# 15. Potential Biodiversity Change: Global Patterns and Biome Comparisons

Osvaldo E. Sala, F. Stuart Chapin III, and Elisabeth Huber-Sannwald

The purpose of the exercise reported in this book was to develop biodiversity scenarios for the year 2100. The scenarios focused on 10 terrestrial biomes and freshwater ecosystems, and were based on global scenarios of changes in the environment and current understanding about the specific biome sensitivity to global change. The first step was to identify the major drivers of biodiversity change at the global scale: changes in land use, climate, N deposition, biotic exchange (the deliberate or accidental introduction of species into an ecosystem), and atmospheric CO2. Chapters 2 and 3 described these global patterns and the models used to predict their changes for the year 2100. Next, we estimated the magnitude of change in drivers for each biome. Finally, we estimated the sensitivity of each biome to a unit change in the drivers. The expected change in biodiversity due to each driver for each biome resulted from multiplying the expected change in each driver times the sensitivity to a unit change in driver. For each biome, Chapters 4 to 14 described the general patterns of biodiversity, the expected changes in drivers, the sensitivity to changes in drivers, and the expected patterns of biodiversity change. A first attempt at synthesizing this effort of developing global biodiversity scenarios has been published (Sala et al. 2000). This final chapter synthesizes the detailed information presented in each chapter highlights similarities and differences among biomes, and develops the global biodiversity scenarios. First, we describe broadly the patterns of biodiversity and the location of high-diversity areas within each biome. Second, we develop global scenarios of biodiversity change by combining the biome-specific information into a common framework.

#### Within-Biome Patterns of Biodiversity

The biological diversity of a biome is determined by the regional matrix of biodiversity and by centers of high species diversity, which contribute substantially to the overall biodiversity of a biome. The causes of diversity patterns differ among biomes depending on the relative importance of long-term geographic isolation, rapid evolutionary change, habitat diversity, and human-induced and natural causes of extinctions. In some areas the elimination of dominant species may be compensated by species from the high-biodiversity areas; however, loss of diversity will be substantial in situations where human impact is focused in these areas. Where is biodiversity concentrated in each biome?

In arctic and alpine tundra, high-biodiversity areas occur in favorable sites with relatively warm temperatures (e.g., steep slopes facing toward the equator or at low altitudes and latitudes). The highly fragmented and isolated locations of alpine sites contribute to the significant proportion of rare and endemic species. Endemism is especially high in the European Alps, as well as in parts of the southern hemisphere and Himalayan alpine region. Both global warming and land-use change will strongly affect the local (mainly in the alpine) and regional (mainly in the arctic) diversity of the tundra.

In the *boreal forest*, the prime diversity areas include early-successional riparian floodplains and decaying logs in late-successional forests. The latter support a rich beetle fauna associated with wood decay and a rich flora of mosses and lichens. The floodplains support many migratory tropical birds. In the Scandinavian countries, a high proportion of the beetle species is threatened due to a long history of extensive forest harvest. Overall, there are relatively few endemic species in the boreal zone.

The savanna biome is species-rich due to its long evolutionary history without major glaciation events, allowing many taxa to co-evolve and co-exist in space and time. The large interannual variability in climate contributes to the diversity of life forms in savannas. Characteristic high-diversity areas within this biome are wetlands and riparian habitats, which provide favorable resource-rich conditions. In addition, there are rocky outcrops and ephemeral hydromorphic vegetation types that harbor specialists with narrow ecological requirements.

The five mediterranean-climate regions of the globe all have high species richness, due in part to their long complex evolutionary history without glaciation events. In addition, early human intervention created a heterogeneous fine-grained pattern of many different land-use practices. Especially in the Mediterranean Basin, a complex mainland and insular geography and a

high topographic variation resulted in unusually high landscape-scale diversity that explains the high level of floristic diversity and endemism in Europe.

The extreme environment of the *desert* has led to the evolution of high species diversity with a wealth of unique adaptations. The geomorphology and topographic diversity create diverse local moisture patterns and microhabitats that allow a multitude of animal and plant species to co-exist. In addition, mobile sand dunes and unique parent materials support areas of unusually high diversity of plants and animals.

Diversity varies enormously among grassland types, with many native grasslands such as the grasslands of the Pampas and the tallgrass prairie having levels of plant diversity as high as those typical of tropical forests, whereas others (e.g., the Patagonian grasslands) have less than 30 species of plants. Levels of plant-species diversity in grasslands are not associated with levels of diversity within other taxa. Grasslands that have high plant-species diversity may have low mammal diversity, but high bird diversity.

Temperate forests of the two hemispheres support a striking diversity in tree species, life form, structure, and function spanning a wide range of climate, geology, and evolutionary histories. Latitudinal and regional patterns in seasonality of temperature and rainfall determine the physiognomic diversity of these forests. The southern hemisphere has particularly high concentrations of endemism.

Tropical forests have particularly high species density. They support 14 of the 18 recognized global areas of highest endemism. Tropical forests also support a diversity of life forms and life histories.

Diversity in *lakes* develops during periods of geographic isolation from other water bodies, particularly in arid environments. In ancient lakes, speciation events are relatively frequent, contributing to high levels of endemism. The biodiversity of *streams* varies regionally, due to differences in history, temperature, hydrology, and geomorphology. The tropical freshwaters are a major reservoir of global fish diversity, whereas North American streams and rivers support the richest freshwater fish fauna of moist temperate regions.

## Global Biodiversity Scenarios for the Year 2100

### The Approach

The task of combining the effects of different drivers on the biodiversity change of different biomes required a common framework. Global models of environmental change express their output in different units [e.g., squared kilometers of land-use change or parts per million (ppm) of CO<sub>2</sub> in the atmosphere]. In addition, biomes differ substantially in current levels of species diversity. We used a business-as-usual scenario generated by global models of climate (Had CM2), potential vegetation (Biome 3) (Haxeltine and Prentice 1996), and land use (Scenario A from the Image 2 model) (Alcamo

1994) to estimate the change in the magnitude of the drivers of biodiversity change for each biome. We ranked the projected changes in drivers from small (value of 1) to large (value of 5) (Table 15.1A). The locations of the 10 biomes selected for this exercise were determined by aggregating the Bailey ecoregions (Bailey 1998).

The next step of the exercise was to estimate, for each biome, the impact that a unit change in each driver has on biodiversity independent of the expected change of the driver (Table 15.1B). As in the approach used to compare expected changes in drivers, we ranked the sensitivity of each biome to a unit change in driver from small (value of 1) to large (value of 5). We calculated the expected change in biodiversity due to the effect of one driver as the product of the expected change times the sensitivity.

Finally, to calculate the total change in biodiversity for each biome, we developed three different scenarios based on different assumptions regarding interactions among the drivers of biodiversity change. The first scenario was based on the assumption that there were no interactions among drivers; consequently, total biodiversity change, for each biome, was calculated as the sum of the effects of each driver. The second scenario was based on the assumption that there were antagonistic interactions among drivers; thus, the driver with the largest effect overshadowed the effects of the other drivers. In the antagonistic-interactions scenario, the biodiversity change of the biome was equal to the effect of the driver with maximum value. The third scenario assumed that there were synergistic interactions among drivers and that the effects on biodiversity of several drivers was larger than the sum of the effects of those same drivers acting independently. In the synergistic-interactions scenario, we calculated the biome change in biome diversity as the product of the effects of each driver.

Our current understanding does not allow us to predict which scenario will most closely represent biodiversity change by the year 2100. Evidence suggests that each scenario is plausible under particular circumstances. For example, the sum of the independent effects on biodiversity of elevated CO<sub>2</sub> and N deposition will be much smaller than the effect of enhanced CO2 and N availability acting together (synergistic interaction). The effects of elevated CO<sub>2</sub> on several aspects of ecosystem functioning is amplified when combined with high N availability (Mooney et al. 1999). It is similarly very likely that the effect of biotic exchange on biodiversity will be enhanced if species introductions occur simultaneously with changes in land use or N availability. Other cases support the antagonistic-interactions scenarios. For example, it is unlikely that climate change or N deposition will further affect the biodiversity of tropical forest stands that have been cut, burned, and planted with a crop. We present the three scenarios as plausible alternatives for global biodiversity change because there is no clear evidence that any single scenario will best represent future patterns. Moreover, we expect that the shape of the interactions among drivers will differ among biomes, among drivers, and with the intensity of the change in drivers.

Table 15.1. (A) The expected changes for the year 2100 in the five major drivers of biodiversity change for the principal terrestrial biomes of the earth. (B) The impact of a large change in each driver on the biodiversity of each biome

	Arctic	Alpine	Boreal	Grassland Savanna	Savanna	Med.	Desert	N Temp.	S Temp.	Tropic
(A) Expected changes in drivers	nges in drive	ırs								
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	0.1
N denosition	1.0	3.0	3.0	3.0	2.0	3.0	2.0	5.0	0.1	2.0
Riotic exchange	1.0	1.0	2.0	3.0	3.0	5.0	3.0	3.0	2.0	2.0
Atmos CO <sub>2</sub>	2.5	2.5	2.5	2.5	2.5	2.5	2.5	2.5	2.5	2.5
(B) Impact of a giv	iven change on	on diversity								
Land use		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
N deposition	3.0	3.0	3.0	2.0	2.0	2.0	1.0	3.0	3.0	0.1
Biotic exchange	1.0	1.0	1.0	2.0	2.0	3.0	2.0	1.5	3.0	1.5
Atmos CO <sub>2</sub>	1.0	1.0	1.0	3.0	3.0	2.0	2.0	1.5	1.5	1.0
								,		

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, as a 2.5-fold increase in elevated CO: as projected by 2100, for N deposition as 20 kg/ha/year, for climate as a 4°C, 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).

#### The Drivers

The IMAGE 2 model projects the largest changes in land use to occur in the tropical forest and southern temperate forest biomes (Table 15.1A). In contrast, biomes located in remote areas, such as the arctic and alpine tundra, which will continue to have low human density, are expected to show the least amount of land-use change. Grasslands, savannas, and mediterranean ecosystems will exhibit intermediate levels of land-use change for reasons that are specific to each biome.

The global circulation model (GCM) used in our exercise as well as GCMs included in the most current version of IPCC (Kattenberg et al. 1996) agreed with predictions of largest changes in temperature at high latitudes; consequently, we assigned the largest change in climate to the high-latitude biomes, arctic tundra and boreal forest (Table 15.1A). In contrast, tropical forest will experience the least climate change, and other biomes will show intermediate values.

Carbon dioxide mixes globally on an annual basis (Fung et al. 1987). We therefore assumed that all biomes will experience the same change in atmospheric CO<sub>2</sub> (Table 15.1A). Patterns of nitrogen deposition vary significantly among regions, with the highest levels occurring in Eastern North America, Western Europe, and Eastern Asia associated with the intensity of industrial and urban activities (Holland et al. 1999). We assigned the highest values for N deposition to northern temperate forests and the lowest to biomes located in regions distant from industrial areas such as the arctic tundra and southern temperate forests (Table 15.1A). Biotic exchange is driven by activities such as trade and agriculture and is therefore related to the pattern of human activity. Remote areas receive fewer exotic species than areas with intense human activity (Drake et al. 1989).

#### The Biome Sensitivity

The sensitivity of biodiversity in a particular biome to changes in each driver is generally poorly documented in carefully controlled experiments. These sensitivities, however, can be estimated from general principles, from ecological patterns of species distribution along gradients, and from changes in diversity that have occurred in response to a variety of human-induced environmental changes. In assigning values of biome sensitivity to each driver, authors of each chapter reviewed the available literature for their biome and consulted widely with other ecologists familiar with that biome. We then used these literature reviews and the experience of chapter authors to develop a set of "sensitivity rankings" that were consistent across biomes.

Land-use change is the driver with the largest impact on biodiversity (Sala 1995). The impact is so large and equally negative for all biomes that we assigned land-use change the maximum value in all biomes (Table 15.1B). Land-use change affects biodiversity primarily by reducing habitat availability. For example, when an area of tropical forest is logged, burned, plowed,

and seeded with a soybean crop, most native plant species disappear, and the below-ground biota are drastically modified (Anderson 1995).

We expect that a given change in climate will have a larger effect in biomes characteristic of extreme environments (Table 15.1B). Climate change likely will affect biodiversity in all ecosystems but the rate of change per unit temperature change will be larger for the arctic, alpine tundra, and desert biomes that possess species narrowly adapted to extreme climatic conditions.

Nitrogen deposition will have the largest effect on ecosystems that are most limited by N (e.g., temperate and boreal forest) and the least effect on biomes that are most frequently limited by other factors [e.g., water availability (deserts) or phosphorus (tropical forests)] (Table 15.1B). N deposition affects biodiversity by changing N availability in the soil. Numerous studies reported a negative relationship between N additions and species diversity (Berendse and Elberse 1990; Huenneke et al. 1990; Tilman 1993). For example, fertilization with 27 gN/m²/year in a grassland, characteristic of the North American tallgrass prairie, resulted, after 11 years, in a 50% reduction in species richness (Tilman 1993). Changes in soil N will alter first the competitive balance of plant species by favoring species with high relative growth rate that can take advantage of this resource. If changes persist in time or space, they will result in local extinctions.

The vulnerability of different ecosystems to invasions is an issue of current debate and one that is attracting a significant research effort. The severity of climate is one of the factors that has been suggested as an important determinant of vulnerability to invasions, with more mesic environments being more vulnerable than xeric ecosystems (Rejmánek 1989). Experimental studies have reinforced the idea that high initial biodiversity may reduce vulnerability to invasions (Levine 2000). The same study, however, highlighted the role of other factors that may overshadow the effect of the original biodiversity level. We assigned the lowest sensitivity to biotic exchange to arctic, alpine tundra, boreal forest, and tropical forest, and the highest to mediterranean ecosystems (Table 15.1B).

The sensitivity of different biomes to elevated CO<sub>2</sub> is associated with the degree of water limitation (Mooney et al. 1991). One of the most consistent effects observed in elevated CO<sub>2</sub> experiments has been a reduction in stomatal conductance and a consequent increase in water-use efficiency (Jackson et al. 1994). We therefore assigned the highest sensitivity values to grasslands and savannas because they are water-limited ecosystems with a combination of functional groups with different rooting patterns, photosynthetic pathways, phenology, and woodiness (Table 15.1B). In contrast, we assigned the lowest sensitivity values to arctic, alpine, boreal forest, tropical forest, and freshwater ecosystems.

## Ranking of Drivers

The exercise of developing biodiversity scenarios yielded a ranking of drivers according to their expected global effect on biodiversity for the year 2100

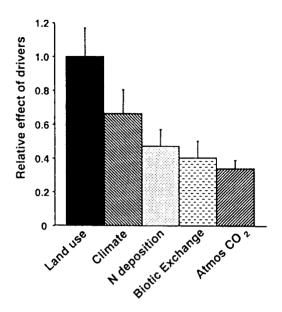


Figure 15.1. Relative effects of the major drivers of changes on biodiversity. The expected biodiversity change for each biome for year 2100 was calculated as the product of the expected change in drivers times the effect of each driver on biodiversity for each biome. Values represent the average across biomes 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. Redrawn with permission from Sala et al. (2000). Copyright 2000 American Association for the Advancement of Science.

(Fig. 15.1). Land-use change is expected to be the driver with the largest effect on biodiversity as indicated by the average effect across biomes. Land-use change will affect biodiversity by changing habitat availability that will result in local and global species extinctions. Climate change is the second most important driver primarily due to the strong effect of warming at high latitudes. N deposition, biotic exchange, and atmospheric CO<sub>2</sub> follow land-use and climate change in the ranking of global effects on biodiversity. Variability among biomes is maximal for land use (Fig. 15.1) due to the large variability among biomes in expected land-use change and the uniformly high sensitivity of all biomes to changes in land use. In contrast, the effect of elevated CO<sub>2</sub> shows small variability because CO<sub>2</sub> is well mixed in the atmosphere and because differences in sensitivity to CO<sub>2</sub> among biomes are relatively narrow (Table 15.1B).

#### Variation Among Biomes

Biomes differ strikingly in the expected effect that different drivers of biodiversity change will have by the year 2100 (Fig. 15.2). Tropical forests and

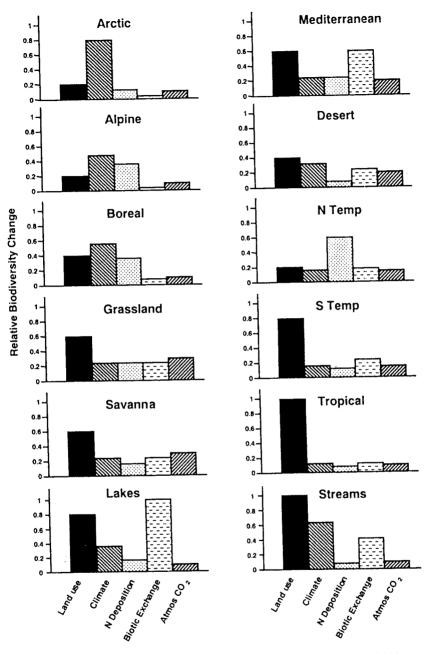


Figure 15.2. The effect of each driver on biodiversity change for each terrestrial biome and freshwater ecosystem type calculated as the product of the expected change of each driver times its effect for each terrestrial biome or freshwater ecosystem. Expected changes and impacts are specific to each biome or ecosystem type and are presented in Tables 15.1 and 15.2. Values are relative to the maximum possible value. Redrawn with permission from Sala et al. (2000). Copyright 2000 American Association for the Advancement of Science.

Table 15.2. (A) Expected changes for the year 2100, in the major drivers of biodiversity change for lakes and streams. (B) The impact of a large change in each driver on the biodiversity of each major freshwater-ecosystem type

	(A) Expected changes in drivers		(B) Impact on diversity	
	Lakes	Streams	Lakes	Streams
Land use	4.0	5.0	5.0	5.0
Atmos CO2	2.5	2.5	1.0	1.0
	2.0	2.0	2.0	1.0
N deposition				
Climate	3.0	4.0	3.0	4.0
Biotic exchange	5.0	3.5	5.0	3.0

Methods and assumptions are as in Table 15.1 (see text).

southern temperate forests will likely be affected mostly by a single factor (i.e., land-use change) whereas the other drivers will have a relatively small effect. Arctic tundra will also likely be affected mostly by a single driver, in this case climate change. In contrast, Mediterranean ecosystems, savannas, and grasslands will likely be affected simultaneously by several factors, all with moderate-to-large effects. Finally, biomes such as northern temperate forests and deserts will likely experience low-to-moderate impacts of all drivers.

Freshwater ecosystems will likely experience large changes in biodiversity that result from changes in land use, biotic exchange, and climate (Table 15.2 and Fig. 15.2). Lakes and streams will both be affected significantly by landuse change because human activities are disproportionately concentrated around waterways. Urban areas and agriculture tend to be located on riparian zones or near them. Human activity results in increase input of nutrients. sediments, and pollutants. Biotic exchange, which results from both intentional human actions and unintentional consequences of these actions, is also relatively larger in freshwater ecosystems than in terrestrial biomes (Lodge et al. 1998). For example, fish stocking in lakes and streams has driven many native fish to extinction, and the unintentional exchange of biota in ballast water that has had large negative effects on the biota of several lakes. N deposition and elevated CO2 will likely have smaller effects in freshwater ecosystems than in terrestrial ecosystems (Tables 15.1 and 15.2). The combined effect of all these factors currently has resulted in a larger decline of biodiversity in freshwater ecosystems than in the most strongly impacted terrestrial ecosystems (Ricciardi and Rasmussen 1999).

Streams in tropical regions will likely be affected most strongly by landuse change, whereas climate change and biotic exchange will have relatively smaller effects. Temperate streams will likely be affected equally by land-use change and biotic exchange (Richter et al. 1997; Harding et al. 1998). Finally, high-latitude streams will likely be affected the most by climate change with land-use change and biotic exchange playing a small role (Oswood et al. 1992). Streams are more sensitive than lakes to changes in climate because of the large effect of climate on run-off and its large effects on stream biodiversity (Poff et al. 1997).

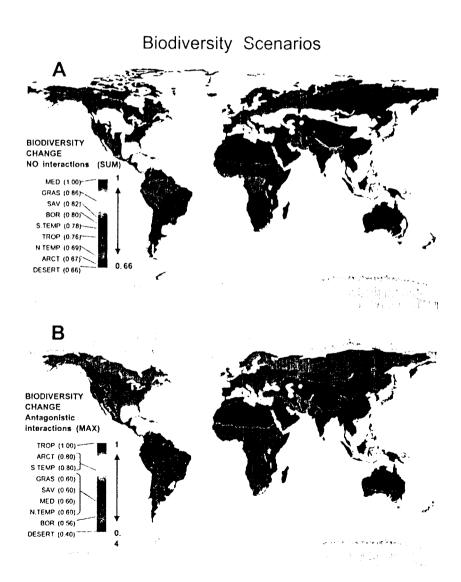
We developed three scenarios of biodiversity change taking into account the effect of all drivers for the ten terrestrial biomes. The three scenarios were based on assumptions of no-interactions, antagonistic interactions, and synergistic interactions among drivers of biodiversity change (Fig. 15.3; see color insert). In the first scenario, which is based on the assumption of no interactions among drivers, mediterranean ecosystems and grasslands appear as the biomes that will experience the largest proportional change in biodiversity, mostly because of the additive effects of most drivers that all have moderate-to-high values (Fig. 15.3A). In contrast, arctic, alpine, and desert ecosystems will experience the least proportional change, mostly as a result of the low-to-moderate effect of most drivers. The range of change from the biome that will change the most to the one that will change the least is relatively narrow in this scenario with the minimum change being 60% of the maximum.

In the second scenario, which was based on the assumption of antagonistic interactions among drivers, the ranking of biomes changed drastically (Fig. 15.3B). Tropical and temperate forests and arctic ecosystems will be the biomes with the largest proportional change in biodiversity, whereas they were among the biomes with lowest change in the previous scenario. Biomes with large changes in this scenario respond to the effect of a single driver, which will be land-use change for tropical and temperate forests and climate for arctic tundra.

In the third scenario, which was based on the assumption of synergistic interactions among drivers, the ranking of biomes is similar to the ranking of the first scenario with the largest proportional change in mediterranean and grasslands biomes and the least proportional change in tropical forest and arctic tundra (Fig. 15.3C). Biomes that will be affected by multiple drivers show larger changes in this scenario than biomes that will be affected by a single factor, even when the expected change of the driver will be very large. The assumption of synergistic interaction among drivers amplifies the differences among biomes. The change expected for the biome with the least change (arctic) will be just 2% of the biome with the largest change (mediterranean ecosystems). The other two scenarios showed narrower differences between the biomes with the highest and lowest expected change.

Despite the differences that result from the three different assumptions about interactions among drivers, common patterns emerge in the comparison of all three scenarios. Mediterranean ecosystems and grasslands appear, in all three scenarios, among the biomes that will experience the greatest proportional change in biodiversity by the year 2100. Savannas, independent

of the scenario chosen, appear as a biome that will experience moderate change. In all three scenarios, deserts and northern temperate forests will also experience moderate-to-low proportional change in diversity. In contrast, the expected change in tropical and southern temperate forests differs dramatically among scenarios. These two biomes range from being the biomes that will show the greatest proportional change in biodiversity in the antagonistic-interactions scenario to being among the biomes that will change the least in the no-interactions and the synergistic-interactions scenarios. All of these



scenarios project *proportional* changes in biodiversity. Because the tropical forest has many more species than the arctic, for example, the changes in absolute number of species lost would be greater in those biomes with greatest current biodiversity.

### Conclusions and Future Research Needs

Biodiversity is quite sensitive in all biomes to drivers of global change. Landuse change appears as the driver with the largest global effect on biodiversity by the year 2100; however, the importance of the different drivers varies enor-



Figure 15.3. Maps of three scenarios of the expected change in biodiversity for the year 2100. Scenario A assumes that 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 results from multiplying the expected change in the driver for a particular biome (Table 15.1A) times the effect of the driver that is also a biomespecific characteristic (Table 15.1B). Scenario B assumes that 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. Scenario C assumes synergistic interactions among the drivers; consequently, the total change is calculated as the product of the changes that result from the action of each driver. The different colors represent the expected change in biodiversity from moderate to maximum for the different biomes of the world ranked according to the total expected change. The numbers in parentheses represent the total change in biodiversity relative to the maximum value projected for each scenario. The biomes are MED (mediterranean ecosystems), GRAS (grasslands), SAV (savannas), BOR (boreal forest), S. TEMP (southern temperate forest), TROP (tropical forest), N. TEMP (northern temperate forest), ARCT (arctic ecosystems), DESERT (desert). Values for alpine, stream, and lake ecosystems are not shown. (Redrawn with permission from Sala et al. 2000. Copyright 2000 American Association for the Advancement of Science.)

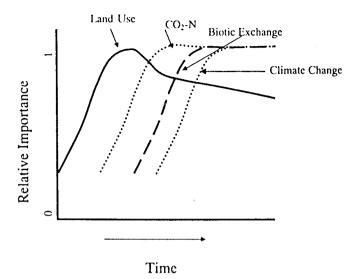


Figure 15.4. Hypothetical diagram of the changes in the importance of each driver of biodiversity change relative to its maximum, from present time to the year 2100. The diagram depicts the changes in importance through time for each individual driver from the lowest (0) to the highest (1), but it does not attempt to make comparisons among drivers. Land-use change is expected to change at the fastest rate and reach the maximum sooner than the other drivers do. The importance of land-use change will likely decline when most of arable land has been converted into cropland. On the contrary, the importance of the other drivers will grow at a slower rate, but it will continue growing until the end of the period of study because of the abundance of the resources and the difficulty of humans in controlling consumption.

mously among biomes ranging from those affected by a single factor, land use or climate, to those affected by most drivers.

In addition to the idiosyncratic geographical patterns of drivers and their differential effects on biodiversity, their relative importance will likely vary with time (Sala et al. 1999). We expect that land-use change will be the driver that will have the steepest rate of change and will achieve a maximum value the soonest (Fig. 15.4). The rate of change in land use has been documented extensively. Since the beginning of the twentieth century a very large fraction of native ecosystems have been transformed into croplands and urban areas (Richards 1993). The rate of change of land use, however, will be reduced in the medium-to-short term when most of the arable land is converted into agricultural land. Changes in the composition of the atmosphere have also been clearly documented (Keeling 1986). The rate of change of greenhouse gases in the atmosphere does not seem to be limited in the medium term due to the abundance of fossil fuels (Schimel et al. 1996) and the difficulties in implementing a global policy that constrains energy consumption. Changes in

climate will result from changes in the composition of the atmosphere and consequently will lag behind changes in the concentration of CO<sub>2</sub> (Kattenberg et al. 1996). The impact of humans on the nitrogen cycle has also been documented (Vitousek 1994), and it is unlikely to decrease in the medium term. The importance of biotic exchange will be magnified by changes in land use, CO<sub>2</sub>, and N deposition and will consequently lag behind them. During the time period explored by this scenario, we expect that the importance of landuse change will grow quickly, but that its relative importance will decline, whereas the other drivers will continue increasing their effects on biodiversity.

This exercise highlights the sensitivity of biodiversity change to the assumptions about interactions among drivers of biodiversity change. We suggest that this is one of the most important sources of uncertainty and that decreasing the level of uncertainty will require a major interdisciplinary research effort. We hypothesize that the shape of the interactions among drivers will vary among biomes and among sets of drivers. The shape of the interaction may also change with the intensity of drivers. At low levels of change, synergistic interactions may prevail, but the antagonistic scenario may be the most realistic at high levels of any driver. Another source of uncertainty in this exercise is the future state of the drivers. Any improvement in the scenarios of change in climate, land use, and CO<sub>2</sub>, will result in a reduction of the uncertainty associated with the biodiversity scenarios.

The scale at which the global scenarios were constructed influences the error of the exercise and limits its applicability. Scenarios were developed for ten terrestrial biomes and two types of freshwater ecosystems. Each of the biome chapters highlighted major differences within biomes that were overshadowed by the scale at which results were synthesized. Most management decisions occur at a finer scale than the one used in this study. Humans manage primarily paddocks, watersheds, and regions and struggle to manage larger units that encompass a variety of ecological, political, and social conditions.

Actions tending to mitigate biodiversity change include those actions that decrease the rate of change of global change drivers. For example, reductions in the rate of change of climate and land use would reduce the rate of change of biodiversity. Those changes should be complemented with specific actions at a finer scale and tailored for the biological, social, and economic conditions of each region. Different management plans will be required for different regions and must be based on a thorough understanding of the ecological and social characteristics of each region. The fine-scale understanding of the determinants of biodiversity change is as important as the understanding of the global patterns and will be an important challenge for the future.

#### References

Alcamo J (1994) Image 2: Integrated Modeling of Global Climate Change. Kluwer Academic Publishers, Dordrecht.

- Anderson JM (1995) The soil system. In: Mooney HA, Lubchenco J, Dirzo R, Sala OE (eds) Global Biodiversity Assessment: Section 6, pp. 406–412. Cambridge University Press, Cambridge, UK.
- Bailey RG (1998) Ecoregions: The Ecosystem Geography of the Oceans and Continents. Springer, New York.
- Berendse F, Elberse WT (1990) Competition and nutrient availability in heathland and grassland ecosystems. In: Grace JB, Tilman D (eds) *Perspectives on Plant Competition*, pp. 93-116. Academic Press, San Diego.
- Drake JA, Mooney HA, di Castri F, Groves RH, Kruger FJ, Rejmanek M, et al. (1989) Biological Invasions: A Global Perspective. John Wiley and Sons, Chichester.
- Fung IY, Tucker CJ, Prentice KC (1987) Application of advanced very high resolution radiometer vegetation index to study atmosphere-biosphere exchange of CO<sub>2</sub>. Journal of Geophysical Research 92D:2999-3015.
- Harding JS, Benfield EF, Bolstad PV, Helfman GS, Jones EBD (1998) Stream biodiversity: the ghost of land use past. Proceedings of the National Academy of Sciences of the United States of America 95:14843-14847.
- Haxeltine A, Prentice IC (1996) BIOME3: an equilibrium terrestrial biosphere model based on ecophysiological constraints, resource availability, and competition among plant functional types. Global Biogeochemical Cycles 10:693–709.
- Holland EA, Dentener FJ, Braswell BH, Sulzman JM (1999) Contemporary and pre-industrial global reactive nitrogen budgets. Biogeochemistry 46:7-43.
- Huenneke LF, Hamburg SP, Koide R, Mooney HA, Vitousek PM (1990) Effects of soil resources on plant invasion and community structure in California serpentine grassland. Ecology 71:478–491.
- Jackson RB, Sala OE, Field CB, Mooney HA (1994) CO<sub>2</sub> alters water use, carbon gain, and yield for the dominant species in a natural grassland. Oecologia 98:257–262.
- Kattenberg A, Giorgi F, Grassl H, Meehl GA, Mitchell JFB, Stouffer RJ, et al. (1996) Climate models—Projections of future climate. In: *Climate Change: The IPCC Scientific Assessment*, pp. 285-358. Cambridge University Press, Cambridge, UK.
- Keeling CD (1986) Atmospheric CO<sub>2</sub> Concentrations. Manna Loa Observatory, Hawaii 1958–1986. Carbon Dioxide Information Analysis Center, Oak Ridge.
- Levine J (2000) Species diversity and biological invasions: relating local process to community pattern. Science 288:852-854.
- Lodge DM, Stein RA, Brown K, Covich WAP, Bronmark C, Garvey JE, et al. (1998) Predicting impact of freshwater exotic species on native biodiversity. Australian Journal of Ecology 23:53-67.
- Mooney HA, Drake BG, Luxmoore RJ, Oechel WC, Pitelka LF (1991) Predicting ecosystem responses to elevated CO<sub>2</sub> concentrations. BioScience 41:96–104.
- Mooney HA, Canadell J, Chapin FS, Ehleringer J, Körner C, McMurtrie R, et al. (1999) Ecosystem Physiology Responses to Global Change. In: Walker BH, Steffen WL, Canadell J, Ingram JSI (eds) *The Terrestrial Biosphere and Global Change: Implications for Natural and Managed Ecosystems: A Synthesis of GCTE and Related Research*, pp. 141–189. Cambridge University Press, Cambridge, UK.
- Oswood MW, Milner AM, Irons JG (1992) Climate change and Alaskan rivers and streams. In: Firth P, Fischer SG (eds) Global Climate Change and Freshwater Ecosystems, pp. 192-210. Springer-Verlag, New York.
- Poff NL, Allan JD, Bain MB, Karr JR, Prestegaard KL, Richter BD, et al. (1997) The natural flow regime: a paradigm for river conservation and restoration. BioScience 47:769-784.
- Rejmánek M (1989) Invasibility of plant communities. In: Drake JA, Mooney HA, di Castri F, Groves RH, Kruger FJ, Rejmánek M, et al. (eds) *Biological Invasions:* A Global Perspective. John Wiley and Sons, New York.
- Ricciardi A, Rasmussen J (1999) Extinction rates of North American freshwater fauna. Conservation Biology 13:1220-1222.

- Richards JF (1993) Land transformation. In: Turner BL II, Clark WC, Kates RW, Richards JF, Mathews JT, Meyer WB (eds) *The Earth as Transformed by the Human Action*, pp. 163–178. Cambridge University Press, Cambridge, UK.
- Richter BD, Braun DP, Mendelson MA, Master LL (1997) Threats to imperiled freshwater fauna. Conservation Biology 11:1081-1093.
- Sala OE (1995) Human-induced perturbations on biodiversity. In: Mooney HA, Lubchenco J, Dirzo R, Sala OE (eds) Global Biodiversity Assessment, Section 5, pp. 318-323, Cambridge University Press, Cambridge, UK.
- Sala OE, Chapin FS III, Gardner RH, Lauenroth WK, Mooney HA, Ramakrishnan PS (1999) Global change, biodiversity and ecological complexity. In: Walker BH, Steffen WL, Canadell J, Ingram JSI (eds) The Terrestrial Biosphere and Global Change: Implications for Natural and Managed Ecosystems, pp. 304–328. Cambridge University Press, Cambridge, UK.
- Sala OE, Chapin FS III, Armesto JJ, Berlow E, Bloomfield J, Dirzo R, Huber-Sanwald E, et al. (2000) Global biodiversity scenarios for the year 2100. Science 287:1770–1774.
- Schimel D, Alves D, Enting I, Heimann M, Joos F, Raynaud D, et al. (1996) Radiative forcing of climate change. In: Houghton J, Meira Filho L, Callander B, Harris N, Kattenberg A, Maskell K (eds) Climate Change 1995: The Science of Climate Change, pp. 76–86. Cambridge University Press, Cambridge, UK.
- Tilman D (1993) Species richness of experimental productivity gradients: how important is colonization limitation? Ecology 74:2179–2191.
- Vitousek PM (1994) Beyond global warming: ecology and global change. Ecology 75: 1861–1876.