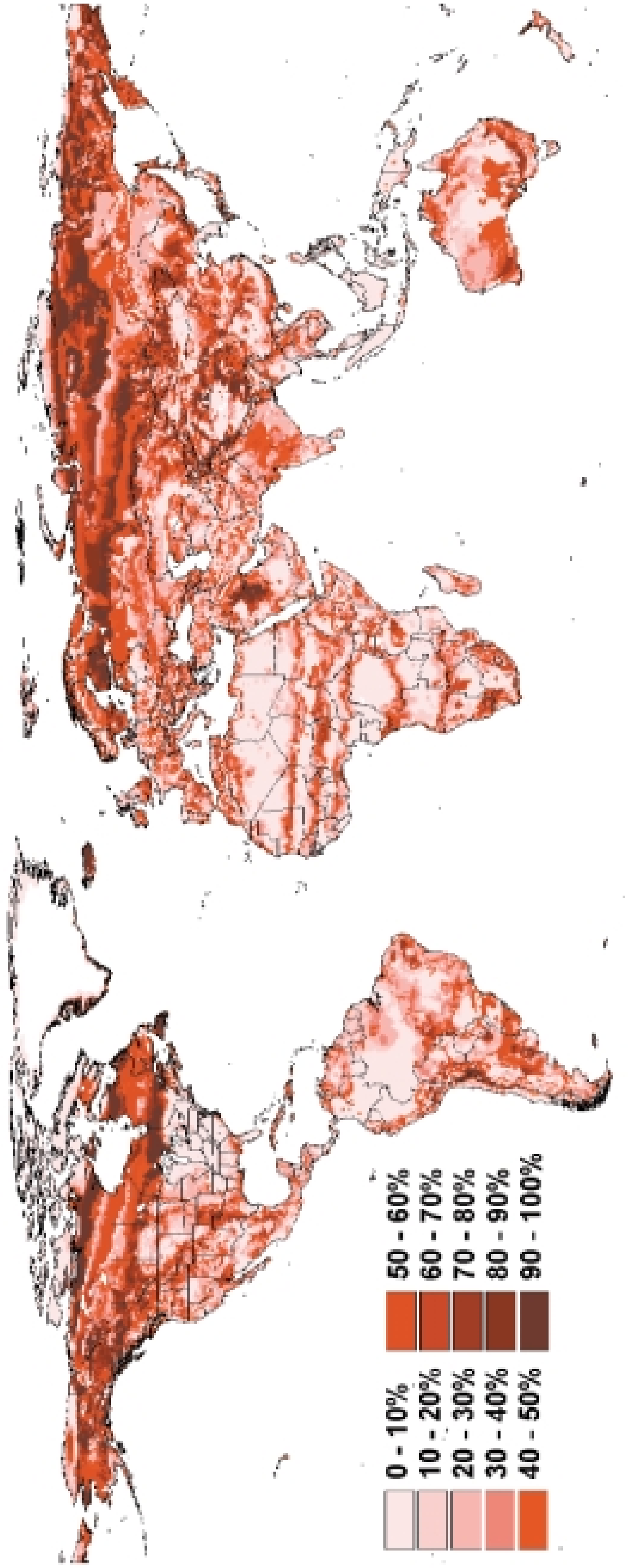
The effect of water barriers in further contributing to migration rates that might be required under 100-year, 2 x CO_2 global warming. Shades of red indicate the percent of models for which future migration rates around water bodies (i.e., using terrestrial migration) were at least 316 metres per year greater than migration rates calculated using "crow-fly" distances.



Map 3

The effect of human development in further contributing to migration rates that might be required under 100-year, 2 x CO_2 global warming. Here, migration rates assuming that human development is off-limits to migration are contrasted with rates that allow migration through any terrestrial grid cell. Shades of red indicate the percent of models for which migration rates excluding human-modified habitats were at least 1,000 m/yr greater than migration rates calculated using all terrestrial cells. In this figure, map grid cells were judged to be human modified if 55% of the cell was composed of anthropogenic habitat (see text for details). The darkest shades indicate the highest consistency among models. Grey areas are the human-modified areas off limits to migration.





Map 4

Loss of existing habitat that could occur under a doubling of atmospheric CO_2 concentrations. Shades of red indicate the percent of vegetation models that predicted a change in biome type of the underlying map grid cell.

As mentioned earlier, the various projections of climate and vegetation change are scenarios, not predictions. In fact, uncertainties in accurate modeling of climate and vegetation are well illustrated in our analysis. Important assumptions about the nature of the coming climate change and the responses of plants to it, such as a cooling effect of sulphate aerosols and a direct CO_2 effect on plant physiology, affected the results that we obtained. The effect of the vegetation model used was especially strong. Differences between the two models nearly swamped the effects of the different climate change scenarios. Significantly, however, our results were robust in the face of this variation among models. All model combinations indicated high migration rates and habitat loss, and within the boreal zone, both vegetation models showed that the time period of warming would have to be increased by approximately an order of magnitude in order to bring future rates into line with post-glacial rates.

- The migration capabilities of organisms are very poorly understood, hence the definition of an “unusually” high migration rate is problematic. A lack of information on plant migration is especially troublesome because although animals can usually migrate more quickly than plants, suitable habitat for animals is often conditional on suitable plant communities. We used 1,000 m/yr as a benchmark of “high” rates based on tree migration during the most recent glacial retreat (e.g., Huntley and Birks 1983). If trees moved at their highest possible rates during glacial times, our calculations suggest that considerable portions of the globe could eventually become devoid of tree cover, with important implications for biodiversity and geochemical cycling (e.g., Solomon and Kirilenko 1997). Unfortunately, it is not clear if the maximum migration rates observed during the Holocene indeed reflected maximum intrinsic rates (Clark 1998). Some lines of evidence suggest that tree capabilities were at a maximum or were exceeded; others suggest that trees can move even more quickly.

- Our calculations of habitat loss are based on losses of existing habitat. At the same time that conditions are becoming unsuitable in one area, they may be improving in another area. Similarly, although habitat patches that persist into the future may decrease in size as judged by loss of existing habitat, new habitat creation may partly compensate for the shortfall (and hence help to ameliorate the species loss predicted from species-area relationships). When viewed from this perspective, the ability of organisms to migrate becomes especially important. If organisms are unable to keep up with the shift, then the future habitat may never materialize. Similarly, if some habitat elements are able to make the transition, but others are not, then organisms may find themselves in a new type of habitat that has not existed before. A good example of the problem of moving an ecosystem from one place to another is provided by what might seem to be a simple task – the reestablishment of plant species into former parts of their ranges. Even this task has proven difficult. Of 29 reintroduction projects in California in the past decade, 10 failed (that is, they failed to result in a new population becoming established). Similarly, in a 1991 study by the British Nature Conservancy Council, only 22% of 144 species reintroductions were deemed successful and more than half appeared to have failed. Successful reestablishment of functioning ecosystems, which might include establishment of self-sustaining populations, pollinators, mycorrhizal fungi, seed dispensers, nutrient cycles, and hydrology, is much less likely (Allen 1994). Certainly, nature will do a better job than humans will, but this example demonstrates the potential problems of moving an ecosystem from one place to another.

• These results pertain only to a doubling of carbon dioxide concentrations. Should atmospheric concentrations rise even higher, and hence cause even more extreme warming, greater loss of existing habitat and reductions in patch area would be expected.

• Our scenarios of migration rates and our conclusions about species loss through loss of existing habitat failed to consider outlier populations. We used sharp biome boundaries and hence implicitly assumed sharp boundaries of species distributions. In fact, species are often found in outlier populations, which can contribute to more rapid migration than along a single population front because of rapid in-filling between populations (Davis et al. 1991, Pitelka et al. 1997, Clark 1998). As noted by Davis (1986), plants continue to compete tenaciously for space even in the face of changed conditions and relictual populations can survive for many years in the absence of flowering and seed set. Although trees and perennials are at a disadvantage with respect to rapidly shifting climate envelopes because of slow maturity and low reproductive rates (Pitelka et al. 1997), these same factors may promote the maintenance of outlier populations that can serve as sources of colonists. These relictual populations also significantly decrease the likelihood of global extinction vs. local extinction. They become especially significant if conditions improve, allowing a species to potentially re-colonize former parts of its range. This importance of outlier populations reinforces the important conservation value of populations that are “outside” of their usual range.

• The potential existence of outlier populations argues for the use of relatively liberal estimates of range sizes in estimating climatically induced migration rates. If a species occurs in only a subset of its climatically possible range, but climate is nonetheless used to model its actual distribution, then estimated climate-induced migration distances will be erroneously high. By defining only 10 biome types, our core calculations implicitly assumed relatively large range sizes and hence provided relatively conservative migration rates. As expected, we found that as the size of modeled distributions decreased, required migration rates increased, albeit not strikingly across the range of sizes that we investigated. Required migration rates may be higher for species with smaller range sizes.

• An important factor relevant to the conservation of rare taxa was our failure to incorporate possible density dependent effects. For example, Schwartz's (1992) simulations showed that rare species never attained their highest migration rates even when suitable habitat was abundant. This is an important concern for many plant species; for example, the Nature Conservancy estimates that one-half of endangered plant taxa in the U.S. are restricted to five or fewer populations (from Pitelka et al. 1997). Schwartz (1992, see also Davis 1989) also noted that climate warming also could especially threaten species with geographically restricted ranges (such as narrow endemics), those restricted to habitat islands, and specialists on uncommon habitats. Thus, the potential for attaining the high-required rates observed here may be even lower for species that are rare in their range.

• In our investigation of migration rates and habitat loss, we did not consider the magnitude of the local climate change. In some areas, new established climatic conditions may differ substantially from preexisting conditions, whereas in other areas, the changes may be less extreme. More extreme change will more quickly reduce the available time for migration and hence possibilities for establishment of new habitat.

• Finally, migration through human modified habitats was treated as an all-or-none process in very large grid cells (0.5 degrees of latitude / longitude). This meant that only relatively extensively developed areas were excluded from migration and that diffusion processes present at small spatial scales were lost (see Dyer 1995). The use of the U.S. Geological Service classification also led to a strong emphasis on agricultural development. Other less intensive forms of development were ignored. For example, Schwartz (1992) noted that compared to the original primary forest, the secondary forests of the northeastern U.S. were of uneven quality, which may influence colonization by slowgrowing shade tolerant trees and exacerbate differences in migration rates among species.

Despite these uncertainties, the magnitude of the effects reported here are of great concern from a biodiversity perspective. Based on existing knowledge, it appears safe to conclude that although some plants will be able to keep up with the rates reported here, others will not. These rates seem unlikely to pose a problem for invasive species and others with high dispersal capabilities, which have migrational capabilities that may typically exceed 1,000 m / yr. For example, Weber (1998) found that when two goldenrod species (*Soldago* spp.) invaded Europe, range diameters increased from 400 to 1400 km between 1850 and 1875 and from 1400 to 1800 km between 1875 and 1990 (see his Figure 3). Assuming a circular range expanding constantly outward, respective migration rates were approximately 20,000 and 1,740 m / yr. Similarly, after its arrival in western North America in about 1880, in approximately 40 years cheatgrass had occupied most of its range of 200,000 km^2 (Mack 1986). Again assuming a circular range, a 40-year period to traverse the radius gives a migration rate of 6,300 m / yr. Animals are presumably able to migrate faster than plants (Davis 1986); for example, water beetles appeared in deglaciated areas long before trees (Morgan et al. 1983). However, as noted above, successful establishment by many animal species may ultimately depend on appropriate floristic and / or structural habitat features.

For many other plant species, however, these rates will likely pose a problem. Aside from setting a possible upper bound on plant migration capabilities, migration rates for invasive species are probably of limited relevance for many plant species. Invasive species often have abnormally high fecundity and dispersal capabilities and in many cases their migration is aided by humans. Troubling information comes from field studies of reinvasions by forest herbs into previously plowed secondary forests. Both Matlack (1994) and Brunet and Von Oheimb (1998) found that distance to oldgrowth was a correlate of understory richness in the successional stands, suggesting migration limitation. Matlack (1994) found no measurable movement for some species and only a small subset (<10% of 51) showed rates as high as 2-3 m/yr. Similarly, Brunet and Oheimb (1998) reported a median migration rate of only 0.3 m/yr (49 species). Other studies (cited in Matlack 1994) have also reported extremely slow movement of forest herbs. At the opposite end of the spectrum from invasive species are species that have evolved *in situ* and might fail to migrate at all. As Brunet and Von Oheimb (1998) pointed out, even though the understory flora appeared to be migrating very slowly, it had evidently migrated into southern Sweden from remote refugia during the last glaciation and therefore had shown much higher migration rates in the past. They suggested that compared to past migration, contemporary migration was limited by such factors such as seed predation, availability of suitable microsites, and vigour of clonal growth. Presumably, the newly-opened colonization sites exposed by the glacier would have presented a very different, and presumably more favourable, environment for migrating species compared to today's already established communities (Dyer 1995). In the absence of significant disturbance, many plant communities, especially forested ones, are quite resistant to invasion, and community-level changes may be delayed for many decades (Pitelka et al. 1997). For example, forest communities modeled by Davis and Botkin (1985) showed 100-200 year timelags in the replacement of dominant species, even though seedlings were available for all species throughout the experiment.

If some species are able to attain the high rates revealed here, whereas others are not, then global warming can be expected to have a "filtering" or "winnowing" effect on plant communities. Matlack (1994) noted that just as agricultural development has put a premium on long-range dispersal of plants, resulting in the selection a recognizable "old-field" flora preadapted to human disturbance, the same mechanism appeared to have selected a high-mobility flora in the successional forest he studied. Global warming is another factor than may result in a "weedier" future, resulting in a subset of plant species comprised of highly mobile species (Sykes and Prentice 1996, Walker and Steffen 1997). Unfortunately, no attempts have been made to characterize the migration capabilities of entire plant communities, hence the magnitude of this winnowing effect is unknown. Some evidence suggests that post-glacial migration limitation has similarly resulted in a subset of highly mobile taxa. If so, given that global warming might require much higher migration rates, it can be expected to result in even greater species loss, especially in nonglaciated areas that previously have not undergone any selection for high mobility taxa. The possibility of high rates of climate change in tropical areas is of particular concern given the presumed importance of long-term climatic stability in contributing to high species diversity and the possibility of much lower intrinsic rates of migration than in the temperate zone.

In conclusion, future migration rates due to global warming may be unprecedented even when judged against rapid post-glacial migration rates. Although migration capabilities are poorly known, it seems likely that these rates will be beyond the capabilities of many species, and will lead to a reduction in biodiversity. Without suitable migration, global warming has the potential to destroy large areas of habitat. For cold-adapted systems, such as arctic and alpine systems, global warming will impose species loss quite irrespective of migrational capabilities. Increases in connectivity among natural habitats within developed landscapes may help organisms to attain their maximum intrinsic rates of migration. However, in order to bring future migration rates into line with even the rapid migration rates of the past, it is apparent that large and rapid reductions in greenhouse gas emissions are required.

Tables

Table 1.

Vegetation types (biomes) used in the analysis. The left column gives the 10 biomes used in the "core" analyses. The other two columns give the original biome classifications used by two global vegetation models.

Core	BIOME3	MAPSS
1. Tundra	Arctic/alpine tundra Polar desert	Tundra Ice
2. Taiga/Tundra	Boreal deciduous forest/woodland	Taiga/Tundra
3. Boreal Conifer Forest	Boreal evergreen forest/woodland	Forest Evergreen Needle Taiga
4. Temperate Evergreen Forest	Temperate/boreal mixed forest	Forest Mixed Warm Forest Evergreen Needle Maritime Forest Evergreen Needle Continental
5. Temperate Mixed Forest	Temperate conifer forest Temperate deciduous forest	Forest Deciduous Broadleaf Forest Mixed Warm Forest Mixed Cool Forest Hardwood Cool
6. Tropical Broadleaf Forest	Tropical seasonal forest Tropical rain forest	Forest Evergreen Broadleaf Tropical
7. Savanna/Woodland	Temperate broad-leaved evergreen forest Tropical deciduous forest Moist savannas Tall grassland Xeric woodlands/scrub	Forest Seasonal Tropical Forest Savanna Dry Tropical Tree Savanna Deciduous Broadleaf Tree Savanna Mixed Warm Tree Savanna Mixed Cool Tree Savanna Mixed Warm Tree Savanna Evergreen Needle Maritime Tree Savanna Evergreen Needle Continental Tree Savanna PJ Continental Tree Savanna PJ Maritime Tree Savanna PJ Xeric Continental
8. Shrub/Woodland	Short grassland	Chaparral Open Shrubland No Grass Broadleaf Shrub Savanna Mixed Warm Shrub Savanna Mixed Cool Shrub Savanna Evergreen Micro Shrub Savanna SubTropical Mixed Shrubland SubTropical Xeromorphic Shrubland SubTropical
Mediterranean		Shrubland Temperate Conifer Shrubland Temperate Xeromorphic Conifer Grass Semi-desert C3 Grass Semi-desert C3/C4
9. Grassland	Dry savannas Arid shrubland/steppe	Grassland Semi Desert Grass Northern Mixed Tall C3 Grass Prairie Tall C4 Grass Northern Mixed Mid C3 Grass Southern Mixed Mid C4 Grass Dry Mixed Short C3 Grass Prairie Short C4 Grass Northern Tall C3 Grass Northern Mid C3 Grass Dry Short C3 Grass Tall C3 Grass Mid C3 Grass Short C3 Grass Tall C3/C4 Grass Mid C3/C4 Grass Short C3/C4 Grass Tall C4 Grass Mid C4 Grass Short C4
10. Arid Lands	Desert	Shrub Savanna Tropical Shrub Savanna Mixed Warm Grass Semi-desert C4 Desert Boreal Desert Temperate Desert Subtropical Desert Tropical Desert Extreme

Table 2.

Countries, U.S. states, and Canadian provinces ranked according to the percent of their territory with unusually high required migration rates (≥1,000 m/yr). Only the first 20 countries and states are shown. Countries had to occupy at least 5 grid cells to be included in the table.

A. Country	Grid Cell Count	Percent[1]
Finland	249	59.9
Uruguay	70	43.9
Kuwait	8	41.1
Russia	11539	38.3
Estonia	26	34.9
Iceland	63	34.6
Sweden	309	34.4
Canada	6228	33.1
Cuba	38	32.1
Latvia	35	31.0
Thailand	171	30.0
Burkina Faso	86	30.0
United Kingdom	131	29.8
Portugal	39	29.5
Benin	39	28.8
Cambodia	62	27.9
Taiwan	13	27.5
Bangladesh	47	27.2
Ireland	38	26.3
Dominican Republic	15	26.2

[1] *Averaged across 14 combinations of global climate and vegetation models.*

B. U.S. State	Grid Cell Count	Percent[1]
Maryland	7	35.7
Tennessee	41	31.9
Utah	92	28.3
Kansas	88	27.8
Delaware	3	26.2
Louisiana	43	25.6
Vermont	14	23.0
Arkansas	55	22.5
Oklahoma	71	22.4
Wyoming	112	21.6
Maine	37	20.1
Arizona	113	19.3
Colorado	112	17.3
Idaho	96	16.1
New Hampshire	12	16.1
New Jersey	9	15.9
New York	56	15.3
Nebraska	86	14.9
Mississippi	47	14.7
Alabama	51	14.7

C. Canadian Province or Territory	Grid Cell Count	Percent[1]
Ontario	500	49.2
Newfoundland and Labrador	203	48.3
Quebec	857	47.0
Manitoba	355	43.0
Alberta	375	33.3
Yukon Territory	341	31.8
Nova Scotia	24	29.2
Northwest Territories	2699	25.9
British Columbia	542	25.5
Saskatchewan	356	24.8
Prince Edward Island	3	11.9
New Brunswick	38	10.9

Table 3.

Increases in required migration rates for: 1) migration that went around water (rather than by straight "crow-fly distances") and 2) migration that went around human development (rather than just around water). For the latter, two anthropogenic habitat loss scenarios were assumed, 55 or 85% (see text). Values are mean (_ SEM) percent of grid cells in the various classes of migration rate increases.

	Shortest-path		**Shortest-path plus 55% habitat loss**		**Shortest-path plus 85% habitat loss**	
Increase class (m/yr)	BIOME3 (n = 6)	MAPSS (n = 8)	BIOME3 (n = 6)	MAPSS (n = 8)	BIOME3 (n = 6)	MAPSS (n = 8)
0-<316	99.1 ± 0.075	98.9 ± 0.181	97.6 ± 0.346	97.0 ± 0.288	99.1 ± 0.146	98.0 ± 0.176
316-<1,000	0.65 ± 0.055	0.63 ± 0.084	1.32 ± 0.199	1.06 ± 0.092	0.53 ± 0.072	0.90 ± 0.059
1,000-<3,162	0.12 ± 0.025	0.21 ± 0.046	0.50 ± 0.075	0.74 ± 0.107	0.25 ± 0.049	0.76 ± 0.102
3,162-<10,000	0.05 ± 0.002	0.13 ± 0.028	0.28 ± 0.083	0.82 ± 0.073	0.13 ± 0.029	0.17 ± 0.008
10,000-<31,622	0.02 ± 0.002	0.08 ± 0.011	0.08 ± 0.016	0.06 ± 0.010	0.01 ± 0.002	0.01 ± 0.002
31,622-100,000	–	0.001 ± 0.0005	–	–	–	–
Undefined[1]	0.08 ± 0.016	0.041 ± 0.005	0.19 ± 0.022	0.30 ± 0.025	0.08 ± 0.008	0.13 ± 0.016

[1] *Cells for which there was no path to a 1 x CO_2 cell of the same biome type.*

Table 4.

Mean (_ SEM) percent of grid cells in six migration rate classes for the two global vegetation models and for assumptions about the time period during which warming under a 2 x CO_2 atmosphere might be achieved (100 and 200 years). Sample size (n) is the number of climate models used for each vegetation model.

	BIOME3 (n = 6)		**MAPSS (n = 8)**	
Migration rate class (m/yr)	**100-yr warming**	**200-yr warming**	**100-yr warming**	**200-yr warming**
0-<316	71.1 ± 1.23	79.6 ± 1.11	61.0 ± 1.75	73.7 ± 1.86
316-<1,000	11.6 ± 0.26	9.6 ± 0.45	17.7 ± 0.10	14.4 ± 0.33
1,000-<3,162	10.6 ± 0.53	8.8 ± 0.52	13.9 ± 0.57	9.3 ± 0.87
3,162-<10,000	5.9 ± 0.57	1.9 ± 0.43	6.6 ± 1.05	2.5 ± 0.66
10,000-<31,622	0.9 ± 0.18	0.1 ± 0.03	0.6 ± 0.22	0.09 ± 0.04
31,622-100,000	0.03 ± 0.008	0.01 ± 0.006	0.03 ± 0.02	0.004 ± 0.0005

Table 5.

Countries, U.S. states, and Canadian provinces ranked according to percent loss of existing habitat. Only the first 20 countries and states are shown. Countries had to occupy at least 5 grid cells to be included in the table.

A. Country	Grid Cell Count	Percent[1]
Iceland	71	81.6
Estonia	26	68.1
Kyrgyzstan	84	67.9
Finland	249	67.9
Latvia	35	56.3
Russia	11620	55.8
Macedonia	11	51.3
Sweden	309	50.6
Georgia	29	50.5
Tajikistan	59	50.4
Bulgaria	47	48.5
Uruguay	70	46.8
Montenegro	6	46.4
Canada	6465	46.3
Bhutan	13	46.2
Mongolia	739	45.9
Azerbaijan	37	45.6
Norway	242	45.1
Romania	112	44.8
Iraq	171	43.4

B. U.S. State	Grid Cell Count	Percent[1]
Maine	37	44.0
Oklahoma	71	42.2
Wyoming	112	41.7
Idaho	96	40.1
Kansas	88	39.9
Utah	92	38.1
Texas	259	36.8
New Hampshire	12	35.1
Colorado	112	35.0
Arizona	113	34.6
Oregon	111	33.5
North Dakota	85	31.5
California	171	30.7
Washington	83	30.4
Montana	182	30.3
Louisiana	43	29.6
Minnesota	97	27.5
Nebraska	86	27.5
New Mexico	122	26.6
Georgia	58	24.8

C. Canadian Province or Territory	Grid Cell Count	Percent[1]
Yukon	346	64.1
Newfoundland and Labrador	203	63.6
Ontario	495	61.4
British Columbia	522	60.4
Quebec	857	59.5
Alberta	375	56.4
Manitoba	355	52.9
New Brunswick	38	44.7
Saskatchewan	356	36.2
Nova Scotia	24	34.2
Northwest Territories	2912	33.0
Prince Edward Island	3	0.0

[1] *Averaged across 14 combinations of global climate and vegetation models.*

Table 6.

Countries, U.S. states, and Canadian provinces ranked according to percent species loss as predicted due to the decrease in the area of persisting habitat patches. Only the first 20 countries and states are shown. Countries had to occupy at least 5 grid cells to be included in the table.

A. Country	Grid Cell Count	Percent[1]
Lesotho	12	5.4
Norway	242	4.3
Sweden	309	3.1
Guinea-Bissau	9	2.9
Byelarus	113	2.9
Albania	12	2.8
Lithuania	39	2.8
Russia	11620	2.8
Iran	624	2.7
Armenia	13	2.7
Turkey	323	2.6
Canada	6465	2.5
Syria	73	2.5
Switzerland	18	2.4
Poland	163	2.4
Nepal	52	2.4
Ireland	38	2.4
Zambia	249	2.4
Finland	249	2.3
China	3781	2.3

B. U.S. State	Grid Cell Count	Percent[1]
Rhode Island	1	3.0
Nevada	121	2.9
Montana	182	2.8
South Dakota	91	2.5
Idaho	96	2.5
Colorado	112	2.2
Wyoming	112	2.2
North Dakota	85	2.2
Washington	83	2.1
California	171	2.0
Oregon	111	2.0
Nebraska	86	2.0
Arizona	113	1.7
New Mexico	122	1.7
Utah	92	1.7
Texas	259	1.6
Oklahoma	71	1.5
Kansas	88	1.2
West Virginia	22	1.0
Kentucky	44	0.8

C. Canadian Province or Territory	Grid Cell Count	Percent[1]
Northwest Territories	2912	3.1
Saskatchewan	356	3.0
Newfoundland and Labrador	203	2.9
Yukon	346	2.7
Manitoba	355	2.5
Quebec	857	2.4
Alberta	375	1.7
British Columbia	560	1.3
Prince Edward Island	3	1.0
Ontario	5000	.9
Nova Scotia	24	0.8
New Brunswick	38	0.6

[1] *Averaged across 14 combinations of global climate and vegetation models.*

Map 5

Percent species loss predicted for habitat patches that will persist in a 2 x CO_2 climate. As habitat is lost, patches become smaller. Based on species-area relationships, the reduction in species richness can be predicted as a function of the decrease in patch area. Shades of red indicate average species loss for 14 combinations of linked climate change/vegetation change models.

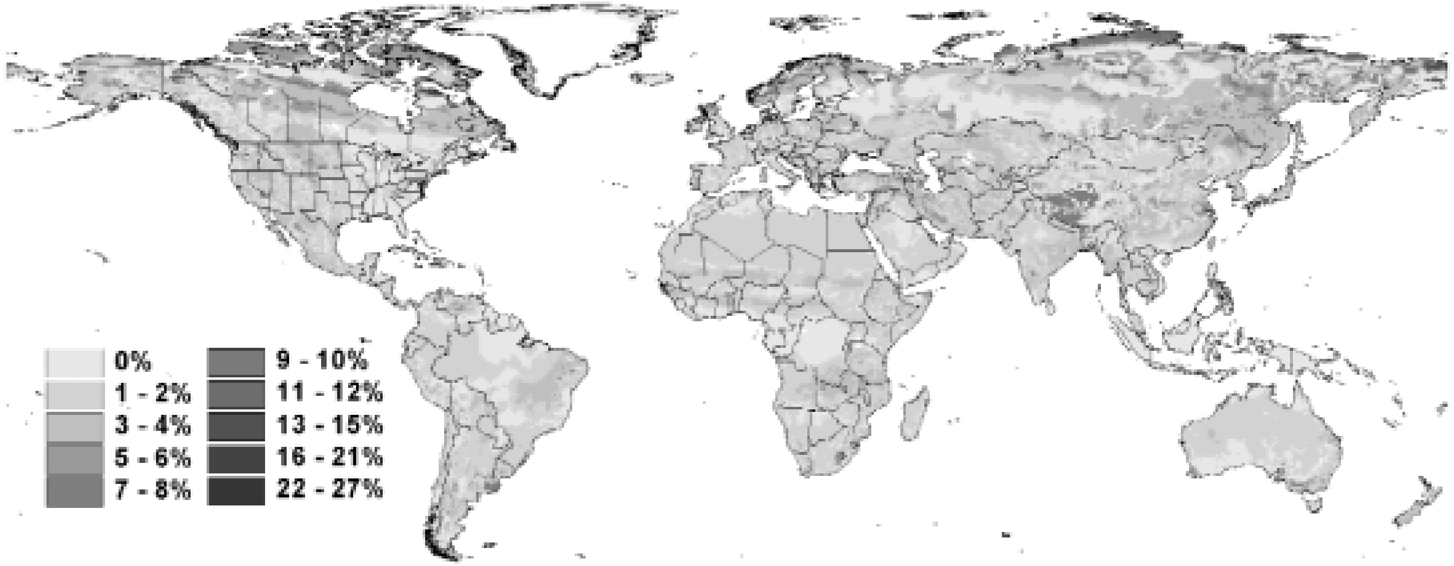


Figure 1.

Schematic representation of three ways in which global warming could lead to species loss.

A - As habitat conditions shift under the influence of warming, species will have to migrate to keep up with the shift. In the area labeled "b", such migration will be required. In the area labeled "a", current habitat conditions overlap with future conditions, hence no migration is required.

B - Because of the shifts in climatic zones, some present-day areas of habitat will become unsuitable in the future. In this example, area "a" (in red) will be lost, whereas area "b" will remain.

C - Areas of habitat loss (in red) will impose reductions in the sizes of existing habitat patches (in dark green). Using species-area relationships, the amount of biodiversity loss can be predicted from the amount of area loss, as show in the two examples. The creation of new habitat (light green) in some cases may ameliorate the species loss.

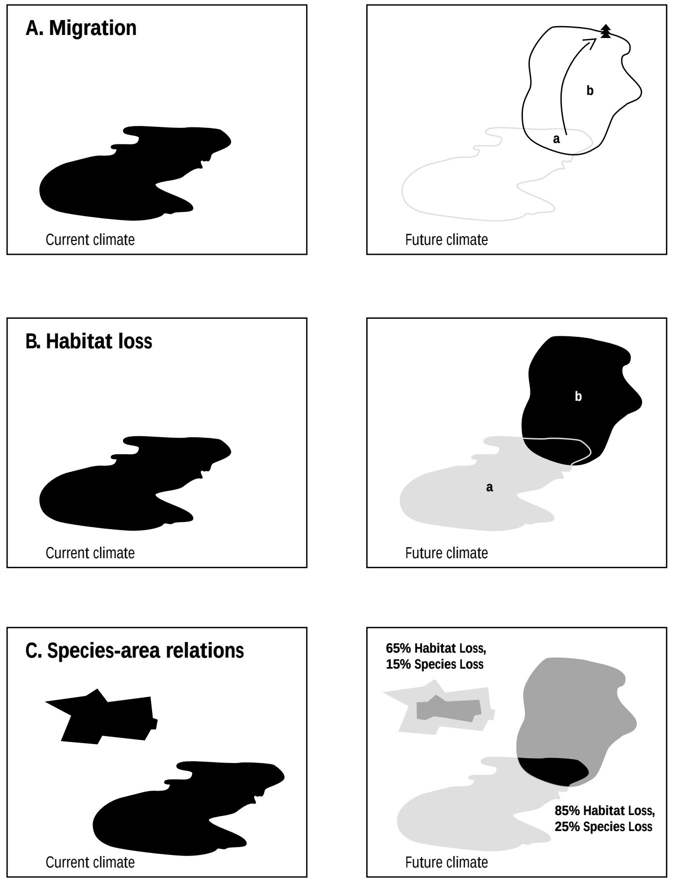


Figure 2.

Migration rates that species might be required to achieve in order to keep up with global warming associated with a doubling of CO_2 concentrations in 100 years. Shown are the average percent of pixels (map grid cells) in various migration rate classes for two global vegetation models (BIOME3 and MAPSS). Dots represent the individual combinations of climate and vegetation models upon which the means are based (14 model combinations in total). Migration rates are in units of metres per year.

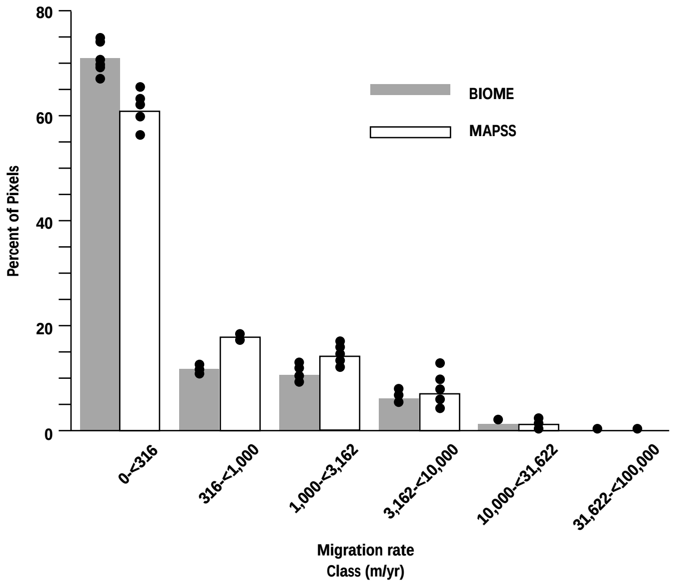


Figure 3.

Migration rates that species might have to achieve in order to keep up with global warming plotted against latitude. Migration rates and mean proportions of map grid cells with unusually high rates (≥1,000 metres per year) are shown for 20-degree latitudinal classes. Positions on the y-axis represent the mean latitudes of the cells within the classes. Results are shown for two global vegetation models (BIOME3 and MAPSS). The triangles indicate results from individual combinations of climate and vegetation models (14 in total).

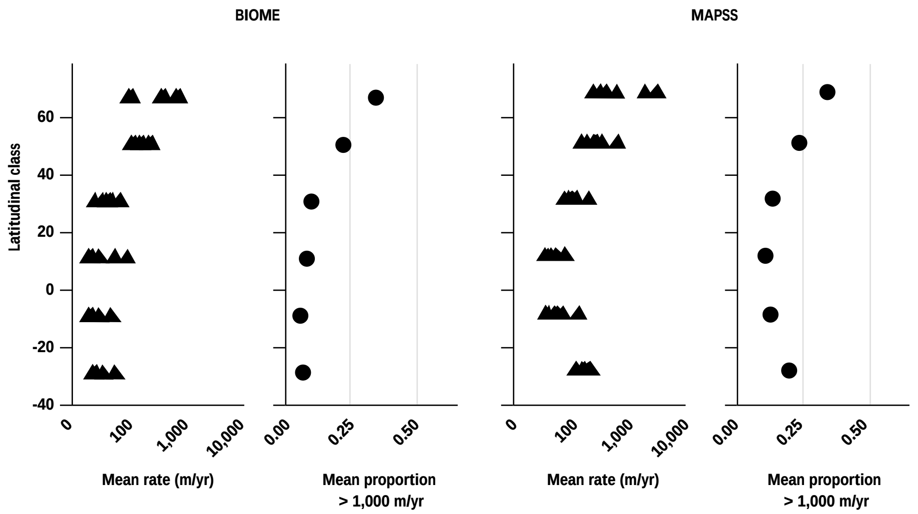


Figure 4.

As Figure 3, except that rates and proportions are shown for the 10 vegetation (biome) types.

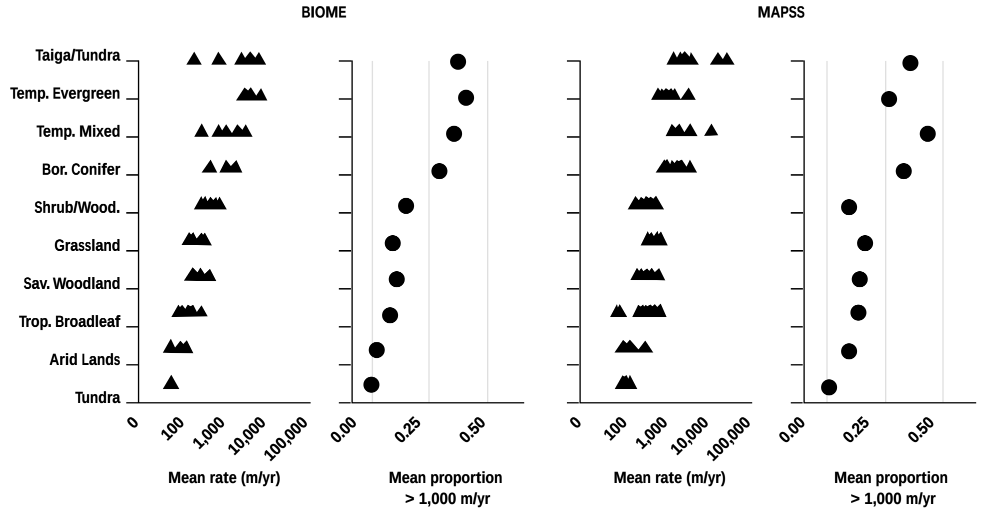


Figure 5.

Figure illustrating how rates of migration of spruce (Picea) observed during the most recent glacial retreat compare with migration rates that might be imposed by global warming.

A. Average (± standard error) required migration rates of grid cells in the boreal biome as a function of the time period during which a 2 x CO_2 climate is achieved. The "best fits" with Picea rates (indicated by the arrows) is observed if the warming occurs during a more than 1,000 year period. That is, best agreement between required rates and historic rates is achieved if one assumes that the warming will take over more than 1,000 years, instead of during the 100 or so years expected.

B. Migration rates that species in the boreal zone would have to achieve in order to keep up with 100-year global warming compared with migration rates observed for spruce (Picea) during the glacial retreat.

C. As B, except that the warming is assumed to occur over the "best fit" time period; i.e., over more than 1,000 years. The "best fit" values (1070 years for BIOME3 and 1150 years for MAPSS) shown by arrows in part A were those that minimized deviations between the heights of histogram bars (as quantified by the sum of the absolute values of the deviations).

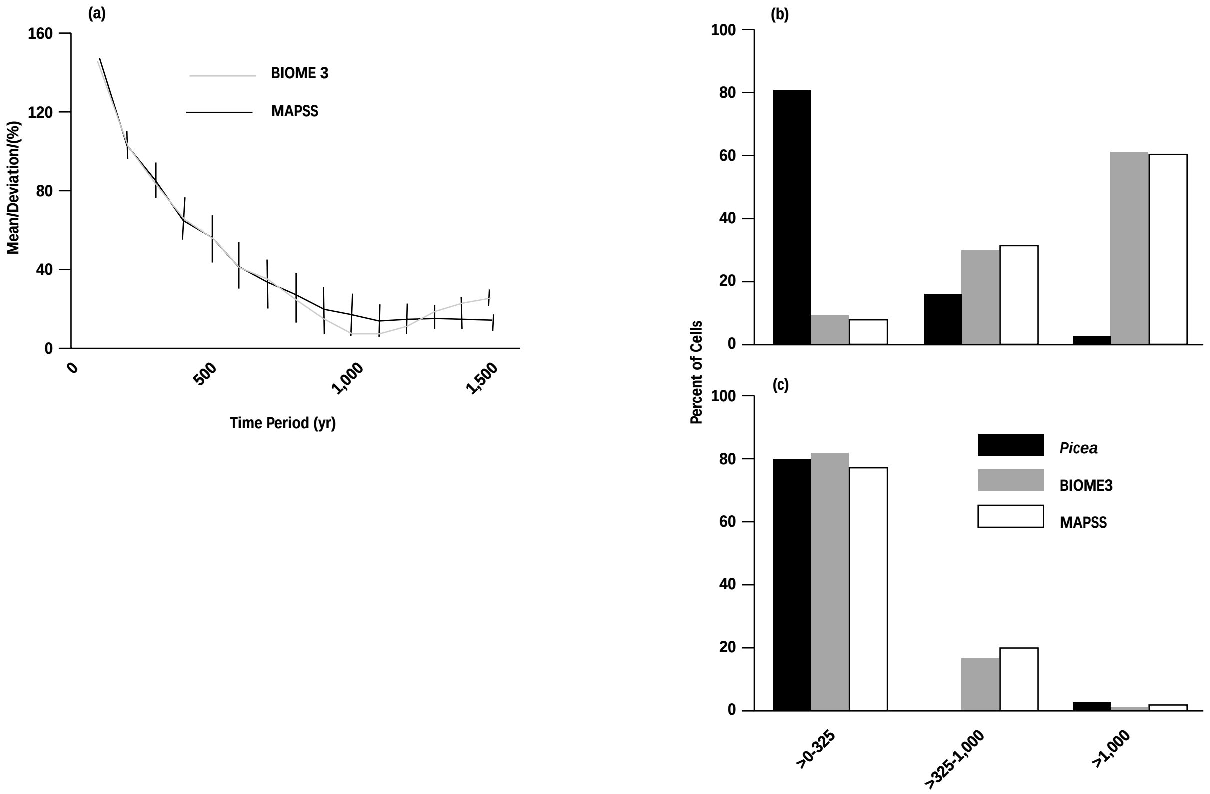
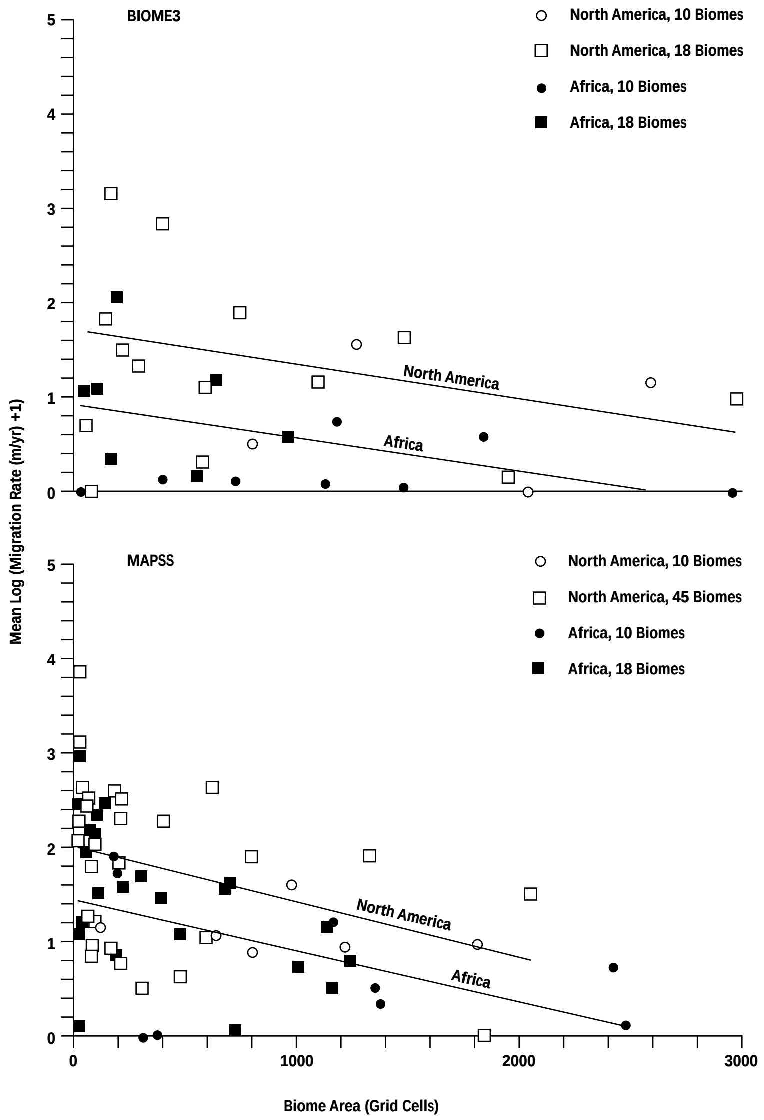


Figure 6.

Estimates of the migration rates under global warming as a function of assumptions about habitat breadth. Mean log-transformed migration rates are plotted against biome area for biomes in North America and Africa. Calculations are for two global vegetation models (BIOME3 and MAPSS) in combination with one climate change scenario (HADGCM2SUL). For each vegetation model, results for two global biome classification schemes are shown: 10 biomes (broad habitat breadth) vs. the original number of biomes used in the model (18 for BIOME3; 45 for MAPSS - narrow habitat breadth). African biome migration rates and areas were calculated separately for biomes north and south of the equator.



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End Notes

[1] *The climate models (General Circulation Models) included older-generation equilibrium models, newer-generation transient models, and models with and without the cooling effects of sulphate aerosols. The vegetation models (MAPSS and BIOME3) included versions with and without direct physiological effects of* CO_2 *(which have been posited to increase the water use efficiency of plants).*

[2] *If the variables are plotted on logarithmic scales, the increase is close to linear.*

[3] *The older general circulation models used simple mixed layer oceans to simulate equilibrium climate under 2 x* CO_2 *forcing and included models from the Goddard Institute for Space Studies (GISS), the Geophysical Fluid Dynamics Laboratory (GFDL-R30), Oregon State University (OSU), and the U.K. Meteorological Office (UKMO). The newer (transient) models included two were from the U.K. Hadley Centre (HADCM2GHG and HADGCM2SUL) and one from the Max Planck Institute for Meteorology (MPI-T106). These models made use of coupled atmospheric-ocean dynamics and in one case (HADGCM2SUL) incorporated the cooling effect of atmospheric aerosols (sulfates). The course grids of the GCMs were interpolated to 0.5degree latitude/longitude grids. Climate change scenarios were created by applying ratios and differences from 1 x* CO_2 *and 2 x* CO_2 *simulations back to a baseline monthly climate dataset (see Neilson et al. 1998). To calculate future climate from the transient GCMs, a 30 year (Hadley Centre) or 10 year (Max Planck Institute) climate average was extracted from the current period (e.g., 1961-1990) and the period approximating 2 x* CO_2 *forcing (e.g. 2070-2099). Neilson et al. (1998) used a similar set of models to investigate global changes in biome area, leaf area index, and runoff.*

[4] *MAPSS and BIOME3 were run under the two Hadley Centre scenarios, whereas only BIOME3 was run under the Max Plank Institute scenario and only MAPSS was run under the GFDL, GISS, OSU, and UKMO scenarios. Global vegetation models that made use of the Hadley Centre and MPI climate were run both with and without direct* CO_2 *effects, whereas in keeping with the VEMAP analyses, the older climate change scenarios were run only with direct* CO_2 *effects (Neilson et al. 1998). MAPSS and BIOME2 (a precursor to BIOME3) produced generally similar results for the coterminous United States. However, compared to BIOME2, the modelled vegetation in MAPSS was consistently more sensitive to water stress, producing drier future outcomes, and had a larger benefit from the direct physiological effects of increased* CO_2*, particularly the ability of plants to use water more efficiently (VEMAP Members 1995).*

[5] *In both distance calculation methods, distances between cell centres were calculated using software from the United States National Oceanic and Atmospheric Association (FORTRAN subroutine INVER1, written by L. Pfeifer and modified by J. G. Gergen) using the 1984 World Geodetic System reference ellipsoid (WGS84). The shortest path calculations made use of Dijstra's algorithm.*

[6] *We classified 0.5-degree cells as "highly" impacted if 55 or 85% of the underlying 1-km-resolution cells were human-modified (i.e., their USGS land cover type designations contained the words "crop," "field," "irrigated," "town," or "urban" [16 of the 94 USGS land cover types]).*

[7] *These comparisons of biome breadths were undertaken for one climate change scenario only (HADGCM2SUL). Biomes with fewer than 20 grid cells were excluded from the plots.*

[8] *Average migration rates were significantly lower for BIOME3 than for MAPSS. Respective log-transformed means (*$\log_{10}$*[migration rate +1]) were 0.93 (sd = 0.10, n = 6) and 1.26 (sd = 0.18, n = 8); ANOVA* $F_{1,12} = 16.07$, $p = 0.002$*. BIOME3 consistently had more cells with low migration rates (<316 m/yr) than MAPSS, comprising on average 71% vs. 61% of cells, respectively (see Figure 2). Conversely, BIOME3 had consistently fewer cells than MAPSS in the 316-1,000 m/yr class, and although not always consistent among the climate models, fewer in the 1,000-10,000 m/yr class.*

[9] *Among MAPSS runs, older climate models had significantly higher log-transformed migration rates than newer models. Respective log-transformed means were 1.38 [sd = 0.18, n = 4] and 1.14 [sd = 0.06, n = 4];* $F_{1,6} = 5.99$, $p = 0.05$*.*

[10] *A two-way ANOVA comparing Hadley Centre results according to the vegetation model and whether or not sulphate cooling was used indicated not only that BIOME3 had lower rates on average than MAPSS, but that models with sulphate cooling had slightly lower average migration rates than the models without cooling. Respective means of log-transformed rates were 0.95 [sd = 0.20, n = 2] and 1.08 [sd = 0.18, n = 2]; ANOVA* $F_{1,1} = 58.05$, $p = 0.08$*.*

[11] *For BIOME3, incorporation of increased water use efficiency through direct* CO_2 *effects led to consistently and significantly lower log-transformed migration rates, however the same was not true for MAPSS. For BIOME3, paired-t = -8.41, p = 0.02, mean difference between pair-specific averages was 0.15, n=3. For MAPSS, paired-t = 0.57, p = 0.66, mean difference between pair averages was 0.01, n=2.*

[12] *After transforming back to nonlogged values, y-intercepts of linear regressions were 109 m/yr for North America and 30 m/yr for Africa for MAPSS and, respectively, 53 and 5 m/yr for BIOME3.*

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