REVIEW: BIODIVERSITY

Global Biodiversity Scenarios for the Year 2100

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Scenarios of changes in biodiversity for the year 2100 can now be developed based on scenarios of changes in atmospheric carbon dioxide, climate, vegetation, and land use and the known sensitivity of biodiversity to these changes. This study identified a ranking of the importance of drivers of change, a ranking of the biomes with respect to expected changes, and the major sources of uncertainties. For terrestrial ecosystems, land-use change probably will have the largest effect, followed by climate change, nitrogen deposition, biotic exchange, and elevated carbon dioxide concentration. For freshwater ecosystems, biotic exchange is much more important. Mediterranean climate and grassland ecosystems likely will experience the greatest proportional change in biodiversity because of the substantial influence of all drivers of biodiversity change. Northern temperate ecosystems are estimated to experience the least biodiversity change because major land-use change has already occurred. Plausible changes in biodiversity in other biomes depend on interactions among the causes of biodiversity change. These interactions represent one of the largest uncertainties in projections of future biodiversity change.

Global biodiversity is changing at an unprecedented rate (*1, 2*) as a complex response to several human-induced changes in the global environment (*3*). The magnitude of this change is so large (*1*) and so strongly linked to ecosystem processes (*4, 5*) and society's use of natural resources (*6, 7*) that biodiversity change is now considered an important global change in its own right (*8*). In our definition of biodiversity, we include all terrestrial and freshwater organisms—including plants, animals, and microbes—at scales ranging from genetic diversity within populations, to species diversity, to community diversity across landscapes. Our definition excludes exotic organisms that have been introduced and communities such as agricultural fields that are maintained by regular human intervention. We do not consider marine systems in this study.

International conventions seek to minimize changes in biodiversity, just as other conventions seek to reduce the atmospheric concentration of CO_2 and chlorofluorocarbons. Scientists and policy-makers are familiar with, and frequently use, scenarios of change in climate or of concentrations of greenhouse gases in projecting the future state of the global environment (*9*). Although biodiversity changes are just as important for the functioning of ecosystems and the well-being of humans, there are currently no scenarios for biodiversity comparable to those of climate and greenhouse gases. Previous exercises have assessed extinction threats as a function of human land use at the global and regional levels (*10, 11*).

Modeling Biodiversity Change

We developed global scenarios of biodiversity change in 10 terrestrial biomes and in freshwater ecosystems for the year 2100 based on global scenarios of changes in environment and land use and the understanding by ecological experts of the sensitivity of biodiversity in each terrestrial biome to these global changes. First, we identified the five most important determinants of changes in biodiversity at the global scale: changes in land use, atmospheric CO_2 concentration, nitrogen deposition and acid rain, climate, and biotic exchanges (deliberate or accidental introduction of plants and animals to an ecosystem). Second, we calculated the expected change of these drivers in each biome. Third, we estimated for each biome the impact that a unit change in each driver has on biodiversity. Finally, we derived three scenarios of future biodiversity for each biome, relative to its initial diversity, based on alternative assumptions about interactions among the drivers of biodiversity change. We assumed that (i) there are no interactions among the various causes of biodiversity change, (ii) there are antagonistic interactions and biodiversity will respond only to the driver to which it is most sensitive, or (iii) there are synergistic interactions and biodiversity will respond multiplicatively to the drivers of biodiversity change. Because the nature of interactions among causes of biodiversity change is poorly known, we present all three alternatives as plausible scenarios of biodiversity change.

Drivers of Change

We used a business-as-usual scenario generated by global models of climate (Had CM2), vegetation (Biome3) (*12*), and land use [A1 scenario of Image 2 (*13*)] to estimate the change in magnitude of the drivers of biodiversity change for each biome between 1990 and the year 2100. Our 10 terrestrial biomes resulted from aggregating the original Bailey ecoregions (*14*). We ranked the projected changes in drivers as small (value of 1) to large (value of 5). We used the A1 scenario of the IMAGE model to estimate changes in land use for each biome (*13*). The IMAGE model projects that most land-use change will continue to occur in the tropical forests and in the temperate forests of South America and that the least land-use change will occur in the arctic and alpine (where human population density probably will remain low) and in northern temperate forests (where reforestation is expected to exceed deforestation, also causing small negative effects on biodiversity) (Table 1). The extent of habitat modification is projected to be modest in desert and boreal forest and intermediate in savannas, grasslands, and Mediterranean ecosystems. Atmospheric CO_2 mixes globally within a

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year (*15*), so we assumed that all biomes would experience the same change in CO_2 concentration. Nitrogen deposition is largest in the northern temperate zone near cities and is smallest in biomes such as the arctic and southern temperate forests, which generally are distant from sources of pollution. Other biomes are intermediate, with regional variation in deposition generally associated with cities or industrial point sources. Climate is expected to warm most dramatically at high latitudes (arctic and boreal zones), to change least in the tropics, and to show intermediate changes in other biomes (*9*) (Table 1). Changes in precipitation are uncertain and are difficult to generalize at the biome level. The pattern of biotic exchange reflects the pattern of human activity. Remote areas with little human intervention receive fewer exotic species than areas that are in the middle of trade routes or that host intense human activity (*16*).

The second step of our exercise was to evaluate, for each biome, the impact that a unit change in each driver has on biodiversity independently of the expected magnitude of change in the driver (Table 2). Land-use change is the most severe driver of changes in biodiversity (*17*). For example, conversion of temperate grasslands into croplands or tropical forests into grasslands results in local extinction of most plant species and the associated animals whose habitat is largely determined by plant species composition. Below-ground organisms are also affected most severely by land-use change (*18*). We assumed no differences among biomes in the response to a unit change in land use and we assigned land use the maximum impact factor because of the consistently large effect of land-use change on biodiversity. The increase in atmospheric CO_2 is expected to have the largest effect on biodiversity in those biomes where plant growth is most limited by water availability and where there is a mixture of C_3 and C_4 species because of known species differences in the effect of CO_2 on water-use efficiency (*19, 20*). For example, changes in atmospheric CO_2 may change the competitive balance between species that differ in rooting depth, photosynthetic pathway, or woodiness as well as associated below-ground organisms (*21*). Therefore, we assigned the maximum impact factor of elevated CO_2 to grasslands and savannas, which are water-limited biomes with a mixture of contrasting plant functional types. Based on the same reasoning, we assigned the smallest impact factors to arctic, alpine, boreal forest, tropical forest, and freshwater ecosystems.

Increased nitrogen deposition should have the largest impact on biodiversity in those biomes that are most nitrogen-limited primarily by giving a competitive advantage to plant species with high maximum growth rates, which then exclude the slower growing species (*22*). Consequently, we assigned the largest impact factor to temperate forests, boreal forests, arctic, and alpine. Biodiversity in deserts and tropical forests may respond least to nitrogen deposition because plant growth is strongly limited by water and phosphorus, respectively (*23*). Grasslands, savannas, and Mediterranean systems received intermediate impact factors because nitrogen and other factors limit plant growth.

A given change in climate is expected to have the largest proportional effect on biodiversity in those biomes characteristic of extreme climates, although biodiversity in all biomes likely will be sensitive to climate. Small changes in temperature or precipitation in arctic, alpine, desert, and boreal forest will result in large changes in species composition and biodiversity. Similarly, we assume that biomes where climate less strongly limits the activity of organisms will experience changes in the distribution of organisms, but the overall effect on proportional change in diversity may be less pronounced than in extreme environments.

Biotic introductions (that is, successful establishment of exotic species) vary according to environmental conditions and biogeographic considerations. Invasions have occurred least frequently in arctic and alpine ecosystems, because of their severe environment (*24*) and the broad longitudinal distribution of much of the high-latitude flora and fauna. In the tropics, we also expect a small proportional change in the diversity of intact ecosystems because of the high initial diversity and because abiotic and biotic factors characteristic of this biome, including its high diversity, minimize the probability of successful establishment by invaders in undisturbed communities (*25*). Conversely, we expect the greatest effect of biotic exchange in biomes such as Mediterranean and southern temperate forests that have long been isolated and exhibit extensive convergent evolution (*26*). Other biomes are intermediate in their connectedness. There is wide variation within most biomes in the successful establishment of biotic introductions, depending on the original diversity and isolation from similar habitats. For example, islands typically have low diversity and are more prone to biotic invasions (*27*).

When averaged across biomes, land-use change is the driver that is expected to have the largest global impact on biodiversity by the year 2100 (Fig. 1), mostly because of its devastating effects on habitat availability and consequent species extinctions. Climate change will be the second most important driver of biodiversity change, mostly as a result of the expected warming at high latitudes. Changes in atmospheric CO_2, biotic exchange, and nitrogen deposition also will have substantial effects on future biodiversity, with the relative importance being regionally variable. Variability among biomes of the impact of the different drivers is maximal for land use, reflecting the broad range of expected changes in this driver and the large sensitivity of all biomes to land-use change. In contrast, atmospheric CO_2 showed the smallest variability of the three drivers because CO_2 is well mixed in the atmosphere

Table 1. Expected changes for the year 2100 in the five major drivers of biodiversity change (land use, atmospheric composition CO_2, nitrogen deposition, climate, and biotic exchange) for the principal terrestrial biomes of the Earth (arctic tundra, alpine tundra, boreal forest, grasslands, savannas, Mediterranean ecosystems, deserts, northern temperate forests, southern temperate forests, and tropical forests).

	Arctic	Alpine	Boreal	Grass-land	Sa-vanna	Med	Desert	N temp	S temp	Tropic
Land use	1.0	1.0	2.0	3.0	3.0	3.0	2.0	1.0	4.0	5.0
Climate	5.0	3.0	4.0	2.0	2.0	2.0	2.0	2.0	2.0	1.0
Nitrogen deposition	1.0	3.0	3.0	3.0	2.0	3.0	2.0	5.0	1.0	2.0
Biotic exchange	1.0	1.0	2.0	3.0	3.0	5.0	3.0	3.0	2.0	2.0
Atmospheric CO_2	2.5	2.5	2.5	2.5	2.5	2.5	2.5	2.5	2.5	2.5

Table 2. Impact of a large change in each driver on the biodiversity of each biome. In this exercise, a unit change of the driver was defined for land use as conversion of 50% of land area to agriculture, for CO_2 as a 2.5-fold increase in elevated CO_2 as projected by 2100, for nitrogen deposition as 20 kg ha^{-1} $year^{-1}$, for climate as a 4°C change or 30% change in precipitation, and for biotic exchange as the arrival of 200 new plant or animal species by 2100. Estimates vary from low (1) to high (5) and result from existing global scenarios of the physical environment and knowledge from experts in each biome (see text).

	Arctic	Alpine	Boreal	Grass-land	Sa-vanna	Med	Desert	N temp	S temp	Tropic
Land use	5.0	5.0	5.0	5.0	5.0	5.0	5.0	5.0	5.0	5.0
Climate	4.0	4.0	3.5	3.0	3.0	3.0	4.0	2.0	2.0	3.0
Nitrogen deposition	3.0	3.0	3.0	2.0	2.0	2.0	1.0	3.0	3.0	1.0
Biotic exchange	1.0	1.0	1.0	2.0	2.0	3.0	2.0	1.5	3.0	1.5
Atmospheric CO_2	1.0	1.0	1.0	3.0	3.0	2.0	2.0	1.5	1.5	1.0

and the range of ecological responses is quite narrow. The other drivers have intermediate variability. In this global analysis, we consider only proportional changes in diversity and give no weighting to the area, initial species diversity, or economic value of biomes.

We performed a simple sensitivity analysis (*28*) of our model by independently increasing and then decreasing by 10% the expected change of each driver. The ranking of drivers (Fig. 1) was not altered in any of the trials in which we increased the expected change of each driver. When we decreased each driver by 10%, in only one trial was the ranking altered: nitrogen deposition switched positions with biotic exchange. These results suggest that modifications of the parameters in ±10% will not modify the result of this exercise with regard to the ranking of drivers. The ranking of relative impact of global-change drivers on biodiversity is relatively insensitive to small changes in drivers because our model assumes no nonlinearities or bifurcations. Our scenarios result from multiplication of the expected changes and biome-sensitivity matrices (Tables 1 and 2) and the linear combination of their product to construct the ranking of drivers and the different scenarios.

Variation Across Biomes

There are large differences among biomes in the causes of future change in biodiversity (Fig. 2). Biomes such as tropical and southern temperate forest show large changes, mostly due to changes in land use with relatively small effects due to other drivers. Arctic ecosystems are also influenced largely by a single factor (climate change). In contrast, Mediterranean ecosystems, savannas, and grasslands are substantially affected by most drivers. Finally, biomes such as the northern temperate forests and deserts show contributions by all the drivers but most of them are moderate.

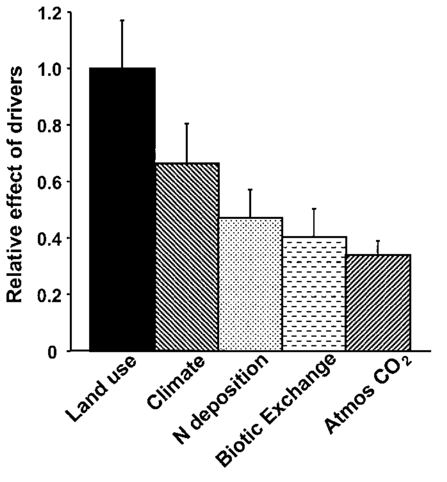

Fig. 1. Relative effect of major drivers of changes on biodiversity. Expected biodiversity change for each biome for the year 2100 was calculated as the product of the expected change in drivers times the impact of each driver on biodiversity for each biome. Values are averages of the estimates for each biome and they are made relative to the maximum change, which resulted from change in land use. Thin bars are standard errors and represent variability among biomes.

Freshwater ecosystems show substantial impacts from land use, biotic exchange, and climate (Fig. 2). Land use is expected to have especially large effects because humans live disproportionately near waterways and extensively modify riparian zones even in terrestrial biomes that otherwise are sparsely populated. This leads to many changes within the waterways, including increased inputs of nutrients, sediments, and contaminants (*29*). In addition, humans use waterways as transportation corridors, sewage disposal sites, and water sources, so that much of Earth's accessible freshwaters are already coopted by humans (*30*). Biotic exchange, in particular, is relatively more important for aquatic (especially lakes) than for terrestrial ecosystems because of both extensive intentional (for example, fish stocking) and unintentional (for example, ballast water releases) releases of organisms (*31*). Carbon dioxide and nitrogen deposition generally had less impact on lakes and streams than on terrestrial ecosystems, but acidic deposition (partly attributable to nitrogen deposition) and its interactions with climate change, land use, and stratospheric ozone depletion are large—especially for boreal lakes (*32*). Recent analyses suggest that, as a result of all these impacts, global freshwater biodiversity is declining at far greater rates than is true for even the most affected terrestrial ecosystems (*33*).

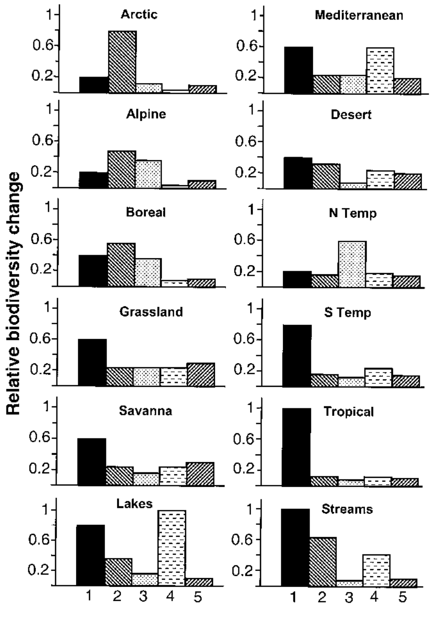

Fig. 2. Effect of each driver on biodiversity change for each terrestrial biome and freshwater ecosystem type calculated as the product of the expected change of each driver times its impact for each terrestrial biome or freshwater ecosystem. Expected changes and impacts are specific to each biome or ecosystem type and are presented in Tables 1 to 4. Values are relative to the maximum possible value. Bars: 1, land use; 2, climate; 3, nitrogen deposition; 4, biotic exchange; 5, atmospheric CO_2.

For streams, variation in expected impact exists along a latitudinal gradient from tropical to temperate to high latitude/altitude regions. In tropical streams, land use is expected to have the greatest effect, with climate and biotic exchange being minimal. In temperate streams, biodiversity will be similarly affected by both land-use change (*34*) and biotic exchange (*35*), which reaches its maximum impact value in this region. In high latitude/altitude streams, climate change is the dominant driver and it is expected to cause the greatest change in biodiversity (*36*), with land use and biotic exchange being minimal. Biodiversity in streams and rivers generally is more sensitive to climate than in lakes because streams have greater responsiveness to runoff; generally, it is less sensitive to biotic exchange because streams are physically harsh and more dynamic temporally (*37*).

To estimate the total change in biodiversity for each terrestrial biome, we provide three alternative scenarios of biodiversity based on the assumptions of no interactions, antagonistic interactions, or synergistic interactions among causes of biodiversity change. In all scenarios, we project that grasslands and Mediterranean ecosystems will experience large biodiversity loss because of their sensitivity to all drivers of biodiversity change, particularly land-use change (Figs. 2 and 3). We did not generate these scenarios

Table 3. Expected changes for the year 2100 in the major drivers of biodiversity change for lakes and streams.

	Lakes	Streams
Land use	4.0	5.0
Climate	3.0	4.0
Nitrogen deposition	2.0	2.0
Biotic exchange	5.0	3.5
Atmospheric CO_2	2.5	2.5

Table 4. Impact of a large change in each driver on the biodiversity of each major freshwater-ecosystem type. Methods and assumptions are the same as in Tables 1 and 2.

	Lakes	Streams
Land use	5.0	5.0
Climate	3.0	4.0
Nitrogen deposition	2.0	1.0
Biotic exchange	5.0	3.0
Atmospheric CO_2	1.0	1.0

for freshwater ecosystems because they are distributed throughout all terrestrial biomes. Projected biodiversity changes in other terrestrial biomes differ dramatically among our three scenarios.

If we assume that diversity will respond to global changes, without any interaction among these drivers of change, we project that Mediterranean and grassland ecosystems will be most sensitive to change (Figs. 2 and 3A). In contrast, arctic, alpine, and desert ecosystems will show only moderate changes in biodiversity for reasons that are specific to each biome. The range of changes among biomes projected by this scenario is relatively small, with the changes in all biomes being within 60% of the maximum change.

If we assume that diversity in each biome will be determined only by the factor that has the greatest impact on diversity, then we project that tropical and southern temperate forests will experience substantial changes in diversity due to land-use change and the arctic will experience change due to climate change (Figs. 2 and 3B). In this scenario, deserts and alpine will show the fewest diversity changes, because there is no single driver to which biodiversity in these biomes is extremely sensitive.

If there are synergistic interactions among all causes of biodiversity change, we project that Mediterranean and grassland ecosystems will experience the greatest biodiversity change because diversity in these biomes is sensitive to all global-change drivers (Figs. 2 and 3C). In this scenario, tropical forest, arctic, and alpine ecosystems will show the fewest biodiversity changes, because there are several drivers of change to which these biomes are relatively insensitive. In contrast to the no-interaction scenario, in this case the range of expected change is quite broad, encompassing two orders of magnitude, because of the effect of synergistic interactions on amplifying differences among biomes.

Uncertainties

This analysis highlights the sensitivity of biodiversity change to our assumptions about interactions among causes of biodiversity change. Which assumptions are most plausible? There is clear evidence for nonlinearities and synergistic interactions among many of the global change drivers. Invasions of exotic species are promoted by human disturbance and changes in climate variability (interaction of biotic exchange, land-use change, and climate change). Elevated CO_2 has the greatest effect on species composition in the presence of nitrogen deposition (interaction of CO_2 and nitrogen deposition). Synergistic interactions may decrease in importance at extreme values of individual drivers of biodiversity change. For example, where land use has been severe and extensive such as in forest clearing followed by seeding of an exotic crop species, further damage to biodiversity by other drivers may not be possible. In such cases, biodiversity change responds only to the driver with the greatest impact. The strength of interactions among drivers in their effects on biodiversity is virtually unknown.

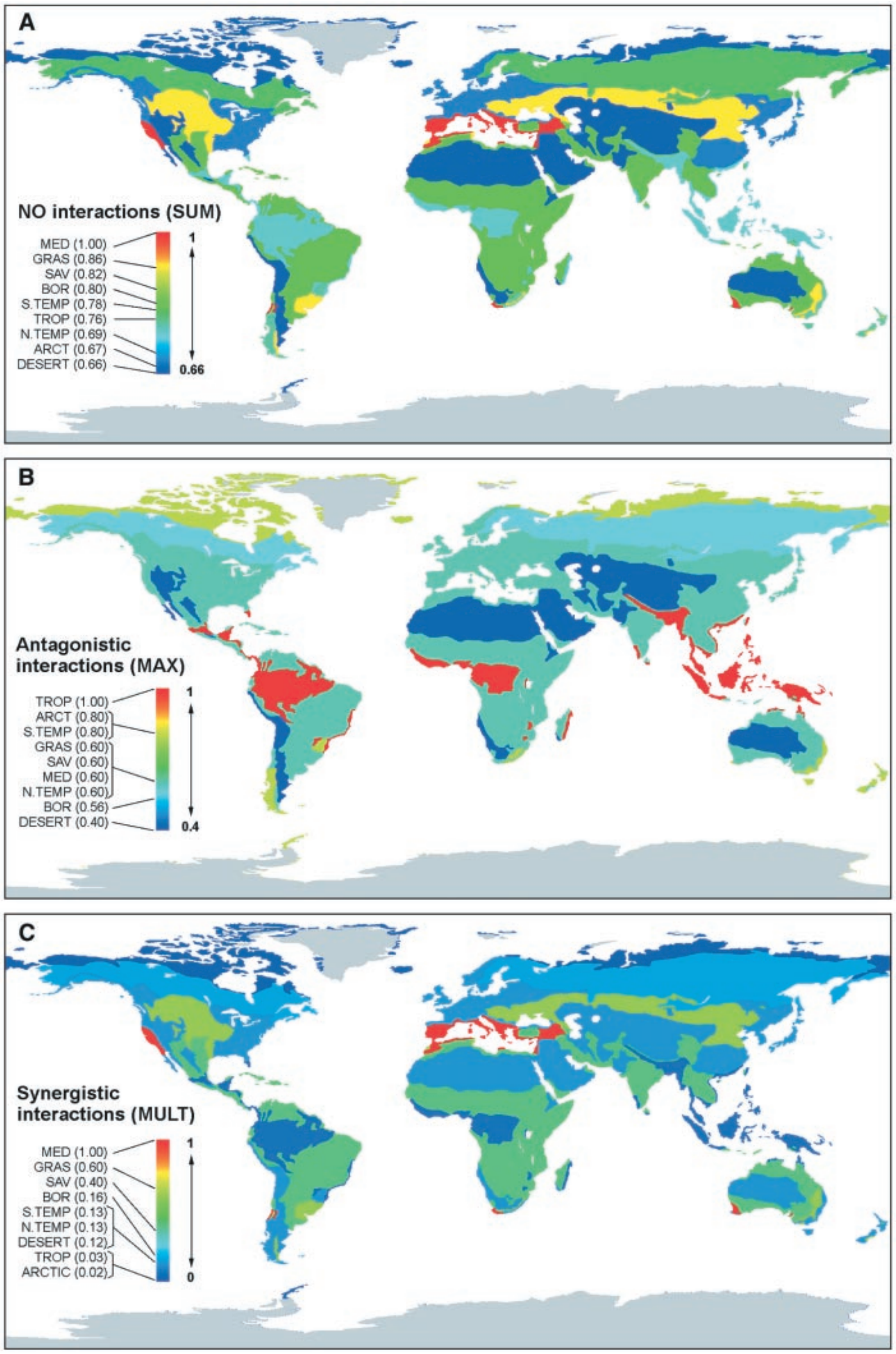

Fig. 3. Maps of three scenarios of the expected change in biodiversity for the year 2100. (**A**) There are no interactions among drivers of biodiversity change; consequently, total change is calculated as the sum of the effects of each driver, which in turn result from multiplying the expected change in the driver for a particular biome (Table 1) times the impact of the driver, which is also a biome-specific characteristic (Table 2). (**B**) Total biodiversity change equals the change resulting from the driver that is expected to have the largest effect and is calculated as the maximum of the effects of all the drivers. (**C**) Interactions among the drivers are synergistic; consequently, total change is calculated as the product of the changes resulting from the action of each driver. Different colors represent expected change in biodiversity from moderate to maximum for the different biomes of the world ranked according to total expected change. Numbers in parentheses represent total change in biodiversity relative to the maximum value projected for each scenario. Biomes are Mediterranean ecosystems (MED), grasslands (GRAS), savannas (SAV), boreal forest (BOR), southern temperate forest (S.TEMP), tropical forest (TROP), northern temperate forest (N.TEMP), arctic ecosystems (ARCT), and desert (DESERT). Values for alpine, stream, and lake ecosystems are not shown.

We hypothesize that future changes in biodiversity will be intermediate between scenarios that consider synergistic interactions or no interactions, but realistic projections of future biodiversity change require improved understanding about interactions among drivers of biodiversity change.

Other uncertainties in our analysis include the magnitude and regional variation in the future changes in drivers, as thoroughly analyzed by Intergovernmental Panel on Climate Change (*38*). This reflects future policies governing (i) the intensity and aerial extent of land-use change, (ii) the protection of biodiversity per unit of land-use change, and (iii) changes in atmospheric composition. Uncertainties in future climate and vegetation reflect the same policy uncertainties (*38*). As a result of the large policy-related uncertainties in drivers, we emphasize that we have presented scenarios rather than predictions of biodiversity change.

We expect large regional variation in biodiversity change within each biome. For example, diversity in islands, lakes, and some streams is particularly vulnerable to biotic exchange because geographic isolation has led to local adaptation and, in the case of islands, often a low biodiversity (*27, 31*). Hot spots of diversity such as riparian corridors and coastal land margins often coincide with hot spots of development, leading to large biodiversity loss. Within-biome variation in climate may cause the greatest biodiversity change near climatically determined boundaries of organism distribution. Other specific local patterns of biodiversity change are less predictable than general trends at larger scales and may reflect interactions among drivers of biodiversity change that are locally important or a consequence of local "surprises." An initial analysis of the causes of regional variation in diversity loss within each biome is being published separately (*39*).

Biodiversity in all biomes is sensitive to global changes in environment and land use and realistic projections of biodiversity change will require an integrated effort by climatologists, ecologists, social scientists, and policy makers to improve scenarios of future changes in the Earth system. This analysis represents an attempt to develop future global biodiversity scenarios. Refinement of these scenarios to the point that they are useful to policy-makers will require quantitative regional analyses and a study of the interactions among factors to which local biodiversity is most sensitive. Mitigation of the expected effects on biodiversity identified in this study should encompass both reduction of the rate of change of the drivers at the global scale and development of management practices specifically tailored for each region according to its biological, social, and economic characteristics.

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