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Global Warming
and Species Loss in
Globally Significant
Terrestrial Ecosystems

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Foreword by WWF

Even our most protected wilderness areas may not survive global warming unscathed. As these unique, diverse habitats are rapidly changed by global warming, animals and people who are dependent on them will face a crisis of survival. Immediate action needs to be taken to protect people, animals and habitats from this global threat. Solutions exist that reduce human-induced emissions of carbon dioxide and other gases which blanket the earth, trap in heat and cause global warming.

Key findings of the new WWF report, *Habitats at Risk: Global Warming and Species Loss in Terrestrial Ecosystems,* underscore the urgent need for immediate action by governments, industry and communities to effectively address this worldwide threat. The report examined the impact of climate change on the terrestrial ecosystems that WWF identified as part of the Global 200 — areas where the Earth's biological wealth is most distinctive and rich, where its loss will be most severely felt, and where we must fight the hardest for conservation. If we double the CO_2 concentration in the next 100 years — an amount less than current predictions of future CO_2 concentrations, the following effects are predicted.

- More than 80 percent of the ecoregions tested will suffer extinctions of plant and animal species as a result of global warming.
- Changes in habitats from global warming will be more severe at high latitudes and altitudes than in lowland tropical areas.
- Some of the most unique and diverse natural ecosystems may lose more than 70 percent of the habitats upon which their plant and animal species depend.
- Many habitats will change at a rate approximately ten times faster than the rapid changes during the recent postglacial period, causing extinctions among species unable to migrate or adapt at this fast pace.

To save these valuable habitats and the species that depend on them, emissions must be significantly reduced worldwide. The Kyoto Protocol, the only global effort to address climate change, is a good first step in the right direction. All countries, including the United States, should immediately put in place strong domestic plans to meet or beat their Kyoto Protocol targets.

The solutions are at hand and the risks are high. Action is needed now.

Jennifer Morgan
Director
WWF Climate Change Campaign

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Executive Summary

lobal warming is perhaps the most pervasive of the various threats to the planet's biodiversity. Unlike other threats also caused by human development, it has the potential to influence all ecosystems, including those that are far from human populations and are still classified as wilderness. Unfortunately, despite this insidious nature, there have been few efforts to assess the potential effects of greenhouse warming on global ecosystems. Those that have been undertaken have focused on flows of energy and matter through ecosystems rather than on the species that make up ecosystems. The implications of global warming for global biodiversity remain largely unstudied.

Here, we assess the threats of global warming to ecoregions that were identified as being of particularly high conservation value from a biodiversity perspective (the "Global 200" of WWF). In a real sense, these ecoregions represent the crown jewels of the planet's biological diversity. These ecoregions are of special significance from a global warming perspective for the same reason that they were chosen for their biodiversity value — namely their broad representation of the planet's biological communities, high species richness, biological distinctiveness, and intactness. The potential for extensive impacts here would signal a key threat to the planet's biodiversity. Indeed, threats to these ecosystems would presumably signal the climate-induced "unnatural adaptation" that is to be avoided under the United Nations Framework Convention on Climate Change (Article 2).

In this study, we used a suite of models of global climate and vegetation change to investigate three important global warming-induced threats to the terrestrial Global 200 ecoregions:

1) Invasions by new habitat types (and corresponding loss of original habitat types)
2) Local changes of habitat types
3) High rates of required species migration.

Seven climate models (general circulation models or GCMs) and two vegetation models (BIOME3 and MAPSS) were used to produce 14 impact scenarios under the climate associated with a doubling of atmospheric CO_2 concentrations, which is expected to occur in

less than 100 years.[1] Previous analyses indicated that most of the variation among the impact scenarios was attributable to the particular vegetation model used, hence we provide results separately for the two models. The models do not provide information on biodiversity *per se,* but instead simulate current and future potential distributions of major vegetation types (biomes) such as tundra and broadleaf tropical rain forest. We were able to use the models to indirectly investigate potential biodiversity change within the ecoregions in several ways:

- To measure the invasion of new biome types into the ecoregions, we compared the future biome composition in the ecoregions with their present-day composition. The appearance of new biome types signals a decline in the original biome makeup of the ecoregion, which in turn signals a decline in species richness in the ecoregion.

- To measure the potential loss of existing habitats, we compared current biome distributions with those projected for the future under the various scenarios, and quantified the percent of change. A change of biome types signals a potential decrease in local species richness if climate-induced extinction is not matched by incoming migration. A simple conceptual model of local species richness is presented to illustrate that both extinction and migration can influence local species richness.

- Losses of existing habitats within the ecoregions were compared against random sets of locations constructed so that they had the same current biome composition as the original ecoregions. These analyses indicated the extent to which the Global 200 ecoregions were vulnerable in the context of their biome composition. Equally important, they provided an assessment of the comparative vulnerability of ecoregions with the same major vegetation types.

- To measure the rates of migration that greenhouse warming might impose on species, we calculated the rates at which major biomes 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 species. More

rapid required migration rates (RMRs) signaled an increased likelihood of local declines in species richness. Required migration rates 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 assumed that the doubled CO_2 climate was reached after 100 years. 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.

- In a sensitivity analysis, we varied the biome classification scheme. A relatively coarse classification scheme (few biome types) is expected to result in less ecosystem change under the warming and hence is relatively conservative. This is analogous with the possibility that species have relatively large geographic distributions and/or wide climatic tolerances. We used two classification schemes: 1) a relatively coarse 10-biome-type scheme, and 2) the original (and more narrow) schemes used by the global vegetation models (18 types for BIOME3; 45 for MAPSS).

SUMMARY OF KEY FINDINGS
Specific Conclusions

- Under the broad definition of biome types, many ecoregions had the same collection of biome types before and after the warming (35% of ecoregions for MAPSS, 51% for BIOME3). However, when a more narrow biome definition was used, only 13–19% showed no change and 13–25% lost greater than 10% of their original biome types. Thus, more than 80% of ecoregions were projected to suffer extinctions as a result of global warming. Northern and Australian biomes tended to be especially hard hit. Ecoregions with the most consistent losses of their original biome types included the Fynbos of Southern Africa and the Terai-Duar Savannas/Grasslands of northeastern India.

- Local biome change was much more pervasive, averaging 21–34% of an ecoregion under the broad biome definition and 32–50% under the narrow definition. If new habitat types fail to reestablish because of failed migration, species loss could be catastrophic in many

cases. In the broad biome classification scheme, 2% of ecoregions on average showed >70% local change and the possibility of catastrophic species loss. In the narrow definition, the percentage increased to 5–19%.

- Amounts of local biome change showed strong latitudinal and altitudinal effects, with greatest change at high latitudes and altitudes and relatively less change in lowland tropical areas. Ecoregions in Canada, Russia, and Asia were especially vulnerable. Under the coarse biome definition, seven ecoregions showed 70% or more change in at least one vegetation model: Ural Mountains Taiga (Russia), Canadian Low Arctic Tundra, Altai-Sayan Montane Forests (Russia/Mongolia), Muskwa/Slave Lake Boreal Forests (Canada), Kamchatka Taiga and Grasslands (Russia), Canadian Boreal Taiga, and Southwestern Australia Forests and Scrub.

- In the context of their particular biome types, certain ecoregions were unusually vulnerable, whereas others were relatively stable. For example, despite its large size, the Canadian Low Arctic Tundra showed 75 and 77% local pixel change (for BIOME3 and MAPSS, respectively) compared to 44 and 57% respectively for random sets with the same biome composition. Other unusually vulnerable ecoregions included the Central Andean Dry Puna (Chile, Argentina, and Bolivia), Daurian Steppe (Mongolia and Russia), and the Ural Mountains Taiga (Russia). Tundra ecoregions of Canada and Russia tended to be relatively vulnerable, whereas those of Fennoscandia and western Alaska tended to be relatively stable. Within the tropics, the South American region tended to be vulnerable, whereas insular southeast Asia and central Africa tended to be stable.

- Average required migration rates (RMRs) were unusually high (often exceeding 1,000 m/yr). Under a broad biome definition, 6–11% of ecoregions had average RMRs above 1,000 m/yr; under a narrow definition, the percentages were 19–42%. Rates of change of this magnitude are approximately 10 times faster than the rapid migrations during the recent post-glacial period and signal the possibility of extinctions as populations fail to reestablish in areas that are newly climatically suitable.

- Unusually high migration rates were shown in northern areas, especially in Canada and Russia, but also in southwestern Australia and New Zealand. Under a nar-

row biome definition, high rates also tended to be prevalent in warm temperate and subtropical areas. Nearly one quarter of the ecoregions, including a wide diversity of ecosystem types, had consistently high rates (>750 m/yr for both global vegetation models [GVMs]).

General conclusions

- Global warming has the potential to cause extinctions in a great majority of the world's especially valuable ecosystems. Losses of habitat types are predicted within the ecoregions and, based on species–area relationships, can be expected to result in losses of biodiversity.

- Depending on species responses to the warming, especially their ability to migrate to new sites, habitat change in many ecoregions has the potential to result in catastrophic species loss.

- The fact that certain ecoregions are of high value from a biodiversity perspective did little to protect them against the effects of global warming. Although some ecoregions were more vulnerable than others, on the whole they faired little better than random regions of the globe.

- High required migration rates (RMRs) were not isolated occurrences within the ecoregions. Instead, in many ecoregions, the *average* RMR was greater than 1,000 m/yr, which is approximately an order of magnitude higher than migration rates frequently observed in the historical and fossil record. Future migration rates may need to be unprecedented if species are to keep up with climate change. 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. Some species with low dispersal capabilities may fail to migrate at all.

- Global warming is likely to have a winnowing effect on the ecosystems within ecoregions, filtering out species that are not highly mobile and favoring a less diverse, more "weedy" vegetation and ecosystems that are dominated by pioneer species, invasive species, and others with high dispersal capabilities.

- High required migration rates tended to be common at high latitudes and altitudes; however, when a narrow biome definition was used, they were also prevalent in subtropical and dry ecosystem types. A narrow biome definition may be more realistic at these sites because of the generally observed decline in geographic range size with latitude.

- In nonglaciated regions, where previous selection for high mobility has not occurred, species may suffer disproportionately. Therefore, even though high RMRs are not as common in the tropics as in colder regions, they may still have strong impacts in terms of species loss.

- The effects of global warming are influenced significantly by species geographic distributions and climatic tolerances. Species with relatively large distributions and greater climatic tolerances are at lesser risk. Island ecoregions, which were largely excluded from this report because of the small number of grid cells that they occupied, may be at special risk because of small populations, limited opportunities for migration, and sea level rise.

- Barriers to migration and habitat loss will exacerbate climate–induced species loss. Human population growth, land–use change, habitat destruction, and pollution stress will therefore exacerbate climate impacts. Increased connectivity among natural habitats within developed landscapes may help organisms to attain their maximum intrinsic rates of migration and help to reduce species loss. Migration is likely to be especially problematic for isolated island ecoregions.

- Reductions in both the rate and amount of warming will reduce species loss. Urgent reductions in carbon dioxide and other greenhouse gas emissions are required to prevent the possibility of widespread, and in some cases catastrophic, species loss.

In conclusion, this study demonstrates that under a wide range of assumptions about future global warming and its effects on major vegetation types, species losses can be expected in most of the planet's globally significant ecoregions. Migration rates required by the warming are unprecedented by historical standards, raising the possibility of extensive, and in many cases, catastrophic, species loss.

Introduction

Global warming resulting from anthropogenic emissions of greenhouse gases is recognized as a key threat to biodiversity (Kappelle et al. 1999, Noss 2001). The direct and indirect threats of the warming include losses of habitat; shifts in climatic conditions and in habitats that surpass migrational capabilities (Davis 1986, Malcolm and Markham. 2000, Malcolm et al. in press); nonsynchronous shifts in habitat conditions (Martin 2001); altered competitive relationships; invasions by generalist species (Walker and Steffan 1997); and biodiversity-unfriendly human adaptive responses (Noss 2001). Evidence suggests that the warming of the past century already has resulted in marked ecological changes, including changes in growing seasons (Myneni et al. 1997, Menzel and Fabian 1999), species ranges (Thomas and Lennon 1999, Parmesan et al. 1999), and patterns of seasonal breeding (Beebee 1995, Brown et al. 1999, Crick and Sparks 1999).

Despite the possibility that global warming rivals other primary threats to biodiversity, there have been few efforts to model the implications of global warming for terrestrial biodiversity, especially at the global level. The significant efforts devoted to investigating the ecological effects of warming instead have been devoted to changes in the functional properties of ecosystems, especially on the ways in which they process energy and matter (e.g., VEMAP Members 1995, Houghton et al. 1996).

This paucity of information on biodiversity is especially notable given the recent efforts to prioritize conservation efforts at the global scale, for example by focusing on distinctive and representative ecoregions (Olson and Dinerstein 1998), centers of endemism (Mittermeier et al. 1998), or intact forested ecosystems (Bryant et al. 1997). The identified regions represent the crown jewels of the planet's biological diversity. They are of special significance from a global warming perspective for the same reason that they were chosen in the first place — namely, their broad representation of the planet's biological communities, high species richness, biological distinctiveness, and intactness. The potential for extensive climate-induced impacts here would signal a key threat to the planet's biodiversity. Indeed, threats to these ecosystems would presumably signal the climate-induced "unnatural adaptation" that is to be avoid-ed under the United Nations Framework Convention on Climate Change (Article 2).

Here, we build on previous efforts to assess terrestrial biodiversity threats at the global scale (Malcolm and Markham 2000, Malcolm et al. in press) by focusing on one of these prioritization efforts: the terrestrial component of the WWF "Global 200" (Olson and Dinerstein 1998). This approach is representational in that within major biome (vegetation) types and geographic realms of the planet, ecoregions were identified that were of particular value from a biological standpoint based on such values as species diversity, uniqueness of the biota, and intactness. We were interested not only in the absolute threat posed to these biologically valuable regions by warming, but, following the same logic of representation, in the relative threats to ecoregions within certain major habitat types.

To undertake the analysis, we capitalized on efforts to assess impacts of global warming on major vegetation types (biomes) and indirectly investigated several factors relevant to species diversity. Rather than using species or habitat distributions themselves, we used the biomes as proxies. Although indirect, this approach is nonetheless highly relevant to biodiversity. The biomes describe major habitat types that often have many species in common. Equally important, mapping of biomes makes use of derived climate variables that are relevant to a wide range of organisms (especially plants) and hence, at least in a heuristic sense, can be thought of as proxies for species climate envelopes.

As detailed below, we evaluated the effects of global warming with respect to three variables: 1) appearances of biome types that were novel to the ecoregion; 2) overall biome change; and 3) migration rates required by the warming. Through a conceptual model of changes in species richness induced by warming, we also show that the potential for species loss may be mediated importantly by migration rates. For biome change, we compare responses not only among the Global 200 ecoregions, but also in the context of expected responses for a given biome type. Finally, in sensitivity analyses, as a proxy for variation in the sizes of species distributions and the breadth of their climatic tolerances, we investigated two biome classification schemes.

METHODS: QUANTIFYING THREATS TO BIODIVERSITY

Potential distributions of major vegetation types were simulated by global vegetation models (GVMs). Based on ecological and hydrological processes and plant physiological properties, these models predict the 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 at the site have stabilized.

To analyze the potential effects of global warming, biomes were mapped both under recent (1961–1990) climates and under future climates that were simulated by general circulation models (GCMs) under a doubling of atmospheric CO_2 concentrations. The 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 geographic scales 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).

Altogether, we used 14 combinations of GVMs and GCMs (the same set used by Malcolm and Markham. 2000; see also Neilson et al. 1998). These included two GVMs (MAPSS [Neilson 1995] and BIOME3 [Haxeltine and Prentice 1996])[1] and seven GCMs, including both "older" and "newer" generation models.[2] These model outcomes cannot be viewed as predictions (VEMAP Members 1995); rather, they 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.

Previous analyses have shown that the greatest source of variation among these 14 models was the vegetation model used (Malcolm et al. in press, Malcolm et al. in prep.). Accordingly, to span the approximate range of model outcomes in the analyses presented here, we provide results separately for the two vegetation models. The Global 200 ecoregions were converted to the same resolution as the 14 model combinations: 0.5 degree

grids of latitude and longitude. Because of the inherently variable responses of regions with small areas, we excluded ecoregions with 10 or less grid cells, reducing the original 140 terrestrial ecoregions to 113. This removed many of the island ecoregions.

A Heuristic Approach to Modeling Biodiversity Change

An attempt to model the effect of climate change on the myriad species in an ecosystem would be a very detailed and difficult undertaking. Basic information is often lacking — for example, information on where species occur and how quickly they might respond to change. Equally problematic are the complex sets of factors and interactions among species that may influence the responses of species to climate change. 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 heuristic approach.

The Appearance of Novel Biome Types

We reasoned that ecoregions would be at particular risk if global warming resulted in replacement of the original biome types with new biome types (figure 1). Biomes are characterized by a particular suite of climatic conditions and, at least within a biogeographic realm, often have many species in common. Replacement of the original biomes with new ones would signal major ecological change. In particular, it would signal a reduction in area of the original biomes that made the ecoregion so valuable in the first place. A reduction in the area of a biome in turn would mean a loss of the some of the original species from the ecoregion, as predicted from species-area relationships.

Notice that the condition that the biomes be "new" to the ecoregion makes this a conservative assessment. Inevitably, many ecoregions will contain many biome types (although they may be dominated by one or a few). Even if an ecoregion contains only one small area of a biome type, a broad future spread of that biome type in the ecoregion would not be judged to be new. A better measure might be an index of similarity of the biome

collection before and after the global warming; however, the approach taken here has the virtue of being simple and transparent. Although conservative, the sensitivity of an ecoregion based on its current makeup makes biological sense. If future biome types already tend to be represented in the area, then source populations will be nearby. It also implicitly assumes that ecoregions that have a relatively diverse biome makeup will be more robust in the face of climate change, an observation that is made frequently (e.g., Markham 1996).

Local Biome Change Of course, the appearance of novel biome types will identify only a fraction of the local biome change in an ecoregion (figure 1). For example, it is possible to imagine an ecoregion in which the set of types is identical under current and future conditions, but where the locations of the biomes have completely changed. This resorting of biomes also has important implications for biodiversity. Provided that organisms are unable to tolerate the new climatic conditions, extinctions will occur. These extinctions may be offset by migrations of species that are suited to the new climate, but only if the populations are able to migrate fast enough to keep up with the warming.

We illustrate this interplay between local extinction and incoming migration in a simple conceptual model

(figure 2). We envisioned a latitudinally arrayed sequence of biomes, with each having a unique set of species. To represent increasing species richness with latitude, the number of species per biome is assumed to increase arithmetically through the sequence. Mean annual temperature, which serves to define species climate envelopes, is assumed to increase smoothly and linearly from one edge of the sequence (the most species-poor edge) to the other. All species were assumed to be able to migrate the same distance x during a time step and to establish and survive at a locality if the locality's temperature was within their original biome's temperature range (i.e., the temperature range of their original biome defined the species climate envelope). The model did not include extinction lags — it was assumed that species outside of their climate envelopes would disappear immediately. Note also that the model is "neutral" in the sense that species did not interact with each other and had equal migration capabilities and climate envelope breadths.

To use the model to investigate the effect of different rates of warming on local extinction and migration (and the resulting change in net species richness), we varied the amount of warming in a given time step. The importance of migration in mitigating change at a location is evident (figure 3). Provided that migrational capabilities

FIGURE 1.

An example of biome change in a Global 200 ecoregion (California Chaparral and Woodlands) that illustrates calculation of: 1) percent new biome types, and 2) percent local biome change. In the first measurement, future biome types that were not originally represented in the ecoregion (lower left figure) are counted and expressed as a percentage of the total number of grid cells in the ecoregion. In the second, grid cells that changed biome type (lower right figure) are counted and expressed as a percentage of the total number of grid cells in the ecoregion. This example is based on simulations that used 10 global biome types, the MAPSS vegetation model (with increased water use efficiency), and the Hadley Centre climate model (with sulphate cooling). Grid cell dimensions are one-half degree of latitude by one-half degree of longitude.

FIGURE 2.

Decreasing speciese richness

Decreasing temperature

Biome x

Species
a,b,c,d

Biome y

Species
e,f,g,h,i,j,k,l

Migration
capabilities

Schematic illustration of a model of changes in local species richness in response to global warming. Biomes were assumed to have unique sets of species, with species richness increasing regularly through the biome sequence. The sequence was underlaid by a smoothly and linearly varying gradient of mean annual temperatures. Species were assumed to have identical migrational capabilities and to be able to persist at a locality only if the annual temperature there was within the range of annual temperatures in their original biome.

FIGURE 3.

Local species richness

Rate within migration capabilities

Rate exceeds migration capabilities

0

0

Rate of temperature increase

Local species richness at a constant time into the future as a function of the rate of warming. Provided that species are able to accompany the shifting climate, more rapid warming leads to greater species richness as species characteristic of warmer biomes invade the community. When the rate of warming exceeds migrational capabilities, a net loss of species occurs, and the loss is greater at higher rates of warming.
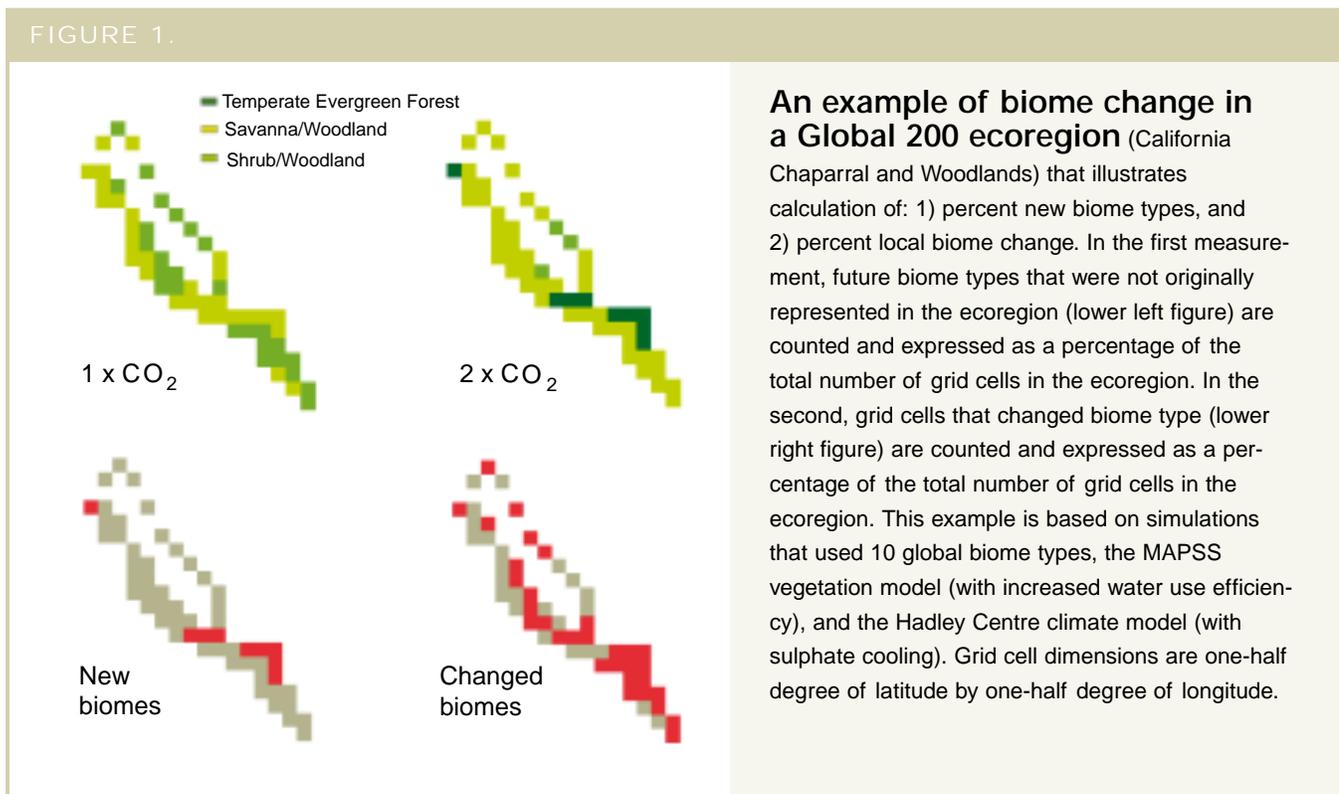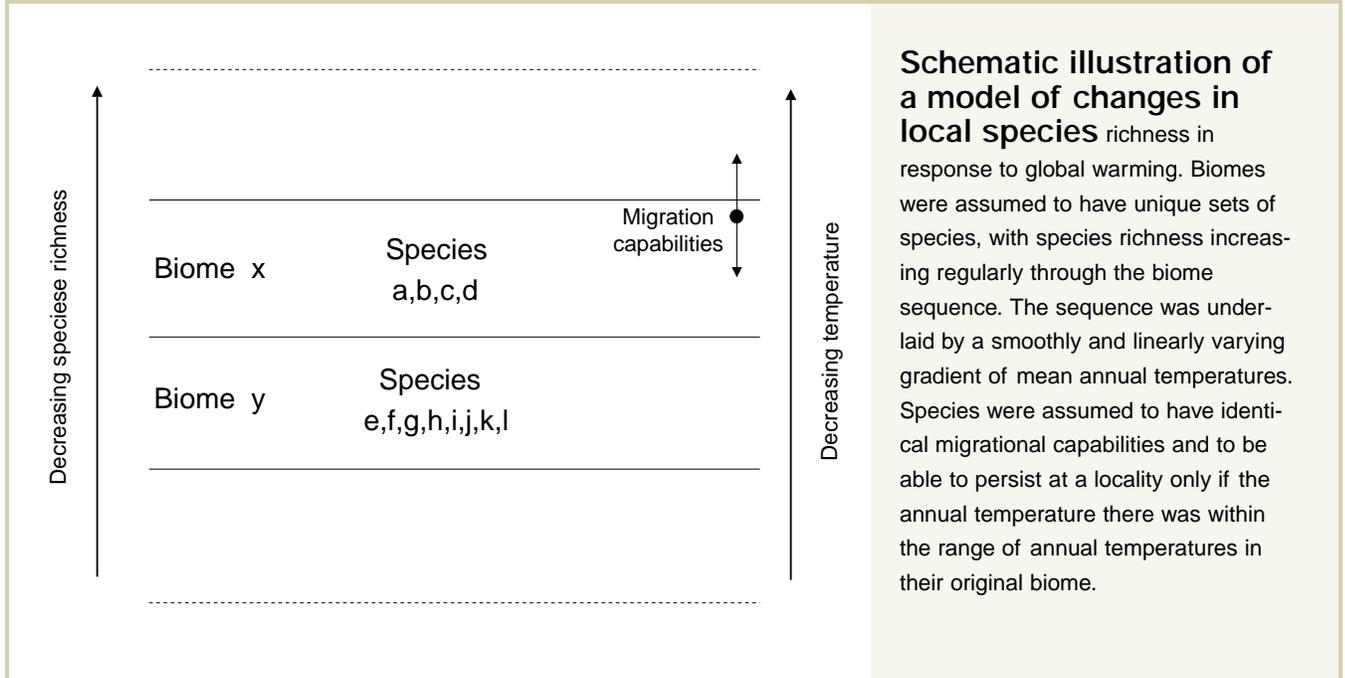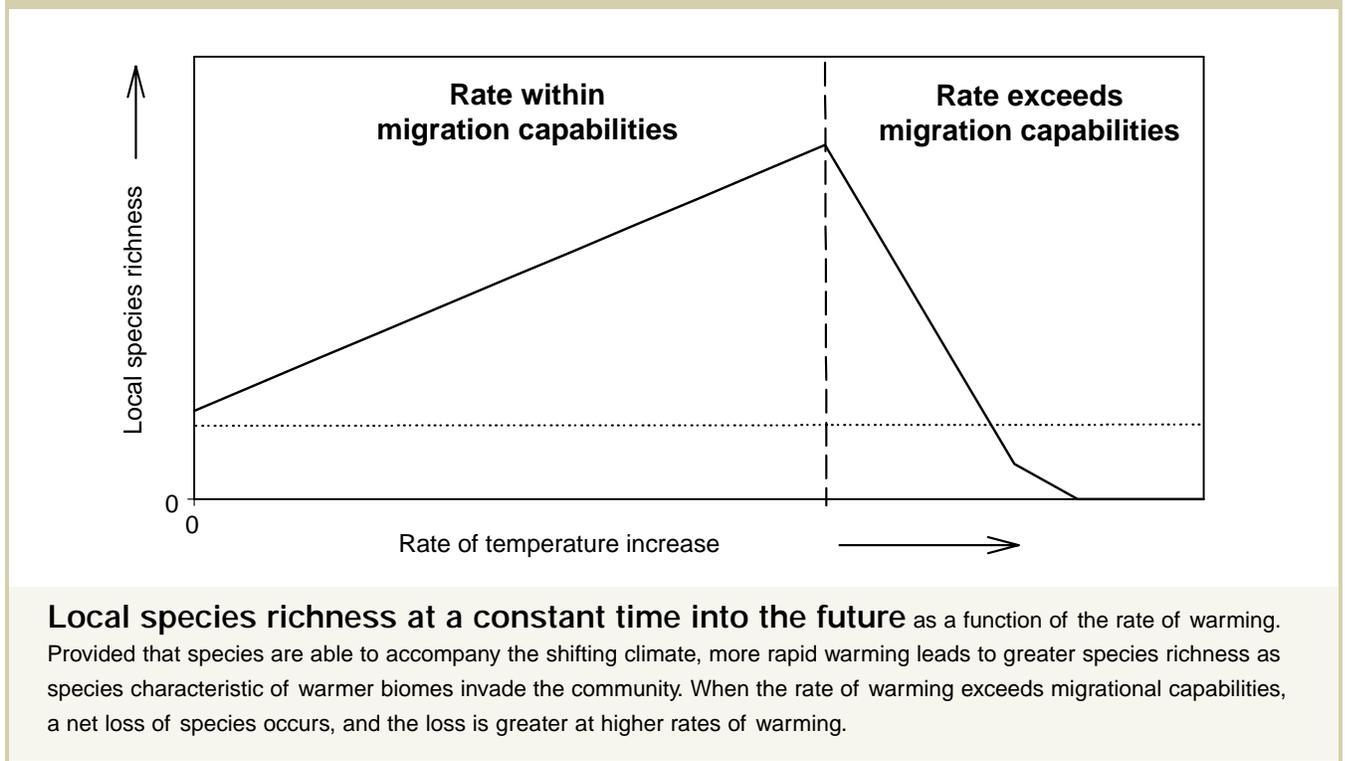
exceeded or equaled the movement of climatic envelopes, the original relationship between species richness and temperature was maintained and higher rates of warming led to higher local species richness (this result-

ed from the replacement of local species by those characteristic of warmer biomes). However, once the shifts in temperature envelopes outpaced migrational capabilities, local extinction began to outweigh immigration and

higher rates of warming resulted in increasingly large declines in species richness.

In this sense, local change can be viewed as a worst-case scenario under climate change if it is assumed that populations go extinct and are not replaced through migration (or, more realistically, are replaced only by climatically tolerant and fast migrating taxa). Our two biome change calculations (appearances of new biome types and local biome change) thus span a spectrum of possible biodiversity outcomes, from decreases in species richness in an ecoregion because of absolute reductions in the amounts of the original habitats, to widespread species loss through failures of populations to keep pace with the warming.

Local Change: Controlling for Biome Types
A global-scale look at local biome change (Malcolm and Markham 2000) showed a strong latitudinal trend, a result that is verified in the analyses presented here. In part, this is due to the greater projected warming in northern regions, and hence the more extensive ecological change expected in those regions. To control for this effect, we also examined local biome change in the context of the particular biomes found in an ecoregion.

This approach allowed us to compare climate change vulnerability among ecoregions with similar biome types (such as among the lowland tropical areas) and to examine a very fundamental question: Are the Global 200 more (or less) sensitive to the effects of global warming than other comparable ecoregions? For example, if the biological value and uniqueness of the Global 200 is partly attributable to historical long-term climatic stability, and that stability carries forward under a doubling of CO_2 concentrations, then lower vulnerability to global warming might be observed. Specifically, we used a bootstrap approach and compared percent change in the ecoregions against percent change in randomly selected collections of grid cells of the same biome composition. For each of the 14 model combinations and 113 ecoregions, we computed 10,000 random collections and tested the null hypothesis that the observed ecoregion percentage could have come from the random collection.[3]

Migration Rates
As noted above, migration capabilities are an important aspect of responses to global warming. Unfortunately, the abilities of organisms to migrate in response to climate changes are not well understood, even for relatively well-known organisms such as trees (see Clark 1998, Clark et al. 1998). Therefore, instead of attempting to predict how fast species and biomes might be able to move, we asked how fast species and biomes might 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 biomes. We could use this information to calculate the speeds that biomes might have to achieve in order to keep up with the warming. Of course, our primary interest was not in the biomes themselves (a biome is, after all, an abstract entity), but rather in the species within them. At least in a heuristic sense, the movement of the biomes provides information on the movements of species. 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. In a more general sense, the "biome climate envelopes" that the vegetation models simulate can be thought of as proxies for "species climate envelopes."

Our calculations of RMRs followed Malcolm and Markham 2000 (core calculations; see also Malcolm et al. in press). To measure required migration 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 straight-line distance between a future locality and the nearest same–biome–type locality in the current climate.[4] To calculate a migration rate, we divided the migration distance by the time period over which the migration occurred. Based on Intergovernmental Panel on Climate Change (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 °C), and sulphate aerosol cooling. Some transient model runs suggest that 2 times 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.

Sensitivity Analyses: Biome Breadths
The above measurements, especially local biome change and RMRs, are influenced by the biome classification scheme used, especially the number of biomes that occur in an area (equivalently, the "breadth" of the definitions).

In general, the use of fewer, more broadly defined climate envelopes can be expected to result in lower biome change and migration rates because existing and future distributions of a biome will show larger areas of overlap and hence larger areas of no biome change and zero migration. Unfortunately for our purposes, species distributions vary enormously in size (as do their climatic tolerances); hence, the utility of using more than one biome classification scheme. We used two: 1) a broadly defined scheme in which 10 global biome types were defined; and 2) the original (and more narrowly defined) schemes of the GVMs (18 biome types for BIOME3 and 45 for MAPSS) (table 1).

RESULTS
Appearances of Novel Biome Types

Provided that biomes were defined broadly (10 biome types), in many cases the same set of biomes types was present before and after the warming. The proportion of ecoregions that underwent no change (i.e., that included the same set of biome types before and after the warming) was relatively high, at 51 and 35% respectively on average for the two global vegetation models (BIOME3 and MAPSS) (figure 4). Only a few ecoregions underwent more than 10% loss of existing biomes (3 and 7% respectively), and only five under went 15% or more change under one or the other of the GVMs. For the five, the percent loss tended to be inconsistent among GVMs (table 2). MAPSS was more sensitive to the warming than BIOME3, a difference between the GVMs that was evident in all analyses.

When biomes were defined more narrowly (18 types for BIOME3 and 45 for MAPSS), loss of existing biome types was more common. Only 19% of ecoregions for BIOME3 and 13% for MAPSS showed no change, and 13 and 25% respectively showed greater than 10% loss of existing biomes (figure 4). This time, 22 ecoregions showed 15% or more loss under one or the other GVM; however, the results again tended to be inconsistent between the GVMs (table 3). Changes in several northern areas were notable because of their large size; however, Australian ecoregions also tended to be hard hit (map 1, table 3). Ecoregions with the most consistent loss of the original biomes under both GVMs included the Fynbos of Southern Africa and the Terai-Duar Savannas/Grasslands of northeastern India.

Local Biome Change

Although ecoregions often maintained the same set of biome types under the doubled-CO_2 climate, most showed high levels of local ecosystem change (figure 5). That is, there was strong spatial re-sorting of the biomes within the ecoregions. For example, under a broad biome definition, absolute change averaged only 1 and 3% for the two GVMs (BIOME3 and MAPSS respectively), whereas local biome change averaged 21 and 34% respectively. Similarly, under a narrow biome definition, GVM-specific absolute changes averaged only 5 and 7% respectively, whereas local change averaged 32 and 50%, respectively. If new habitat types fail to reestablish through migration, these changes in many cases have the potential to result in catastrophic species loss (~70% local change)(see Andre 1994, Fahrig 1997, in press). For the broad biome classification scheme, proportions of ecoregions that showed >70% local change averaged only approximately 2% for the two GVMs, but increased to 5 and 19% for the narrow biome definition (figure 6).

Amounts of local change at the global scale showed a strong latitudinal/altitudinal effect, with greatest change at high altitudes and latitudes and relatively less change in tropical lowland areas (map 2). Ecoregions in Asia, Russia, and Canada showed relatively high amounts of change and covered large areas. A primary effect of a narrow definition of biome change was to increase habitat change in subtropical areas. In the listings of local change under either GVM, tundra/taiga, montane, and temperate forests were prominent (tables 4, 5). For many, high amounts of change were predicted by both GVMs. For the coarse classification scheme, seven ecoregions showed 70% or more change in at least one GVM (Ural Mountains Taiga, Canadian Low Arctic Tundra, Altai-Sayan Montane Forests, Muskwa/Slave Lake Boreal Forests, Kamchatka Taiga and Grasslands, Canadian Boreal Taiga, and Southwestern Australia Forests and Scrub). Drier ecosystems tended to be more prominent under the more narrowly delimited classification scheme, especially for MAPSS (table 5).

A comparison of the amounts of local change against randomly chosen sets of pixels of the same biome types showed that some ecoregions were especially vulnerable to climate change in a comparative context, whereas others were relatively stable (tables 6, 7; map 3). Unusually vulnerable ecoregions included the Central Andean Dry Puna, the Daurian Steppe, the Ural Mountains Taiga, and the Canadian Low Arctic Tundra.
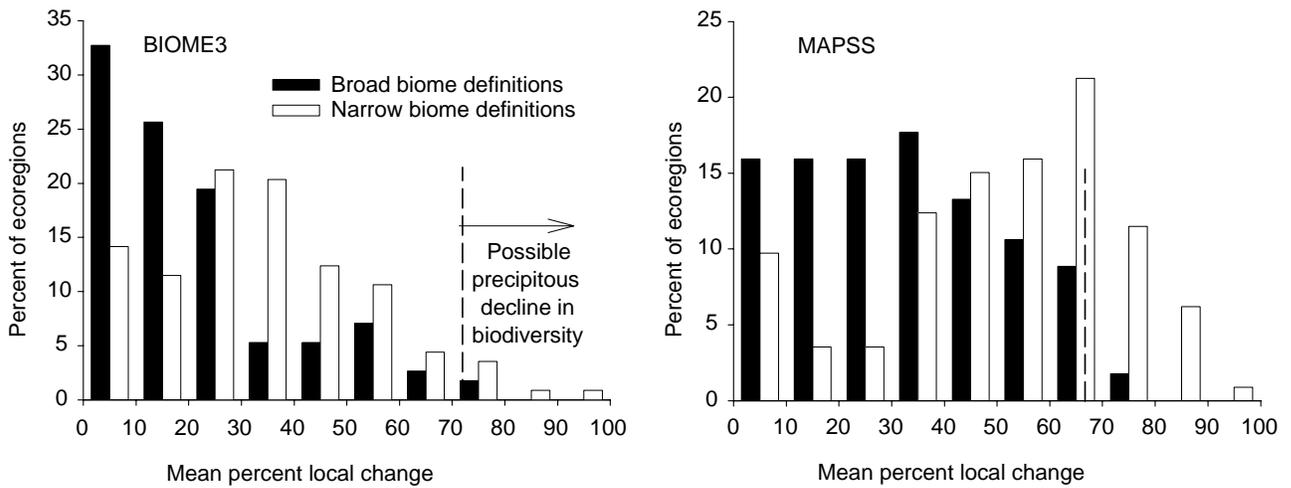
FIGURE 4.
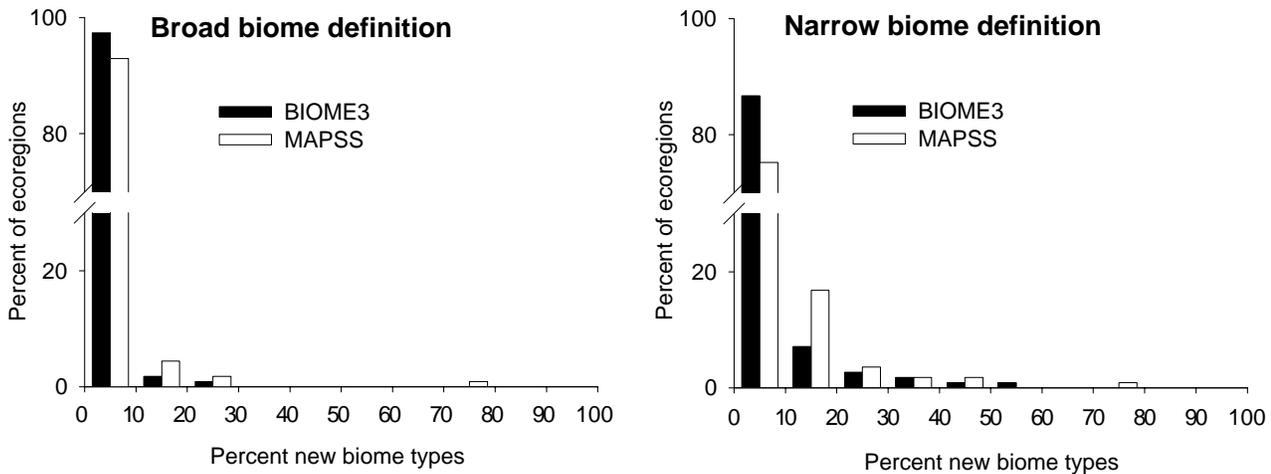
Percent of ecoregions plotted according to average percent of area that became novel biome types under scenarios of doubled CO_2 concentrations. The percentage area for each ecoregion was calculated as the average across multiple climate scenarios for each global vegetation model (BIOME3 or MAPSS). The left figure shows the distribution under a broad biome definition (10 biome types); the right figure is under a narrow biome definition (18 types for BIOME3 and 45 for MAPSS).
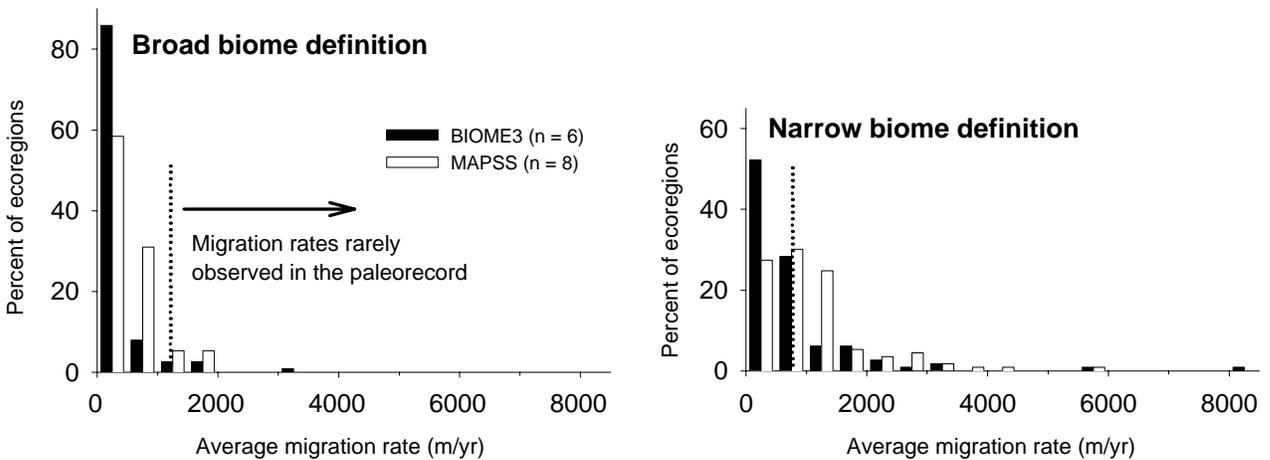
FIGURE 5.
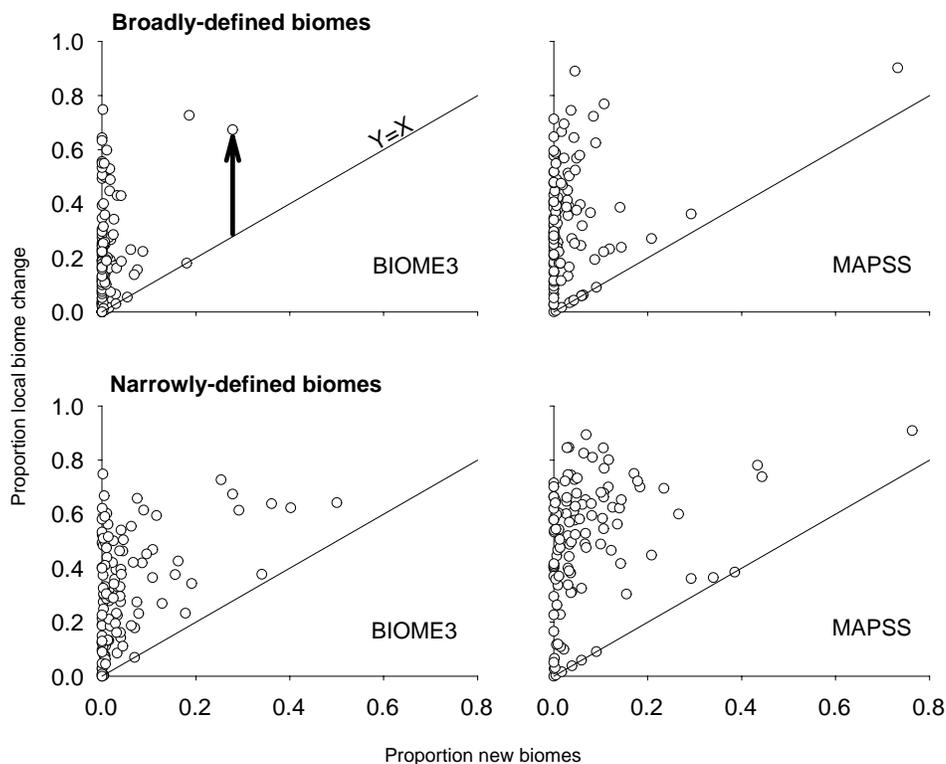
Proportional change of biome types plotted against proportion of novel biome types. As indicated by the arrow, local change may indicate substantially more habitat loss if existing habitats fail to reestablish elsewhere.

Percent of ecoregions plotted according to average percent change of biome types under scenarios of doubled CO_2 concentrations. The percentage area for each ecoregion was calculated as the average across multiple climate scenarios for each global vegetation model (BIOME3 [left figure] or MAPSS [right figure]). In each figure, results are shown for a broad biome definition (10 biome types) and a narrow biome definition (18 types for BIOME3 and 45 for MAPSS).

Percent of ecoregions plotted according to average required migration rates (RMRs) under scenarios of doubled CO_2 concentrations. The migration rate for each ecoregion was calculated as the average across multiple climate scenarios for each global vegetation model (BIOME3 or MAPSS). The left figure shows the distribution under a broad biome definition (10 biome types); the right figure is under a narrow biome definition (18 types for BIOME3 and 45 for MAPSS).

Despite its large size, the last showed usually high change, at 75 and 77% for the two GVMs (BIOME3 and MAPSS, respectively) compared to 47 and 57% respectively for the random sets. Especially stable regions included the Central and Eastern Miombo Woodlands, the Valdivian Temperate Rain Forests/Juan Fernandez Islands, and the Appalachian and Mixed Mesophytic Forests. Tundra ecoregions of Canada and Russia tended to be vulnerable, whereas those of Fennoscandia and western Alaska tended to be more stable. Strong contrasts were shown within the tropics. Within the South American region, most areas showed vulnerability (with the exception of eastern Columbia and the northwestern Amazon). In southeast Asia, insular areas tended to show stability, whereas mainland areas tended to be more vulnerable. In tropical Africa, the central region tended to be relatively stable, whereas western, southern, and eastern Africa tended to be vulnerable.

Required Migration Rates

Required migration rates (RMRs) were strongly affected by the GVM type and the breadth of biome definitions. As was true of the other measurements, BIOME3 was less sensitive than MAPSS, and the assumption of narrow biomes increased vulnerability (figure 7). For example, under the 10-class biome definition, average ecoregion RMRs for the two GVMs (BIOME3 and MAPSS, respectively) were 313 and 502 m/yr, whereas under the narrow definition they were 766 and 1,075 m/yr. Percentages of ecoregions that showed average rates above 1,000 m/yr (unusual in the paleo record) were 6, 11, 19, and 42%, respectively.

Examination of the spatial distribution of RMRs showed strong similarities to the pattern of local biome change. Under a coarse biome classification, unusually high rates were shown in northern areas, especially in Canada and Russia, but also in southwestern Australia and New Zealand (map 4). Consistently high rates (>750 m/yr for both GVMs) were dominated by tundra and taiga areas (table 8). Finer subdivision of biomes led to much higher rates in warm temperate and subtropical areas; only the lowland tropics still had relatively low rates (map 4). High rates were especially prevalent in North America, Europe, Asia, Australia, eastern and southern Africa, and southern South America. Nearly one quarter of the ecoregions, including a wide diversity of ecosystem types, had consistently high rates (>750 m/yr for both GVMs) (table 9).

DISCUSSION

These results indicate that global warming has the potential to strongly affect species richness in the Global 200 ecoregions. Even if ecosystems are assumed to be able to perfectly keep up with the warming, an outright loss of species is expected in many ecoregions because of reductions in the area of the original habitat types.

Under our broad biome definition, which was very conservative because it divided the planet's ecosystems into only 10 vegetation types, the areas lost tended to be small, with only 3–7% of ecoregions on average losing 10% or more of their habitat. However, under a narrow biome definition, 22 ecoregions lost 15% or more of their original biome types in at least one of the vegetation models. Because of the strong relationship between the area of a habitat and the number of species that it contains, this loss of habitat can be expected to result in species extinctions. This species loss will arise from a combination of factors, including reduced population sizes of the various species that dwell in the habitat and reduced numbers of micro-habitats in the habitat.

In the present analysis, it is difficult to calculate the number of species extinctions that can be expected as a result of the area loss, in part because the various biomes within an ecoregion differ with respect to their species richness, and in part because the relationship between area and species richness within a biome type varies according to the spatial scale examined (e.g., Hubbell 2001). A very rough figure assuming a continental species-area exponent of 0.15 would mean species loss of some 2–3% of the biota under 15% habitat loss.[5] In a species-rich ecoregion such as the Fynbos of southern Africa, which averaged 32% loss, the expected 5–6% species loss would imply the eventual loss of thousands of species.

As indicated by the conceptual model, however, species loss could be much higher if the rate of warming exceeds migrational capabilities. Under the worst-case scenario that populations fail to move altogether due to migration limitation, species loss could increase markedly. In the Fynbos, for example, loss of habitat would increase from 32% to 58%. In the Canadian Low Arctic Tundra, the average percent biome change was 76%, which, using an exponent of 0.15, would translate into species loss of 19%. However, use of a species area relationship for habitat loss of this magnitude may seriously underestimate species loss. For example, a variety of

spatially explicit habitat loss models suggest threshold effects (Fahrig in press) wherein sufficiently high habitat loss (typically in the order of 70–80%) may lead to a precipitous increase in extinction probabilities (Andrén 1994, Fahrig 1997).

In the present analysis, 2% of ecoregions showed habitat loss of this magnitude under the coarse biome definition, whereas the average figures for the narrow biome definition were 5 and 19% (for BIOME3 and MAPSS, respectively) (table 5). The mere possibility of catastrophic species loss in 19% of the world's most valuable ecoregions (22 of the 113 considered here) indicates the potentially serious consequences of the projected warming.

A relevant issue is the overall vulnerability of the Global 200 to global warming compared to random locations. Apparently, the factors that give rise to the biological value of these regions do little to protect them against the ravages of climate change. Indeed, in some cases, as discussed below, factors such as low dispersal capabilities and high endemism may make them more vulnerable to climate change.

Of course, the possibility of such radical species loss depends both on migration rates and extinction rates. Although the invasion of new biome types implies a loss of some of the original biota of an ecoregion, it is possible in some cases that the original habitats could reestablish elsewhere. The exception is for many tundra and taiga habitats (including those at high elevations), which are projected to show a net decline globally. These habitats literally have nowhere to go in a warmer world. The same may also apply to arid ecosystems (Neilson et al. 1998, Malcolm et al. in prep).

This reestablishment of new populations will depend on successful migration, which makes the high required migration rates reported here of concern. Typical migration rates observed during the glacial retreat were 100-200 m/yr; the *average* rates of many of the ecoregions in this analysis were an order of magnitude higher. Incredibly, nearly one quarter of ecoregions had average rates of greater than 750 m/yr. Added to this is the possibility that our rates are underestimates because of a conservative estimate of the time period of the warming (100 years).

Unfortunately, the significance of these high rates is difficult to determine with certainty, and little can be said other than that some species presumably will be able to attain them, whereas others will not. The net effect will be a filtering effect, with subsequent ecosystems consisting of the fastest migrating (often weedy) species. Surprisingly, even the migration capabilities of temperate trees (a well studied group) are poorly understood. They appear to have been able to keep up with retreating glaciers (Prentice et al. 1991), but plant demographers have a hard time understanding how they could migrate even that fast (Clark 1998).

The importance of dispersal rates in determining migration capabilities raises the specter of low migration capabilities in some ecoregions. For example, the high species richness in the Cape Floristic Province of southern Africa may be related to low dispersal capabilities (nearly 3,000 species are ant-dispersed [Mittermeier et al. 1999]), with the possibility of low migration capabilities. Matlack (1994) obtained evidence that forest understory plants reinvaded secondary forests at very low rates (less than 1 m/yr typically), with ant-dispersed species performing especially poorly.

A related issue is geographic range size. For virtually all of the variables investigated here, the breadth of the biome definitions influenced the results. Again, it is difficult to make any definitive statements as to what definition might be more relevant. The relationship between average biome area and average range size shows considerable variation. For example, for common U.S. tree species east of the 100th meridian, even the coarsest (10-type) biome classification underestimated average range sizes (Malcolm et al. in press). From Iverson et al. (1999), 75 tree taxa mapped by Little (1971, 1977; cited by Iverson et al. [1999]) had average range sizes of 1.59 million km^2, which was larger than the average 10-class biome sizes for the same region (0.67 million km^2 for both BIOME3 and MAPSS). By contrast, for 819 species in the genus *Eucalyptus* in Australia, average range size was 0.11 million km^2 (Hughes et al. 1996). This was smaller than the average areas of our narrowest biome definitions in the same region (0.85 million km^2 for BIOME3 [18 biome types] and 0.45 million km^2 for MAPSS [45 biome types]).

This emphasizes that the use of biome distributions as proxies for species climate envelopes, even in a heuristic sense, must be treated with caution. Given the average increase in geographic range size with latitude (Rapoport's rule), it seems likely that a coarse biome definition makes more sense at high latitudes, whereas finer definitions make more sense at low latitudes. The prevalence of endemic species (which tend to have small

geographic ranges) in the ecoregions raises the possibility that even our narrow-definition estimates of habitat change and required migration rates are underestimates.

The expectation of systematic variation in relevant life history traits among ecoregions outlines the importance of investigating vulnerability within the context of the major habitat types (which vary systematically with latitude). Generally lower levels of habitat change and required migration rates in tropical compared to temperate regions may not be particularly relevant if tropical species have lower migration capabilities, for example. Of course, the enormously high species richness in tropical regions makes these ecosystems of special concern regardless. There, losses of just a few percentages of the biota potentially translate into tens of thousands of species or more.

Although these calculations indicate the potential seriousness of the problem posed by climate change for the planet's species and ecosystems, they also outline some of the difficulties in obtaining realistic projections of the possible impacts of climate change on species richness. Perhaps most surprising are the strong differences in vegetation change between the GVMs. These differences tend to greatly exceed those attributable to differences among the GCMs (Malcolm et al. in press, Malcolm et al. in prep). However, in a relative sense, the two models indicate similar effects of the warming, suggesting that the overall effect of the warming could be reasonably assessed despite these differences.

The conceptual model presented here illustrates the potentially important roles of migration and extinction in determining species loss; however, it does not include several factors that can be expected to importantly affect overall responses to climate change. These factors in turn significantly complicate attempts to equate vegetation change with species loss (or gain). Perhaps most significant among these is the degree to which climate change increases local extinction rates. Any such extinctions will depend on a number of factors, including the longevity of the organisms involved (which is highly relevant over the short time scale during which a doubling of CO_2 concentrations are expected [<100 years]) and the extent to which distributions are determined by climate. However, although wide tolerances may reduce extinction rates, they also may reduce migration rates because of fewer opportunities for species newly migrating into an area (the "zero sum" dynamics of Hubbell [2001]).

Thus, although wide climatic tolerances may reduce the effects of the warming in the short term, they may exacerbate future species loss by further reducing possibilities for migration. If distributions are determined by biotic interactions, the net effect of a changing climate becomes very difficult to predict, with the possibility that some taxa will maintain populations outside of their normally observed climate envelopes. In fact, the validity of the climate envelope modeling approach in a predictive capacity remains to be established, although recent success using the approach has been obtained in predicting recent changes in distributions of European birds (R. Green pers. comm.).

Finally, the analysis here fails to consider preexisting anthropogenic influences. Many of the species in the Global 200 ecoregions are already threatened by human activities (Olson and Dinerstein 1998). Schwartz (1992, see also Davis 1989) noted that climate warming could especially threaten species with geographically restricted ranges (such as narrow endemics), those restricted to habitat islands, and those that are specialists in uncommon habitats. This is an important concern for many plant species; for example, The Nature Conservancy estimates that one-half of the endangered plant taxa in the United States is restricted to five or fewer populations (Pitelka et al. 1997). Rarity can be expected not only to increase extinction rates (MacArthur and Wilson 1967) but, along with losses of natural habitats, to reduce the potential for migration (see Schwartz 1992). Similar arguments apply to island ecoregions, which were largely excluded from this report because of the small number of grid cells that they occupied. The biodiversity of islands may be at special risk because of small populations, limited opportunities for migration, and sea level rise.

In conclusion, a relatively large collection of global climate and vegetation models all indicate the potential for massive vegetation change in globally significant ecoregions under projected climates associated with a doubling of CO_2 concentrations. This vegetation change has the potential to result in substantial species loss through reductions in the overall amounts of habitat; and in some cases, it may result in catastrophic species loss, especially if the rate of warming exceeds the capabilities of species to migrate. However, the relationship between species loss and climate-induced vegetation change is poorly understood, as are species migration capabilities. Efforts to test the validity of the climate-envelope approach are needed, as are further efforts to model the interplay between local extinction and migration.
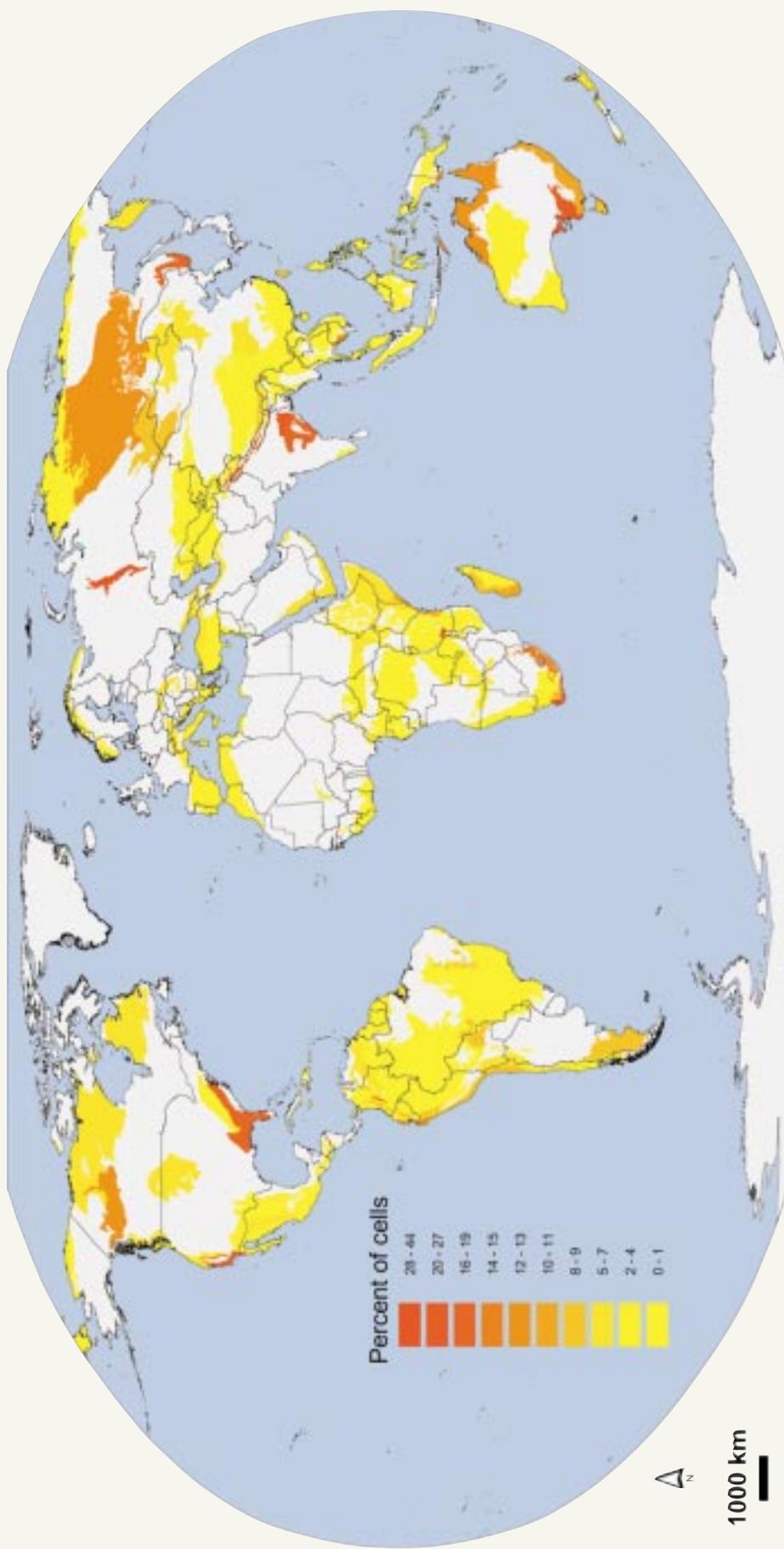
MAP 1.

Percentages of ecoregion grid cells that became novel biome types under scenarios of doubled CO_2 concentrations, averaged across 14 combinations of global vegetation and climate models. Biomes were classified into 18 types for the vegetation model BIOME3 and 45 types for the vegetation model MAPSS.

Percent of cells

28 - 44
20 - 27
16 - 19
14 - 15
12 - 13
10 - 11
8 - 9
5 - 7
2 - 4
0 - 1

1000 km

Percent of cells

70 - 77
62 - 69
54 - 61
47 - 53
39 - 46
31 - 38
24 - 30
16 - 23
8 - 15
0 - 7

N

1000 km

Percent of cells

- 71 - 78
- 63 - 70
- 55 - 62
- 47 - 54
- 40 - 46
- 32 - 39
- 24 - 31
- 16 - 23
- 8 - 15
- 0 - 7

N

1000 km
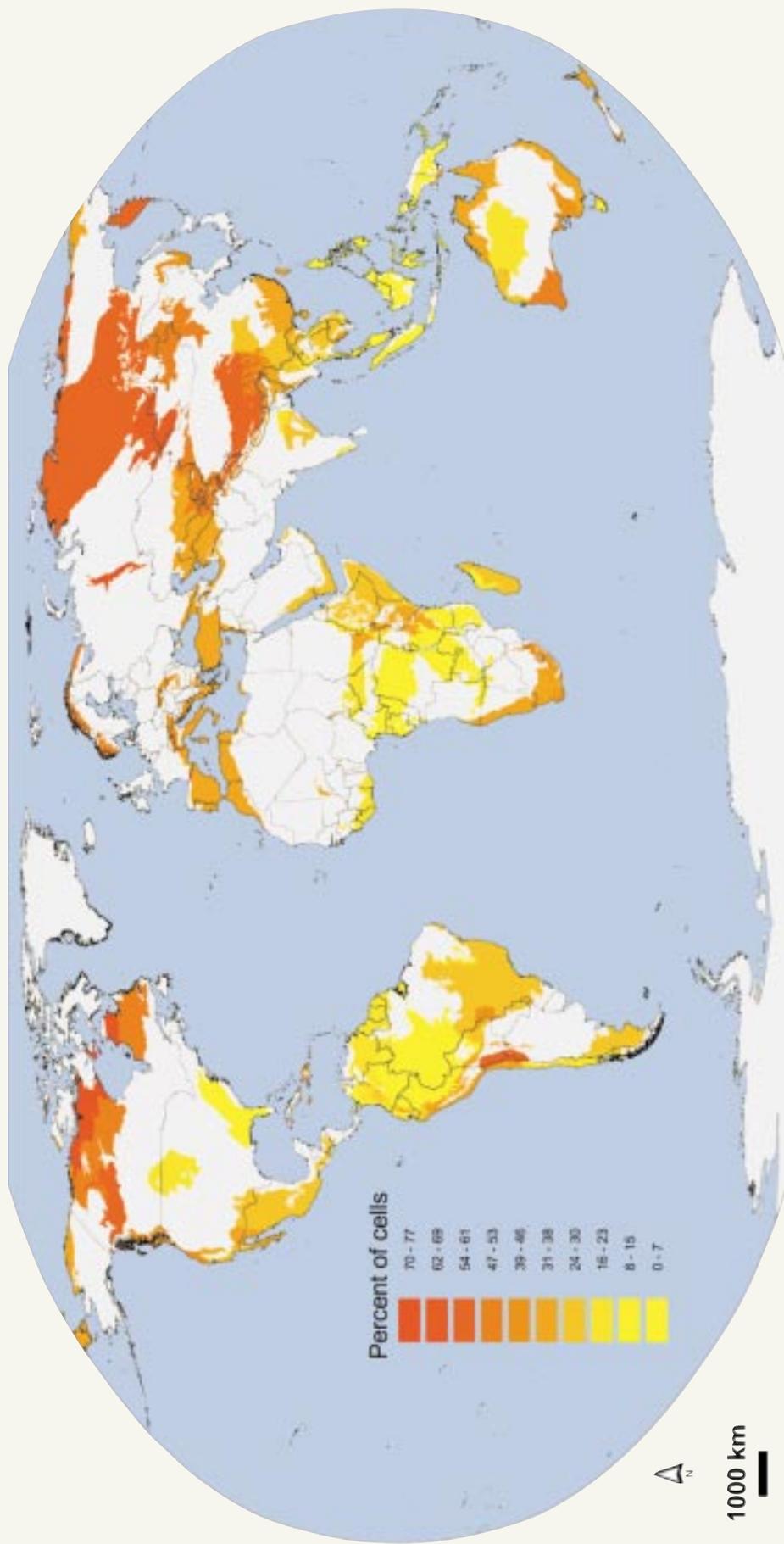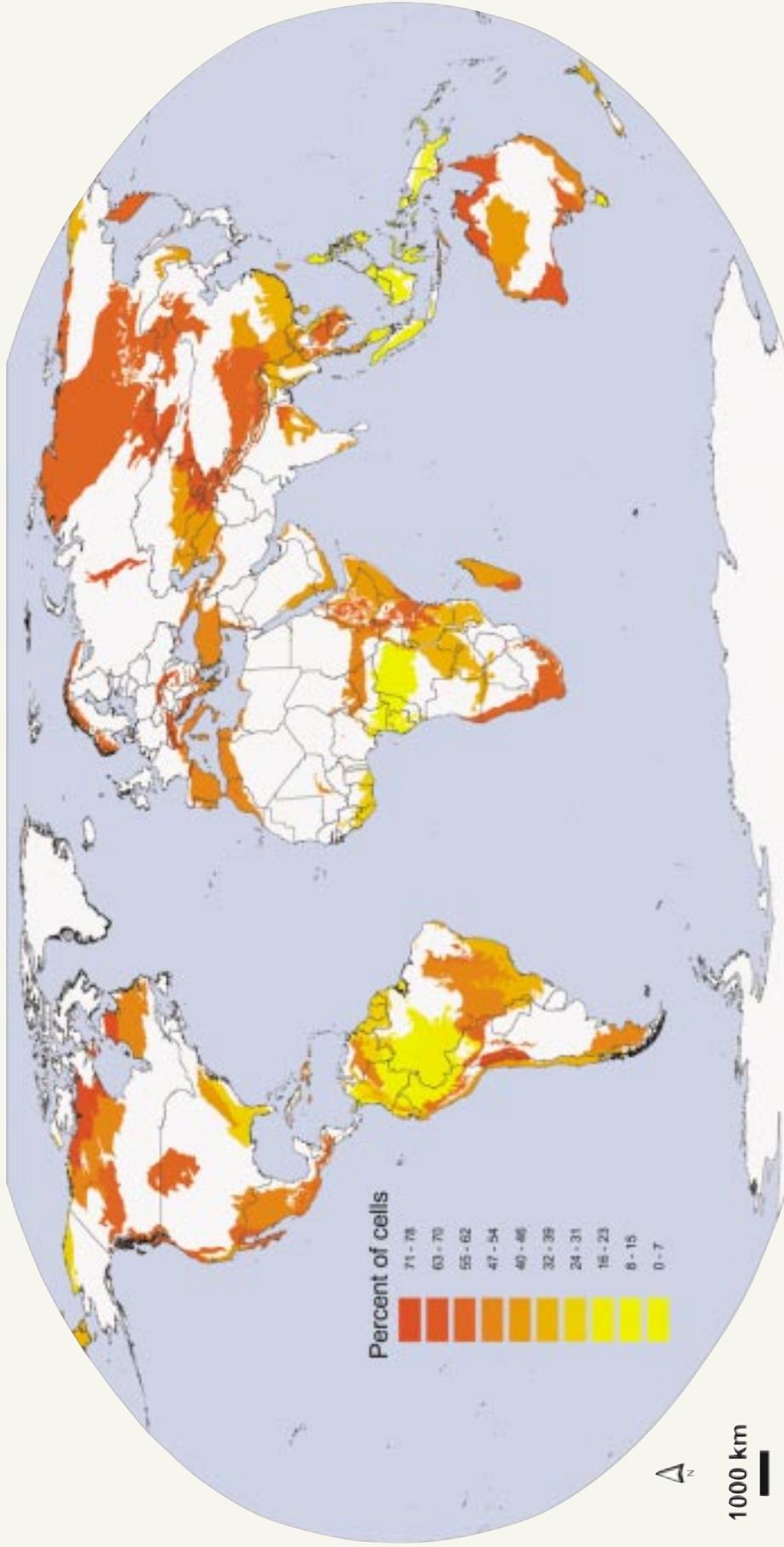
MAP 2.

Percentages of ecoregion grid cells that changed biome types under scenarios of doubled CO_2 concentrations, averaged across 14 combinations of global vegetation and climate models. In the upper map, biomes were classified into 10 types; in the lower map, they were classified into 18 types (BIOME3) or 45 types (MAPSS).

MAP 3A

Average

0 - 10
11 - 20
21 - 30
31 - 40
41 - 50
51 - 60
61 - 70
71 - 80
81 - 90
91 - 100

0 - 10
11 - 20
21 - 30
31 - 40
41 - 50
51 - 60
61 - 70
71 - 80
81 - 90
91 - 100

N

1000 km

Average

0 - 10	0 - 10
11 - 20	11 - 20
21 - 30	21 - 30
31 - 40	31 - 40
41 - 50	41 - 50
51 - 60	51 - 60
61 - 70	61 - 70
71 - 80	71 - 80
81 - 90	81 - 90
91 - 100	91 - 100

1000 km
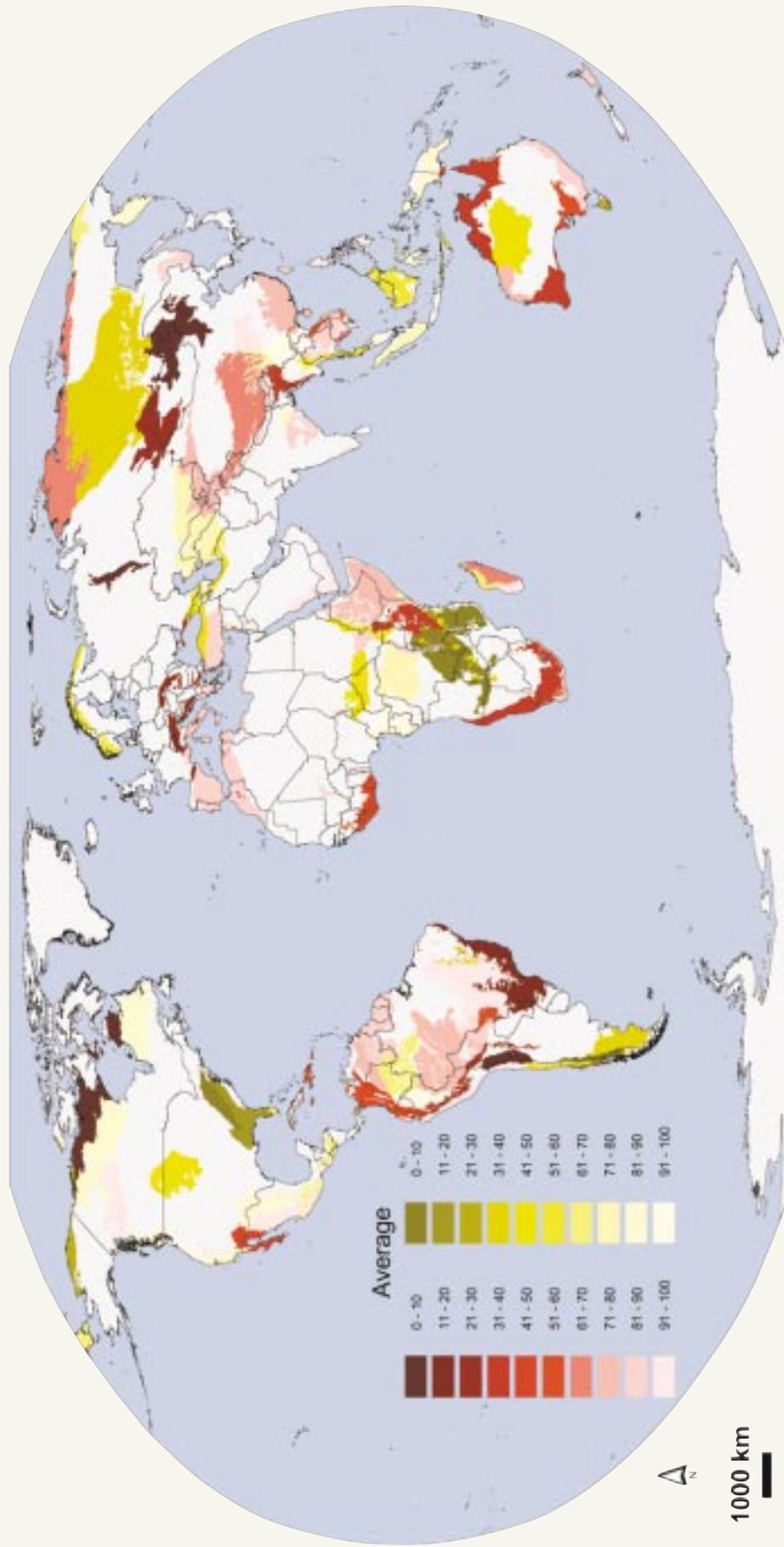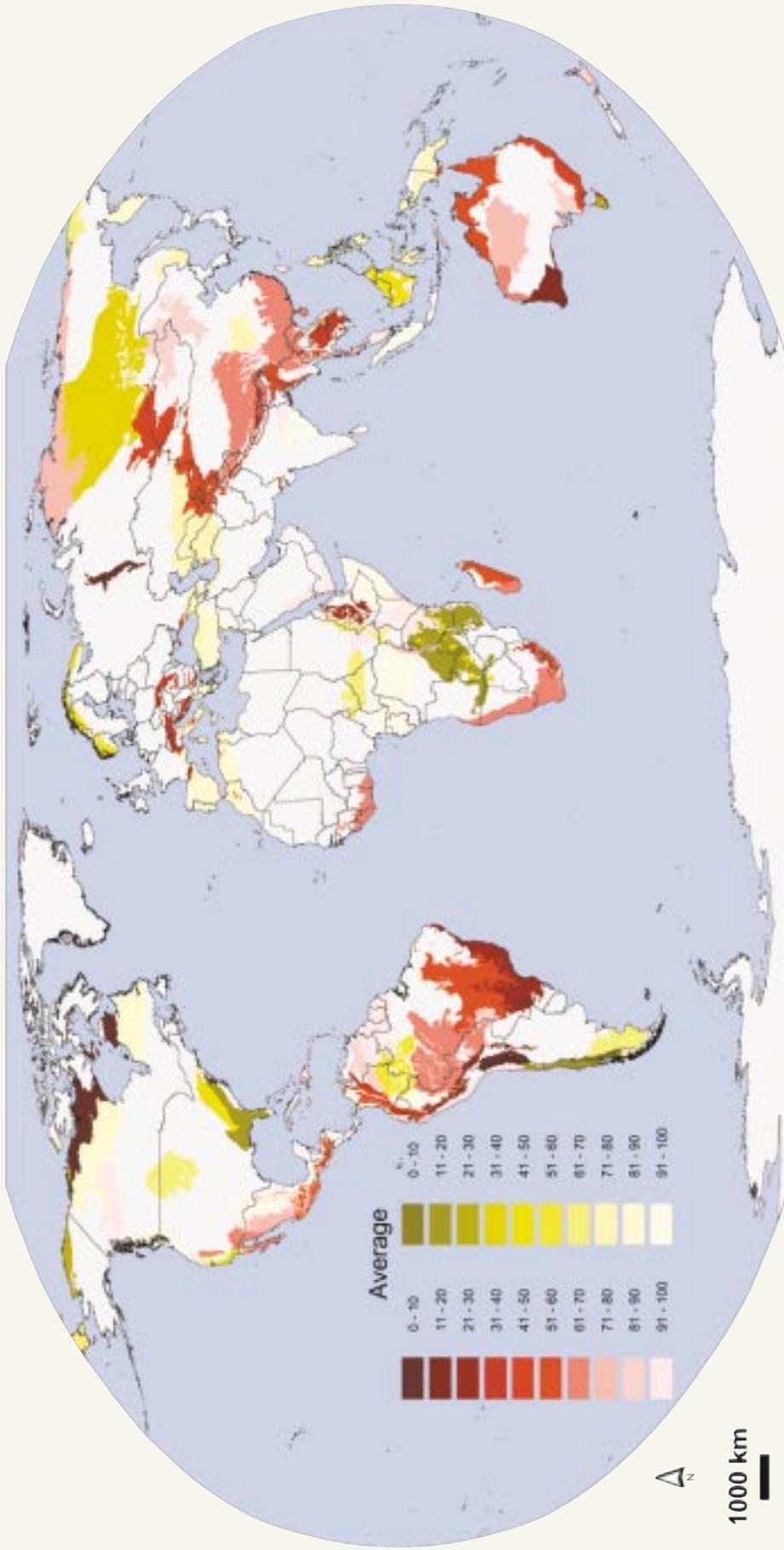
MAP 3.

Comparisons of local biome change between ecoregions and randomly drawn collections of grid cells with the same biome composition. Numbers represent tests of significance between the two (two-sided, type I probabilities), averaged across 14 combinations of global vegetation and climate models. Yellow shades symbolize ecoregions that were relatively stable; that is, they underwent less change than the random collections. Red shades symbolize ecoregions that were relatively vulnerable; that is, they underwent more change than the random collections. For both, smaller numbers indicate a stronger difference between the ecoregion and the random set. In the upper map, biomes were classified into 10 types; in the lower map, they were classified into 18 types (BIOME3) or 45 types (MAPSS).

Average rate

1500 - 1932
1250 - 1499
1000 - 1249
750 - 999
500 - 749
250 - 499
0 - 249

N

1000 km

Average rate
- 1500 – 4317
- 1250 – 1499
- 1000 – 1249
- 750 – 999
- 500 – 749
- 250 – 499
- 0 – 249

N

1000 km

MAP 4.

Average RMRs (required migration rates) within ecoregions, averaged across 14 combinations of global vegetation and climate models. In the upper map, biomes were classified into 10 types; in the lower map, they were classified into 18 types (BIOME3) or 45 types (MAPSS).
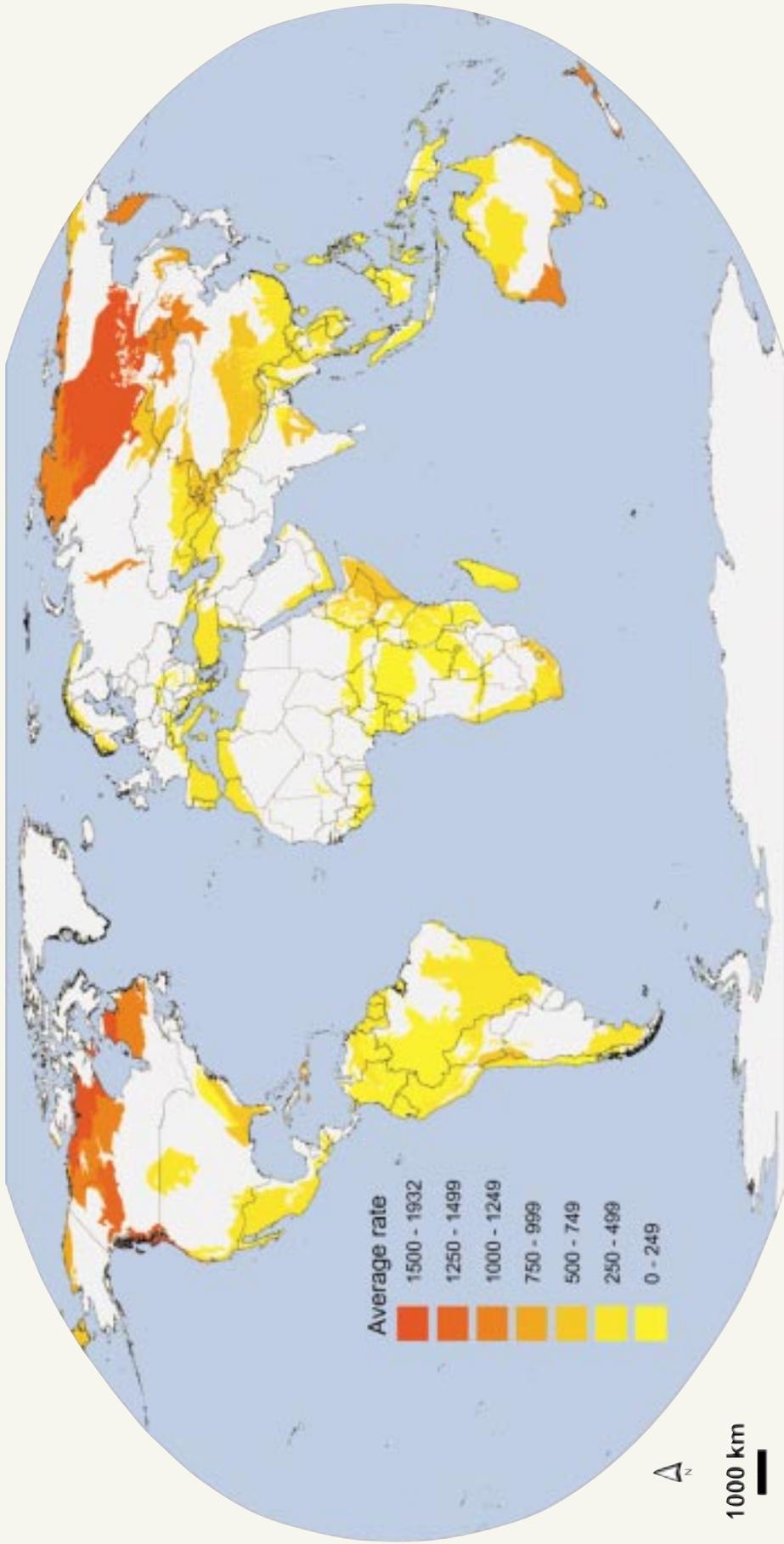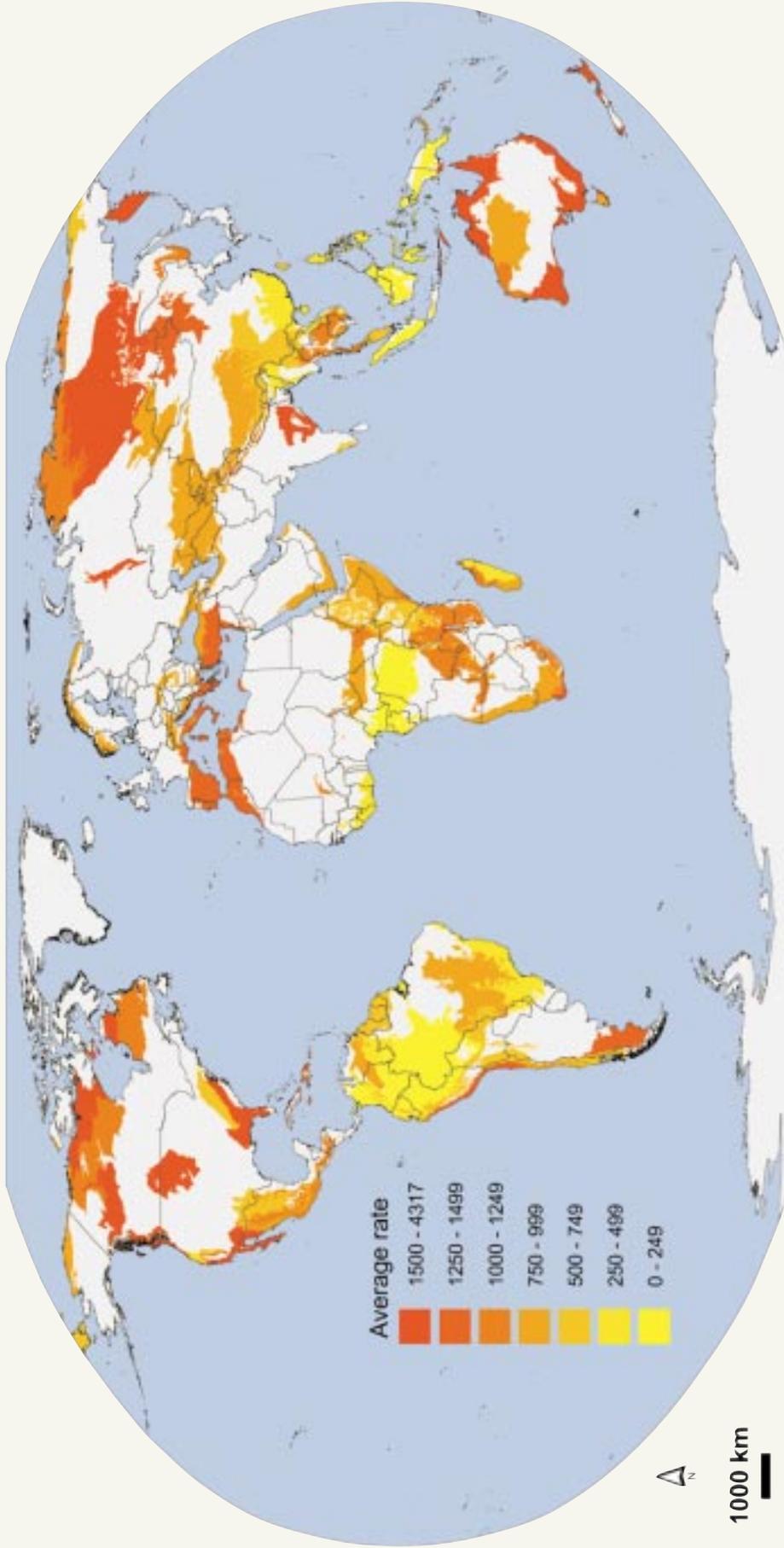
TABLE 1.

Classification scheme used to define 10 major vegetation types from the original types used in two global vegetation models (BIOME3 and MAPSS).

	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.

Ecoregions with relatively large percent increases in the appearance of new biome types (>15% of pixels on average for either BIOME3 or MAPSS) under a broad biome definition (10 biome types).

Ecoregion ID	Ecoregion name	Number of pixels	PERCENT NEW BIOME TYPES BIOME3 (n = 6)	MAPPS (n = 8)	Weighted average
83	Ural Mountains Taiga	114	1.03	73.25	42.299
91	Terai-Duar Savannas & Grasslands	12	18.05	20.83	19.639
71	Russian Far East Temperate Forests	94	0	29.25	16.714
84	East Siberian Taiga	2656	27.81	1.34	12.684
81	Muskwa/Slave Lake Boreal Forests	339	18.58	4.57	10.574

TABLE 3.

Ecoregions with relatively large percent increases in the appearance of new biome types (>15% of pixels on average for either BIOME3 or MAPSS) under a narrow biome definition (18 biome types for BIOME3; 45 for MAPSS).

Ecoregion ID	Ecoregion name	Number of pixels	PERCENT NEW BIOME TYPES BIOME3 (n = 6)	MAPPS (n = 8)	Weighted average
83	Ural Mountains Taiga	114	1.03	76.32	44.053
118	Fynbos	31	15.59	44.35	32.024
91	Terai-Duar Savannas & Grasslands	12	36.11	20.83	27.379
120	Southern Australia Mallee & Woodlands	117	2.28	43.38	25.766
103	Southern Rift Montane Woodlands	12	6.94	38.54	24.997
55	Chhota-Nagpur Dry Forests	41	50	3.35	23.343
75	Southeastern Coniferous & Broadleaf Forests	222	0	33.95	19.4
33	Eastern Deccan Plateau Moist Forests	119	40.2	3.04	18.966
121	California Chaparral and Woodlands	55	6.97	26.59	18.181
68	Western Himalayan Temperate Forests	32	8.86	23.44	17.191
71	Russian Far East Temperate Forests	94	0	29.25	16.714
52	Nusa Tenggara Dry Forests	23	34.06	1.09	15.22
57	Tumbesian-Andean Valleys Dry Forests	36	16.2	14.24	15.08
105	Drakensberg Montane Shrub & Woodlands	72	8.57	17.88	13.89
81	Muskwa/Slave Lake Boreal Forests	339	25.37	4.57	13.484
90	Northern Australia & Trans-Fly Savannas	385	29.13	0.39	12.707
84	East Siberian Taiga	2656	27.81	1.34	12.684
35	Cardamom Mountains Moist Forests	15	4.44	18.33	12.377
8	East African Coastal Forests	34	19.12	4.41	10.714
64	Eastern Australia Temperate Forests	204	0.33	17.1	9.913
65	Tasmanian Temperate Rain Forests	21	0	15.48	8.846
3	Cameroon Highlands Forests	15	17.78	0	7.62

TABLE 4.

Ecoregions with relatively large proportional changes in local biome types (>0.50 proportion of pixels on average for either BIOME3 or MAPSS) under a broad biome definition (10 biome types).

Ecoregion ID	Ecoregion name	Number of pixels	PROPORTION LOCAL BIOME CHANGE		
			BIOME3 (n = 6)	MAPPS (n = 8)	Weighted average
83	Ural Mountains Taiga	114	0.598	0.9024	0.77194
114	Canadian Low Arctic Tundra	607	0.7482	0.7688	0.75997
79	Altai-Sayan Montane Forests	441	0.4891	0.723	0.62276
81	Muskwa/Slave Lake Boreal Forests	339	0.7271	0.5241	0.6111
109	Central Andean Dry Puna	108	0.5494	0.6471	0.60523
112	Eastern Himalayan Alpine Meadows	45	0.4296	0.6949	0.5812
85	Kamchatka Taiga & Grasslands	161	0.1615	0.8905	0.57807
84	East Siberian Taiga	2656	0.674	0.4763	0.56103
110	Tibetan Plateau Steppe	586	0.4303	0.6445	0.5527
116	Taimyr & Russian Coastal Tundra	1227	0.5058	0.5792	0.54774
96	Daurian Steppe	515	0.5556	0.5182	0.53423
115	Fenno-Scandia Alpine Tundra & Taiga	248	0.342	0.6663	0.52731
82	Canadian Boreal Taiga	1097	0.2297	0.745	0.52416
111	Middle Asian Montane Steppe & Woodlands	400	0.5492	0.4754	0.50703
119	Southwestern Australia Forests & Scrub	190	0.1868	0.7132	0.4876
108	Northern Andean Paramo	14	0.2857	0.625	0.47959
77	European-Mediterranean Montane Mixed Forests	217	0.3157	0.5484	0.44867
105	Drakensberg Montane Shrublands & Woodlands	72	0.2014	0.5955	0.4266
68	Western Himalayan Temperate Forests	32	0.5001	0.3672	0.42416
120	Southern Australia Mallee & Woodlands	117	0.1923	0.578	0.4127
37	Greater Antillean Moist Forests	29	0.1667	0.5689	0.39653
73	Klamath-Siskiyou Coniferous Forests	20	0.6333	0.2125	0.39284
118	Fynbos	31	0.1559	0.5686	0.39173
72	Pacific Temperate Rain Forests	138	0.6437	0.193	0.38616
64	Eastern Australia Temperate Forests	204	0.1087	0.5888	0.38304
74	Sierra Nevada Coniferous Forests	20	0.5333	0.2687	0.3821
35	Cardamom Mountains Moist Forests	15	0.1111	0.5167	0.34287
117	Chukote Coastal Tundra	264	0.0695	0.513	0.32293
33	Eastern Deccan Plateau Moist Forests	119	0.5294	0.1323	0.30249
128	Carnavon Xeric Scrub	95	0.0298	0.5027	0.30003

TABLE 5.

Ecoregions with relatively large proportional changes in local biome types (>0.70 proportion of pixels on average for either BIOME3 or MAPSS) under a narrow biome definition (18 biome types for BIOME3; 45 for MAPSS).

			PROPORTION LOCAL BIOME CHANGE		
Ecoregion ID	Ecoregion name	Number of pixels	BIOME3 (n = 6)	MAPPS (n = 8)	Weighted average
83	Ural Mountains Taiga	114	0.6024	0.909	0.7776
114	Canadian Low Arctic Tundra	607	0.7482	0.7688	0.75997
109	Central Andean Dry Puna	108	0.591	0.8102	0.71626
112	Eastern Himalayan Alpine Meadows	45	0.5408	0.8444	0.71429
79	Altai-Sayan Montane Forests	441	0.5011	0.801	0.67247
119	Southwestern Australia Forests & Scrub	190	0.3772	0.8454	0.64474
54	Indochina Dry Forests	146	0.516	0.7012	0.62183
81	Muskwa/Slave Lake Boreal Forests	339	0.7271	0.5241	0.6111
94	Northern Prairie	325	0.2892	0.8254	0.5956
105	Drakensberg Montane Shrublands & Woodlands	72	0.419	0.7222	0.59226
118	Fynbos	31	0.3763	0.7379	0.58293
120	Southern Australia Mallee & Woodlands	117	0.3162	0.781	0.5818
130	Sonoran-Baja Deserts	128	0.2266	0.8467	0.58094
85	Kamchatka Taiga & Grasslands	161	0.1615	0.8936	0.57984
115	Fenno-Scandia Alpine Tundra & Taiga	248	0.342	0.7334	0.56566
8	East African Coastal Forests	34	0.3431	0.7279	0.56299
124	Namib-Karoo-Kaokoveld Deserts	290	0.3316	0.722	0.55469
101	Pantanal Flooded Savannas	54	0.3056	0.7153	0.53971
64	Eastern Australia Temperate Forests	204	0.2492	0.75	0.53537
82	Canadian Boreal Taiga	1097	0.232	0.745	0.52514
37	Greater Antillean Moist Forests	29	0.1954	0.7457	0.50986
35	Cardamom Mountains Moist Forests	15	0.1111	0.7	0.44761

TABLE 6.

Ecoregions that were unusually vulnerable or stable in comparison to random selections that had the same collection of biome types. The direction of change (either stable or vulnerable) was the same for the two global vegetation models, and the average (two-tailed) test of significance between the ecoregion and random set was P < 0.1 for both models. Calculations were under a broad biome definition (10 biome types).

			BIOME3 (N=6)			MAPSS (N=8)		
Ecoregion ID	Ecoregion name	Number of pixels	Obs. prop. biome change	Exp. prop. biome change	P[1]	Obs. prop. biome change	Exp. prop. biome change	P[1]
Vulnerable								
109	Central Andean Dry Puna	108	0.5494	0.4145	0	0.6471	0.4969	0.1
96	Daurian Steppe	515	0.5556	0.3408	0	0.5182	0.4091	0
83	Ural Mountains Taiga	114	0.598	0.4116	0	0.9024	0.4979	0
114	Canadian Low Arctic Tundra	607	0.7482	0.4445	0	0.7688	0.5741	0
Stable								
88	Central and Eastern Miombo Woodlands	620	0.0831	0.1991	0	0.1659	0.3004	0
76	Valdivian Temp. Rain Forests / Juan Fern. Is.	102	0.2108	0.4397	0	0.1154	0.402	0
69	Appalachian and Mixed Mesophytic Forests	146	0	0.1252	0	0.0428	0.362	0

[1] Probability from two-tailed bootstrap test.

TABLE 7.

Ecoregions that were unusually vulnerable or stable in comparison to random selections that had the same collection of biome types. The average direction of change (either stable or vulnerable) was the same for the two global vegetation models and the average (two-tailed) test of significance between the ecoregion and random set was P < 0.1 for both models. Calculations were under a narrow biome definition (18 biome types for BIOME3; 45 for MAPSS).

			BIOME3 (N=6)			MAPSS (N=8)		
Ecoregion ID	Ecoregion name	Number of pixels	Obs. prop. biome change	Exp. prop. biome change	P[1]	Obs. prop. biome change	Exp. prop. biome change	P[1]
Vulnerable								
83	Ural Mountains Taiga	114	0.6024	0.4515	0.1	0.909	0.503	0
109	Central Andean Dry Puna	108	0.591	0.4564	0	0.8102	0.6132	0
114	Canadian Low Arctic Tundra	607	0.7482	0.4745	0	0.7688	0.5738	0
Stable								
76	Valdivian Temp. Rain Forests / Juan Fern. Is.	102	0.2255	0.4584	0	0.3822	0.5998	0

[1] Probability from two-tailed bootstrap test.

TABLE 8.

Ecoregions that had unusually high average migration rates (> 750 m/yr for both BIOME3 and MAPSS) under a broad biome definition (10 biome types).

			AVERAGE MIGRATION RATE (M/YR)		
Ecoregion ID	Ecoregion name	Number of pixels	BIOME3 (n = 6)	MAPPS (n = 8)	Weighted average
84	East Siberian Taiga	2656	3310.3	898.64	1932.21
72	Pacific Temperate Rain Forests	138	1663.1	1929.62	1815.4
114	Canadian Low Arctic Tundra	607	1638.93	1609.18	1621.93
81	Muskwa/Slave Lake Boreal Forests	339	1586.7	1067.71	1290.13
83	Ural Mountains Taiga	114	793.05	1554.74	1228.3
119	Southwestern Australia Forests and Scrub	190	1290.39	1052.61	1154.52
116	Taimyr and Russian Coastal Tundra	1227	1281.8	995.08	1117.96

TABLE 9.

Ecoregions that had unusually high average migration rates (> 750 m/yr for both BIOME3 and MAPSS) under a narrow biome definition (18 biome types for BIOME3; 45 for MAPSS).

			AVERAGE MIGRATION RATE (M/YR)		
Ecoregion ID	Ecoregion name	Number of pixels	BIOME3 (n = 6)	MAPPS (n = 8)	Weighted average
90	Northern Australia and Trans-Fly Savannas	385	5959.67	929.28	3085.16
121	California Chaparral & Woodlands	55	1092.33	4001.13	2754.5
72	Pacific Temperate Rain Forests	138	2190.18	2806.32	2542.26
119	Southwestern Australia Forests & Scrub	190	1693.11	2811.06	2331.94
84	East Siberian Taiga	2656	3310.31	900.22	1933.12
33	Eastern Deccan Plateau Moist Forests	119	3026.07	1020.89	1880.25
83	Ural Mountains Taiga	114	794.85	2534.12	1788.72
118	Fynbos	31	1038.29	2121.06	1657.02
114	Canadian Low Arctic Tundra	607	1642.44	1609.18	1623.43
81	Muskwa/Slave Lake Boreal Forests	339	2279.66	1084.05	1596.45
55	Chhota-Nagpur Dry Forests	41	2648.53	790.9	1587.03
96	Daurian Steppe	515	1517.29	1330.54	1410.58
82	Canadian Boreal Taiga	1097	848.25	1540.18	1243.64
68	Western Himalayan Temperate Forests	32	998.72	1392.78	1223.9
54	Indochina Dry Forests	146	1604.18	880.25	1190.51
105	Drakensberg Montane Shrub. & Woodlands	72	1258.6	1101.09	1168.59
8	East African Coastal Forests	34	834.53	1401.34	1158.42
116	Taimyr & Russian Coastal Tundra	1227	1288.07	995.08	1120.65
29	Kayah-Karen/Tenasserim Moist Forests	74	1380.77	864.79	1085.92
128	Carnavon Xeric Scrub	95	758.47	1241.3	1034.37
88	Central & Eastern Miombo Woodlands	620	812.17	1152.75	1006.79
79	Altai-Sayan Montane Forests	441	808.51	1129.47	991.92
92	Llanos Savannas	130	992.63	782.7	872.67
125	Madagascar Spiny Thicket	41	794.74	914.51	863.18
93	Cerrado Woodlands & Savannas	645	905.9	822.64	858.32
98	Zambezian Flooded Savannas	58	799.65	770.42	782.95

Acknowledgements

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1   MAPSS and BIOME3 were run under the two Hadley Centre scenarios, whereas only BIOME3 was run under the Max Plank Institute for Meteorology (MPI) scenario and only MAPSS was run under the Geophyical Fluid Dynamics Laboratory (GFDL), Goddard Institute for Space Studies (GISS), Oregon State University (OSU), and the United Kingdom Meteorological Office (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 Vegetation/Ecosystem Modeling and Analysis Project (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).

2   The older general circulation models used simple mixed layer oceans to simulate equilibrium climate under 2 times CO_2 forcing and included models from GISS, GFDL-R30, OSU, and UKMO. Of newer (transient) models included, two were from the U.K. Hadley Centre (HADCM2GHG and HADGCM2SUL) and one from the Max Plank 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 0.5 degree 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 (MPI) climate average was extracted from the current period (1961-1990) and the period approximating 2 x CO_2 forcing (2070-2099). Neilson et al. (1998) used a similar set of models to investigate global changes in biome area, leaf area index, and runoff.

3   Because we did not have any prior expectation as to whether the ecoregion value would be larger or smaller than the random value, we calculated two-tailed tests of the hypothesis.

4   In both distance calculation methods, distances between cell centers 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).

5   If the logarithm of species richness is plotted against the logarithm of area, a more-or-less linear relationship is typically observed. 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.

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