

Research, part of a Special Feature on [Scenarios of global ecosystem services](#)
The Future of Vascular Plant Diversity Under Four Global Scenarios

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ABSTRACT. Biodiversity is of crucial importance for ecosystem functioning and human well-being. Using quantitative projections of changes in land use and climate from the four Millennium Ecosystem Assessment (MA) scenarios, we project that reduction of habitat by year 2050 will result in a loss of global vascular plant diversity ranging from 7–24% relative to 1995, after populations have reached equilibrium with the reduced habitat. This range includes both the impact of different scenarios and uncertainty in the SAR relationship. Biomes projected to lose the most species are warm mixed forest, savannahs, shrub, tropical forest, and tropical woodlands. In the 2000–2050 period, land-use change contributes more on a global scale to species diversity loss than does climate change, 7–13% vs. 2–4% loss at equilibrium for different scenarios, respectively. However, after 2050, climate change will become increasingly important.

Key Words: *biodiversity; global environmental change; millennium ecosystem assessment; scenarios.*

INTRODUCTION

Despite continued conservation efforts, biodiversity loss is estimated to be occurring at 100–10,000 times the background rate of the fossil record for the Cenozoic (May et al. 1995, Pimm et al. 1995, Duraiappah et al. 2005). Loss of habitat through land-use change, introduction of alien species, direct exploitation, e.g., hunting and trade, climate change, and pollution have all been identified as causes of biodiversity loss (Hilton-Taylor 2000, Sala et al. 2000). Although several studies indicate the importance of biodiversity for ecosystem functioning and human well-being (Daily 1997, Reid et al. 2005), the number of scenario studies examining the future of biodiversity is small. Moreover, such studies are generally limited in scope, drivers, or scenarios. An important reason for this is that not many models exist that can quantitatively relate biodiversity to changes in variables that are covered in different scenarios. Sala et al. (2000) provided a global assessment of different pressures on biodiversity and showed that changes in land use were projected to be the major drivers of biodiversity loss, followed by climate change, nitrogen deposition, biotic exchange, and atmospheric CO₂ composition. The methods used, however, were qualitative, and the authors used only one scenario. UNEP's Global Environment Outlook

3 (UNEP 2002) provided four quantitative scenarios for loss of natural ecosystems ranging from 5–13% loss in the period 2000–2030, but this study did not quantify species losses. More recently, Thomas et al. (2004) examined the impact of climate change on biodiversity; their analysis of a set of case studies projected that climate change will commit 15–37% of the species in these case studies to extinction. They also suggested that climate change may in fact be the most important driver of biodiversity loss over the next 50 yr. This suggestion, however, was not based on a thorough analysis of land-use impacts within their samples.

Recently, the Millennium Ecosystem Assessment (MA) scenarios have been developed to provide a comprehensive overview of the possible changes in drivers of changes to ecosystems and their services (Reid et al. 2005, Carpenter and Pingali 2006, Sala et al. 2006). Here, we use these comprehensive scenarios to evaluate changes in global and local plant diversity from land use and climate change, the two most important pressures identified by Sala et al. (2000). Loss of global diversity is important because it corresponds to an irreversible loss of potentially valuable genetic libraries and existence values (Myers 1997, Pereira and Cooper 2006). Local population losses, which will occur at an even faster rate (Hughes et al. 1997), are also important

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as they directly affect local ecosystem services (Pereira and Cooper 2006). Our assessment uses the species-area relationship (SAR) to project the potential loss of species based upon the loss of natural habitats described by the MA scenarios. As the method is subject to considerable uncertainty, a sensitivity analysis of the major parameters was performed.

METHODS

The scenarios of the Millennium Ecosystem Assessment

Our assessment was based on the four comprehensive scenarios developed by the Millennium Ecosystem Assessment (MA) to assess potential changes in ecosystem services and their impact on human well-being. These MA scenarios are developed using both qualitative, i.e., storytelling, and quantitative, i.e., modeling, approaches that mutually support each other. The modeling approach uses several global models that were coupled for this assessment, i.e., for a selected number of main variables the output of one model is used as input of the next model (Alcamo et al. 2006). The four Millennium Assessment scenarios are: (1) "Global Orchestration," a globalized world with an economic development focus and rapid economic growth (GO); (2) "Technogarden," a globalized world with a focus on environmental technology (TG); (3) "Order from Strength," a regionalized world with a focus on security (OS); and (4) "Adapting Mosaic," a world with a focus on regional and local socioecological management (AM) (see also Table 1). For this paper, we used the implementation of these scenarios in the IMAGE 2.2 model (Alcamo et al. 1998, IMAGE-team 2001), as this model, within the larger set of models, was responsible for providing an integrated description of land-use change and climate change. IMAGE 2.2 is a dynamic earth-system model, describing global environmental change in terms of chains of driving forces, pressures, state, and response variables, which cover both the natural environment and the socioeconomic system. IMAGE 2.2 generated spatially explicit information at $0.5^\circ \times 0.5^\circ$ on land use and climate change, based on paths for indirect drivers such as population, economy, energy use, and diet. In IMAGE, a crop module based on the FAO agro-ecological zones approach computes yields of seven crops and pastures, estimating the areas used for their production as determined by

climate and soil quality (Alcamo et al. 1998). IMAGE also includes a modified version of the BIOME model (Prentice et al. 1992) to compute changes in potential vegetation for 14 biome types.

The methodology applied to assess biodiversity losses

We have estimated both global and local losses of biodiversity. The method used for local losses is described at the end of this section. For global losses, we used the land cover projections of the MA scenarios produced by IMAGE model in conjunction with the species-area relationship (SAR) to explore possible trends in future, global vascular plant biodiversity. The SAR is a well-established empirical relationship describing how the number of species relates to area (Rosenzweig 1995) and is defined as $S = c A^z$, where S is the number of species, A the habitat area, c is the species density and z the slope of the relationship. The SAR has been used earlier to estimate biodiversity loss when native habitat is reduced by deforestation (e.g., May et al. 1995, Pimm et al. 1995, Brook et al. 2003) or climate change (Thomas et al. 2004).

We applied SAR to a set of global biogeographical units, which can be seen as large areas of relatively uniform climate that harbor a characteristic set of species and ecological communities. We applied SARs independently for each unit; thus, assuming that the overlap in numbers of species is low relative to the number of species that are endemic to each of them. The units are defined on the basis of the intersection of the 14 natural biome types of the IMAGE model and the 6 biogeographic realms of Olson et al. (2001). It should be noted that our results depend on the definition of these units: too few regions imply lack of sensitivity to detail, whereas too many regions imply that the degree of endemism is low possibly resulting in double counting. Therefore, we tested the influence of the definition of these units in the sensitivity analysis discussed in the Results section. The definition of the 14 natural biome types of the IMAGE model is based on climate characteristics and soil types, primarily to assess the impact of climate change on natural vegetation patterns, and the carbon cycle (for a list see the legend of Fig. 1). In the model, the location of these biomes changes over time as a result of land use and climate change. The IMAGE biomes

Table 1. Main assumptions and results in the model about drivers of ecosystem change in each scenario.

	Global Orchestration	Technogarden	Order from Strength	Adapting Mosaic
World population (billions)	Lowest 2000: 6.1 2050: 8.2 2100: 6.9	Medium 2000: 6.1 2050: 8.9 2100: 8.7	Highest 2000: 6.1 2050: 9.7 2100: 10.6	High 2000: 6.1 2050: 9.6 2100: 9.9
Income (average annual GDP pc growth rate: 2000–2100)	Highest (2.5%)	High (2.3%)	Low (1.2%)	Medium (1.8%)
Global GHG emissions (GtC-eq)	High 2000: 9.8 2050: 25.6 2100: 19.5	Low 2000: 9.8 2050: 7.1 2100: 5.5	High 2000: 9.8 2050: 20.3 2100: 25.2	Medium 2000: 9.8 2050: 18.0 2100: 16.0
Global average mean temperature increase (°C)	High 2000: 0.6 2050: 2.0 2100: 3.5	Low 2000: 0.6 2050: 1.5 2100: 1.9	High 2000: 0.6 2050: 1.7 2100: 3.3	Medium 2000: 0.6 2050: 1.9 2100: 3.0
Per capita food consumption	High	High	Low	Low
Agricultural Yield change	High	Medium-high	Low	Medium

resemble those used to define biomes or ecoregion divisions in other studies (Bailey 1989, Olson et al. 2001), and the intersection between IMAGE biomes and realms is similar to the one that is at the basis of Olson's ecoregions. The IMAGE biomes and the six biogeographic realms are shown in Fig. 1. The intersection, e.g., boreal forest in Neartic region, boreal forest in Palearctic region, cool conifer forest in Palearctic region etc., creates a total of 65 biogeographical units.

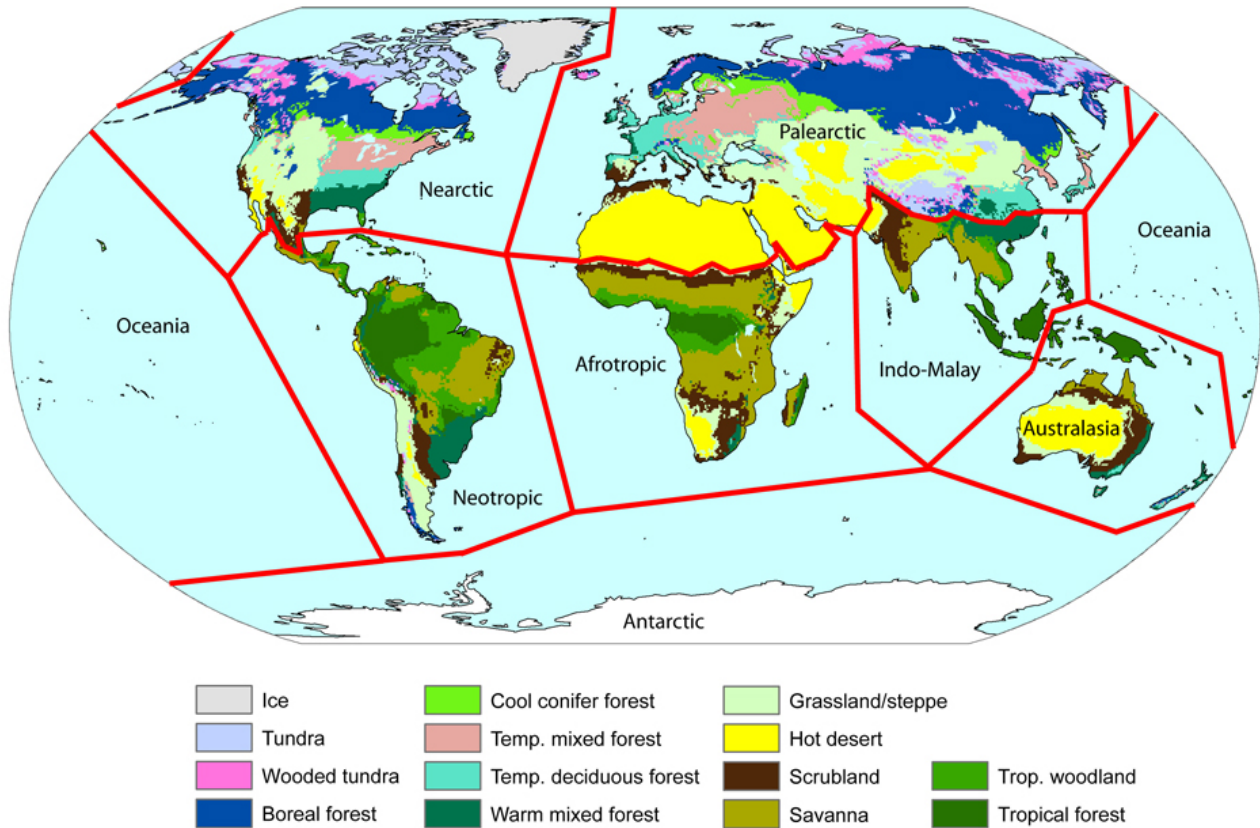
We also assumed that the SAR can be applied in one direction only: habitat loss leads to inferred extinction of species, but increase in area does not lead to a similar increase in species, as timescales examined are extremely short on an evolutionary timescale. For simplicity, we also assume that the diversity of human-dominated vegetation for the

purpose of the SAR calculations is zero. Therefore the number of global species at time $t1$ is:

$$\frac{S_{t1}}{S_0} = \frac{\sum_{i=1}^{65} c_i \text{Min}(A_i(t \leq t1), A_i(2000))^z}{\sum_{i=1}^{65} c_i A_i(2000)^z} \quad (1)$$

where $A_i(t)$ is the area of biome i at time t , and equals the original biome area A_i plus the net change in area of the biome by conversion to agriculture or abandonment of agricultural land $\Delta A G_i(t)$, plus the

Fig. 1. The biogeographical units used as basis for the species-area relationships. Each unique combination of one of the 14 natural biome types of the IMAGE model and the biogeographic realms of Olson et al. (2001) is defined as an unit, e.g., all boreal forest in the Palearctic realm. The realms "Oceania" and "Antarctic" have not been considered separately in the analysis, leaving a total of six realms.



net change in area due to climate change $\Delta AC_i(t)$, which is described in the last section of this text.

$$A_i(t) = A_i(2000) + \Delta AG_i(t) + \Delta AC_i(t) \quad (2)$$

It should be noted that considerable lag time exists between habitat loss and species extinctions (Tilman et al. 1994, Brooks et al. 1999). Therefore, SAR calculations do not refer to the actual number of species lost, but to the number of species that would become globally extinct when populations

relax to equilibrium with the reduced habitat. We do not know precisely how long this time lag is, and it certainly depends on the life history of individual species. Studies on the relaxation time for bird (Brooks et al. 1999, Ferraz et al. 2004) and plant species (Leach and Givnish 1996) suggest that about half of the losses may occur over a period of decades to a century.

In contrast to the loss of biodiversity at the global scale, local changes in species abundance and local extinctions are directly proportional to losses in habitat. Species and the ecosystem services that those species provided often disappear immediately after a piece of native habitat is converted into an

agricultural or urban patch. Moreover, another important difference between local and global losses of biodiversity is the reversibility of the phenomenon. Local losses could be reversed as a result of abandonment or active conservation practices. Populations can invade from adjacent patches naturally or assisted by human intervention. Ecosystem services derived from local diversity can therefore increase or decrease as a result of gains and losses of habitat. Therefore, in our assessment of local biodiversity change, we assumed changes to be fully proportional to the change in area; thus, in Eq. 1, z is set to 1, and the assumption of irreversibility is removed.

Climate change

Climate change will influence ecosystems at several scales, and several methods have been used to assess the potential impact of climate change on biodiversity. A common and relatively simple method to study the impact of climate change on the distribution of biogeographic units is to describe their climatic envelope and compare them against climate change scenarios provided by global circulation models (Prentice et al. 1992, Cramer and Leemans 1993, Malcolm and Markham 2000). Such approaches depict large-scale vegetation shifts as a consequence of climate change. The IMAGE 2.2 follows this approach, including, however, a transient response for actual vegetation as a function of distance, migration rates, and original and new vegetation types, whereby the function alters the actual land-cover type (van Minnen et al. 2000). Real changes could be much more complex because it is individual species that respond to climate change and not entire biomes. Solomon and Leemans (1990), for instance, concluded that future climate change could lead to large-scale synchronization of disturbance regimes, leading to the emergence of early phase succession vegetation with opportunistic generalist species dominating over large areas. Some models focus on the distribution of individual species in response to climate change, whereas other models also describe the ecological interactions between these species (Kleidon and A. 2000, Sitch et al. 2003).

On the basis of the available material in IMAGE, it is possible to estimate the impact of climate change via the species-area-curve relationship, but we need to account for reduced biodiversity in remaining areas in cases where climate change is occurring too

fast for species to adapt. We assumed that this would be particularly important if rapid climate change leads to a difference between actual and potential vegetation (Leemans and Eickhout 2004). If we assume that $A_i(t)$ is the total area, i.e., actual natural vegetation, of biome i , $AO_i(t)$ the remaining part of the original area covered by this biome in year 2000, $AA_i(t)$ the new area covered by this biome where actual vegetation equals potential vegetation, and $AN_i(t)$ the new area of the potential vegetation of that biome where the actual vegetation has not yet been adapted. To estimate the biodiversity loss through climate change, represented by the factor $\Delta AC_i(t)$ in Eq. 2), we did calculations for three different cases:

1. Biodiversity adapts on the basis of the adaptation speed in IMAGE: $\Delta AC_i(t) = \Delta AO_i(t) + \Delta AA_i(t) + k \Delta AN_i(t)$
2. Biodiversity does not adapt, causing all changes from the original potential vegetation to be marked as losses: $\Delta AC_i(t) = \Delta AO_i(t)$
3. Biodiversity adapts immediately to climate change, which means that only where the total biome area of potential vegetation declines, will biodiversity loss occur. $\Delta AC_i(t) = \Delta AO_i(t) + \Delta AA_i(t) + \Delta AN_i(t)$

Here, k is a constant accounting for the loss of biodiversity in areas that could not adapt immediately. For simplicity we chose k to result in a 50% loss of species for the relevant area. The results of these three methods are indicated in the Appendix. As method 1 gives results in between the two extreme cases, i.e., no adaptation and full adaptation, this method was chosen as the default option.

Assessment of the relevant parameters (c and z)

Information on the biodiversity of each biogeographical unit was obtained from a global map of the local diversity of vascular plants (Barthlott et al. 1999). As the map of plant diversity included more detail, a GIS system was used to calculate average c - values over each biogeographical unit. Although in general, each realm-biome unit is

not very heterogeneous in diversity, this averaging may underestimate the diversity of species in cases in which both hotspots and low-diversity areas occur.

For the z -value, we used a compilation of 82 values from studies that surveyed species-area relationships in vascular plants. It has been shown that the z -value can vary with the type (Rosenzweig 1995) and scale (Crawley and Harral 2001) of sampling. Here, we analyzed the effect of the biome and of the type of sampling, i.e., continental, islands, and interprovincial, see Fig. 2). A very clear relationship was found between the type of sampling and the reported z -values, with the average z -value on the provincial SAR being larger than z -values on island and on continental SARs as shown on the left-hand side panel of Fig. 2. With respect to the effect of the biome, we found that z -values for tropical forests were somewhat higher than the average values. Finally, the histogram of the z -values of island SARs on the right-hand side panel of Fig. 2 suggests they follow a lognormal distribution.

Several studies have used the island SAR to predict biodiversity loss (May et al. 1995, Pimm et al. 1995, Brooks et al. 1999), based on the argument that habitat conversion results in islands of native habitat in a sea of human-modified habitat. However, Rosenzweig (2001) has suggested the use of the provincial SAR, arguing that over the long term, each native habitat fragment will behave as an isolated province. At the other extreme one could argue that over the short term, the species that go extinct are those endemic to the area of lost habitat, and are best described by the continental SAR (Rosenzweig 1995, Kinzig et al. 2001). Here, we have chosen to use the island z -values for our central estimates. We used a mean z -value of 0.34 as derived from the literature for island studies. For tropical forest, we used a z -value 20% higher than the mean. At the other extreme, we used z -values 20% lower than the mean for tundra. To give the full range of possibilities, we also made our calculations using the mean values for the other two types of SAR, i.e., 0.25 for continental and 0.81 for provinces. In addition, a Monte Carlo analysis was performed using the log-normal distribution of island z -values.

RESULTS

Loss of vascular plant diversity

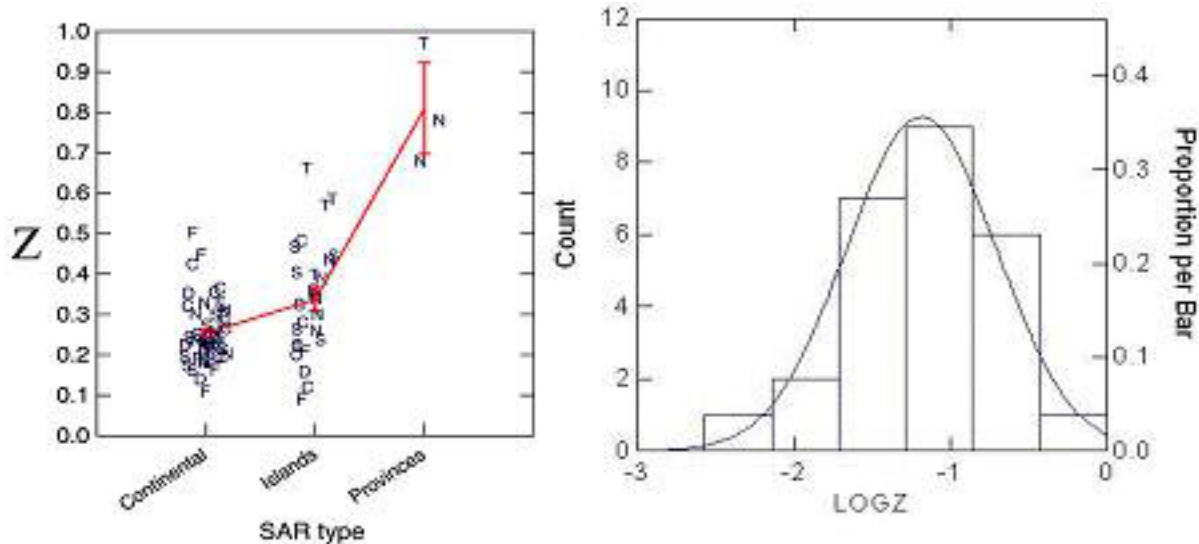
In all scenarios, agricultural expansion will continue to reduce the size of natural biomes globally (Table 2 and Figure 3a). The largest decline occurs for the *OS* scenario, mostly as a result of a large increase in food consumption resulting from the large increase in population and the low yield improvement (see Table 1). In contrast, the *TG* scenario leads to the lowest decline of natural habitat, given the combination of a relatively low population increase, low meat demand and high yield improvements. The other two scenarios *GO* and *AM*, result in intermediate values.

Habitat loss is not uniformly distributed across the different biomes of the world (Table 2). The least amount of change will occur in the Arctic and temperate ecosystems, but in most scenarios, reforestation is expected to exceed deforestation. In tropical regions, however, the total size of natural biomes is projected to decrease by 15–30% by 2050, depending on the scenario. The tropical biomes experience the highest losses as these are also the areas with the largest increases in population and corresponding food demand. In the temperate zones, in contrast, most of the land-use changes have already occurred, and continuing yield improvement could lead to some abandonment of agricultural areas and corresponding increases in natural habitats. In the two scenarios with a regional focus, i.e., *OS*, *AM*, this trend is less dominant, mostly based on the assumed slower yield improvement. Temperate deciduous forests form an exception to the increased habitat area in temperature zones as it is reduced under most scenarios.

The changes in local biodiversity (Fig. 3, left panel) correspond to changes in total area of natural ecosystems. Total natural area is more or less stable in temperate zones. However, in the tropical zone, local biodiversity decreases by about 15–20% in 2050, then more or less stabilizes in the two scenarios *AM* and *TG*, and decreases continuously from 15–30% in 2050 to 30–40% in 2100 in scenarios *GO* and *OS*.

The SAR calculations indicate that global plant diversity at equilibrium is projected to decline in all scenarios, mainly due to land-use change (Fig. 3b).

Fig. 2. Z values reported in studies on the species-area relationship in vascular plants. The points in the left panel correspond to individual studies and are labelled with the biome category of the area studied: T: tropical forest and tropical woodland; F: temperate deciduous forest, C: boreal forest, coniferous forest, wooded tundra and tundra; S: warm mixed forest, shrubland and savannah; D: grassland and desert; N: no specific biome. The red line joins up the means in each type; the error bars represent standard errors. The right panel shows the histogram of z-values of the species-area relationship in island studies of vascular plants, both oceanic islands and habitat fragments in mainland, fitted with a lognormal distribution. Source Sala et al. (2006). Copyright (c) 2005 Millennium Ecosystem Assessment. Reproduced by permission of Island Press, Washington, D.C.



The sharpest rate of decline in global biodiversity at equilibrium occurs between 1995 and 2020 between 7% and 10%. Compared to 1995, the 2050 equilibrium loss varies from 10–16%, and the 2100 loss varies from 13–23%. The sharpest biodiversity decrease, driven by the fastest population growth and low yield improvement, occurs in the *OS* scenario. The lower biodiversity loss in *TG* results from stabilization of the human population and transfer of advanced agricultural technologies to developing countries. In other words, the proactive attitude towards environmental protection assumed in the *TG* scenario is able to reduce the equilibrium loss from 16–10% in 2050 and from 23–13% in 2100 compared to the worst scenario. In the *AM* scenario, the relatively low loss figures also result from the lower increase in food demand in developing countries.

The rate of habitat loss and the corresponding loss

in equilibrium biodiversity in 2050 exceeds 0.1% annually in all four scenarios. It is lowest in *AM* and *TG*, implying that biodiversity is likely to be lost at a much higher rate than indicated in the Cenozoic fossil record. Our results also indicate that in the next two decades, extinction rates are likely to be similar to those experienced in the recent past, and thus, not substantially reduced as called for under the Convention of Biodiversity. Using the rate of biodiversity loss in the 1970–2000 period as a baseline, we find the *TG* and *AM* scenarios to have slightly lower rates of loss than do the baseline during in the 2000–2020 period, i.e., 10–15%, and the *GO* and *OS* scenarios to have higher rates of loss, i.e., 10–40%.

There are major differences among the different biomes in terms of global biodiversity loss (Fig. 4). As tropical ecosystems face the largest area loss, they also suffer the highest biodiversity losses at

Table 2. Change in land cover in 2050.

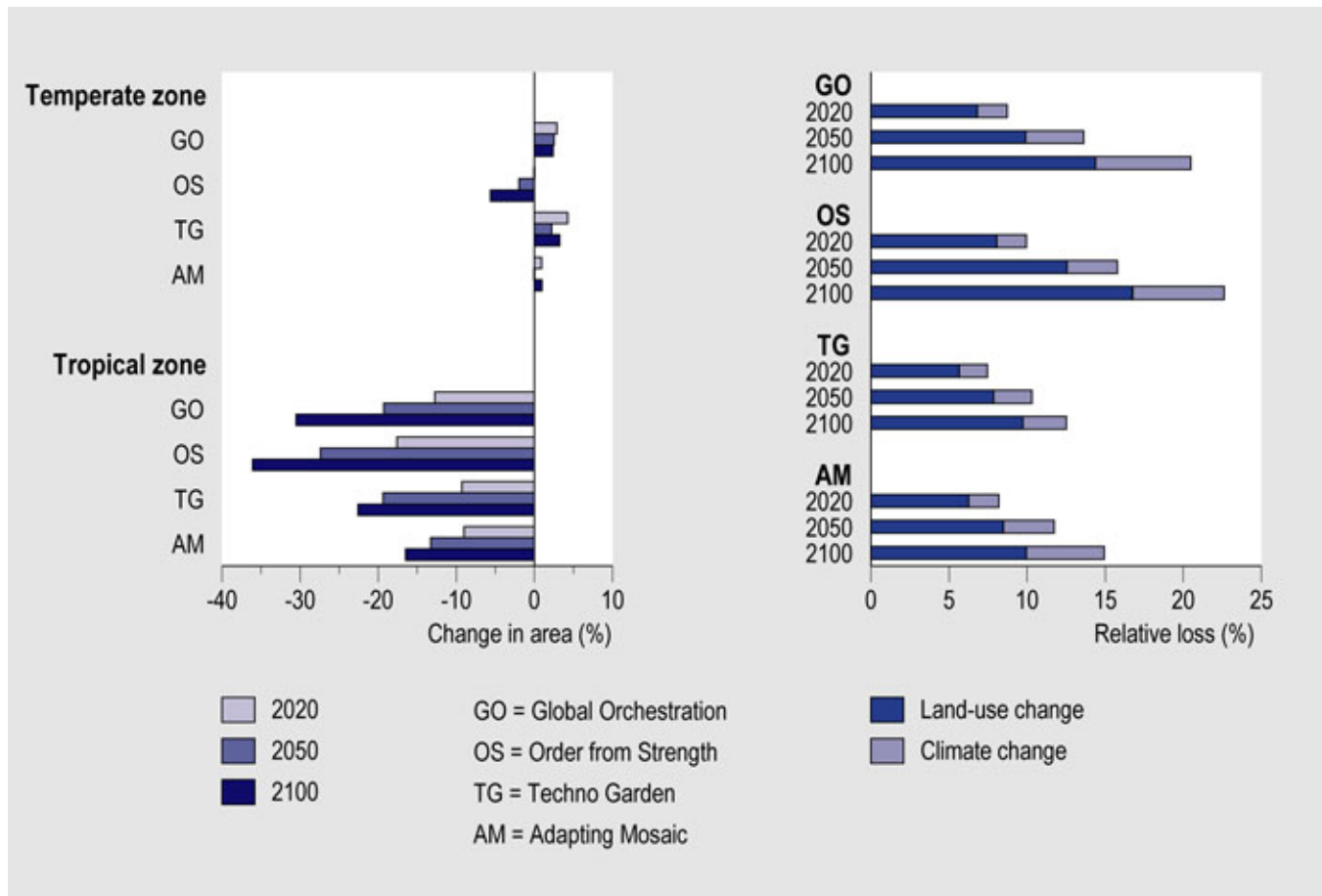
	2000		2050		
	Mha	OS	(Change relative to 2000)		
			TG	GO	AM
Agricultural land	3357	124%	109%	109%	107%
Extensive grassland	1711	100%	100%	99%	100%
Regrowth of forests	446	117%	103%	141%	123%
Ice	231	97%	96%	97%	96%
Tundra	768	95%	94%	95%	95%
Wooded tundra	106	78%	83%	79%	81%
Boreal forest	1509	103%	103%	103%	103%
Cool conifer	168	112%	116%	117%	114%
Temperate mixed	201	117%	143%	130%	124%
Temperate deciduous	145	76%	107%	91%	82%
Warm mixed	95	65%	115%	83%	80%
Steppe	804	86%	91%	93%	93%
Desert	1678	98%	99%	98%	99%
Shrub	207	59%	88%	82%	88%
Savannah	705	45%	64%	57%	73%
Tropical woodland	483	88%	104%	107%	109%
Tropical forest	670	78%	89%	85%	89%

equilibrium. In terms of absolute numbers of species, tropical forest, tropical woodland, savannah, and warm mixed forest account for 80% of all plant species lost at equilibrium by 2050, i.e., 25,000–40,000 different species. Global maps of the losses in biodiversity show the largest losses to occur in the Afrotropic region, where the largest expansion of agricultural land occurs in all scenarios, driven by both a rapidly increasing population and strong increases in per capita food consumption. The second important region in terms

of relative losses is the Indo-Malayan region. The Palearctic region, in contrast, experiences the lowest losses in biodiversity through loss of habitat.

In the first decades, land-use change clearly represents the most important driver of biodiversity loss. In time, however, the impact of land-use change gradually stabilizes because of a stabilizing human population, increases in agricultural yields, and reduced suitability of remaining ecosystem areas for agriculture. In contrast to land-use change,

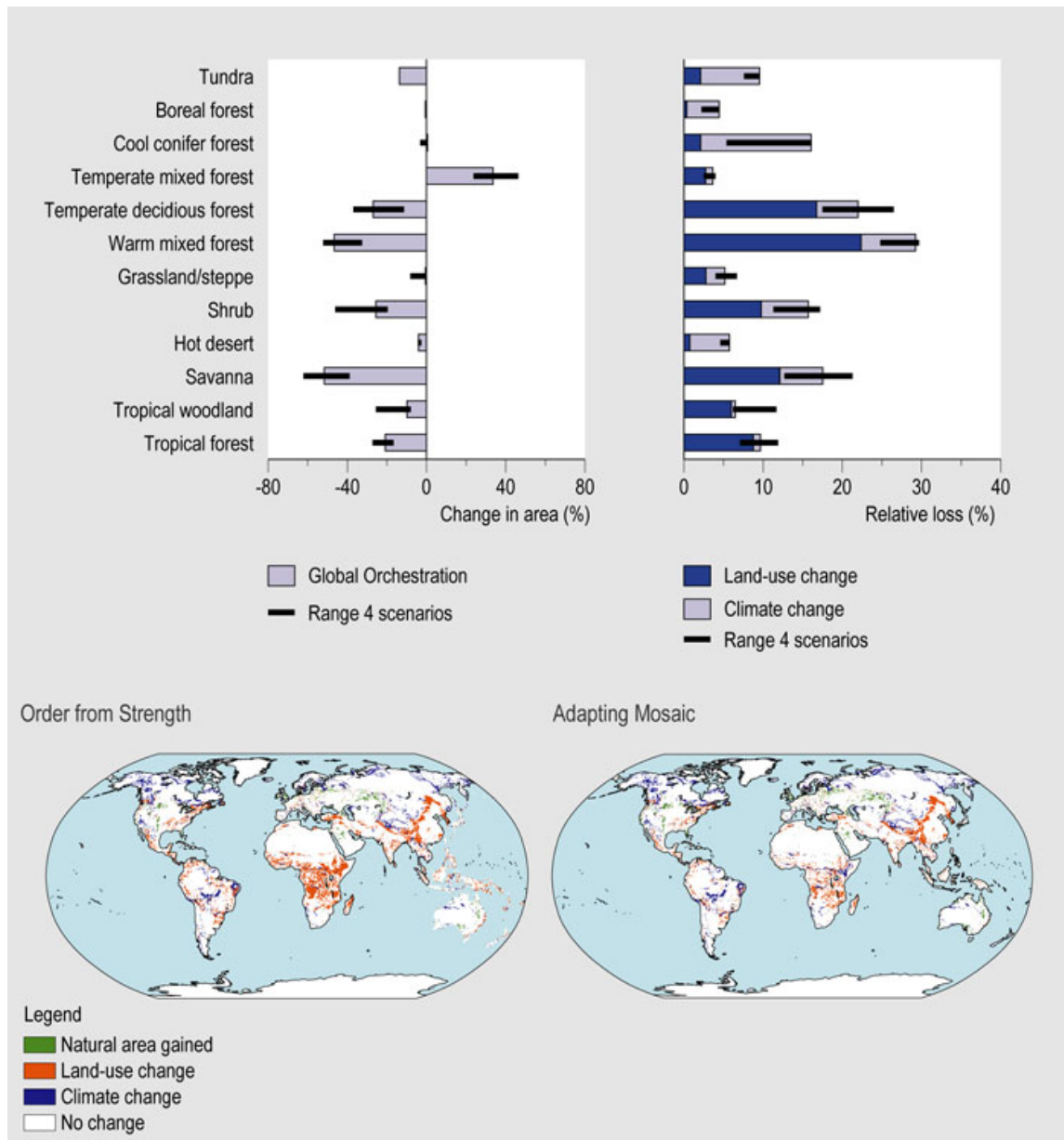
Fig. 3. Changes in the area of natural habitat in the temperate and tropical regions (left) and losses of global vascular plant diversity when populations reach equilibrium with reduced habitat due to conversion to agriculture and climate change (right). Figure is shown for the four Millennium Assessment scenarios. The habitat and biodiversity changes are given relative to the year 1995.



the impact of climate change increases with time, in particular under the *GO* and *OS* scenarios. In the *TG* scenario, the assumed ambitious climate policies reduce climate impacts by more than 60% compared to the *GO* and *OS* scenarios. Our results also show that, in tundra, boreal forests, and cool conifer forest, climate change is projected to be the major cause of biodiversity loss, varying from 5% to almost 15% species loss at equilibrium. Note, however, that for these biomes, land-use change has relatively low impact in comparison with other biomes. In contrast, land-use change is the main driver of biodiversity loss in temperate forests, warm mixed forests, savannah, and tropical forest,

leading to a 7% to nearly a 25% species loss at equilibrium. The contribution of climate change for plant diversity loss in these ecosystems varies between 1% and 8% loss of species. Thus, land-use change in the 2000–2050 period is the dominant driver of species loss at equilibrium at the global level because climate change is found to be less important for biomes such as tropical forest and tropical woodlands, and as a result of their high number of species play an important role in the aggregated results.

Fig. 4. Changes in 2050 in area of different biomes and vascular plant biodiversity in equilibrium with reduced habitat, relative to 1995. Top left panel shows the area of different biomes and top right panel vascular plant biodiversity at equilibrium, both for the Global Orchestration scenario. The uncertainty bars indicate the maximum and minimum values in the total set of scenarios. The bottom panels show changes in natural habitat extent due to land-use change and climate change at a resolution of 0.5° x 0.5°, for the two most extreme scenarios. Order from Strength, left and Adapting Mosaic, right. From "Ecosystems and Human Well-being: Scenarios, Volume 2" by Steve R. Carpenter, et al., eds. Copyright (c) 2005 Millennium Ecosystem Assessment. Reproduced by permission of Island Press, Washington, D.C.



Uncertainty analysis

This assessment faces several important uncertainties including the value for the slope of the SAR, the effect of habitat fragmentation, the overlap in species composition among different biomes, and the remaining biodiversity after conversion of natural land into agricultural land. Some of them can be bound by means of formal uncertainty analysis such as the sensitivity to the slope of the species-area relationship using z -values for different SAR types and performing a Monte-Carlo analysis to replicate the statistical distribution of island z -values.

As stated in the methods section, it is an open question as to which type of SAR best describes the response of biodiversity to land-use change, particularly when one compares short-term responses, i.e., decades, with long-term responses, i.e., millennia. Here, we used the island SAR, which gives intermediate estimates of biodiversity loss. When the z -values for the continental and provincial SARs, i.e., 0.25 and 0.81, respectively are used, our results for 2050 biodiversity loss for the *GO* scenario (Fig. 5) range from 12% for continental to 20% for provincial z -values). However, the general trends remain the same.

In the Monte-Carlo simulation, based on the statistical distribution of island z -values reported in literature, z -values were drawn from the log-normal distribution shown in Fig. 2. In total, 500 Monte-Carlo simulations were performed. The mean, the 25–75%, and 5–95% range of the predicted extinctions are reported. The 90% confidence interval of island z -values from the Monte-Carlo analysis shows a range from 8–21% for the *GO* scenario, and from 7–24% for all scenarios. The 50% confidence interval for the *GO* scenario shows a range from 10–17% and from 9–18% for all scenarios.

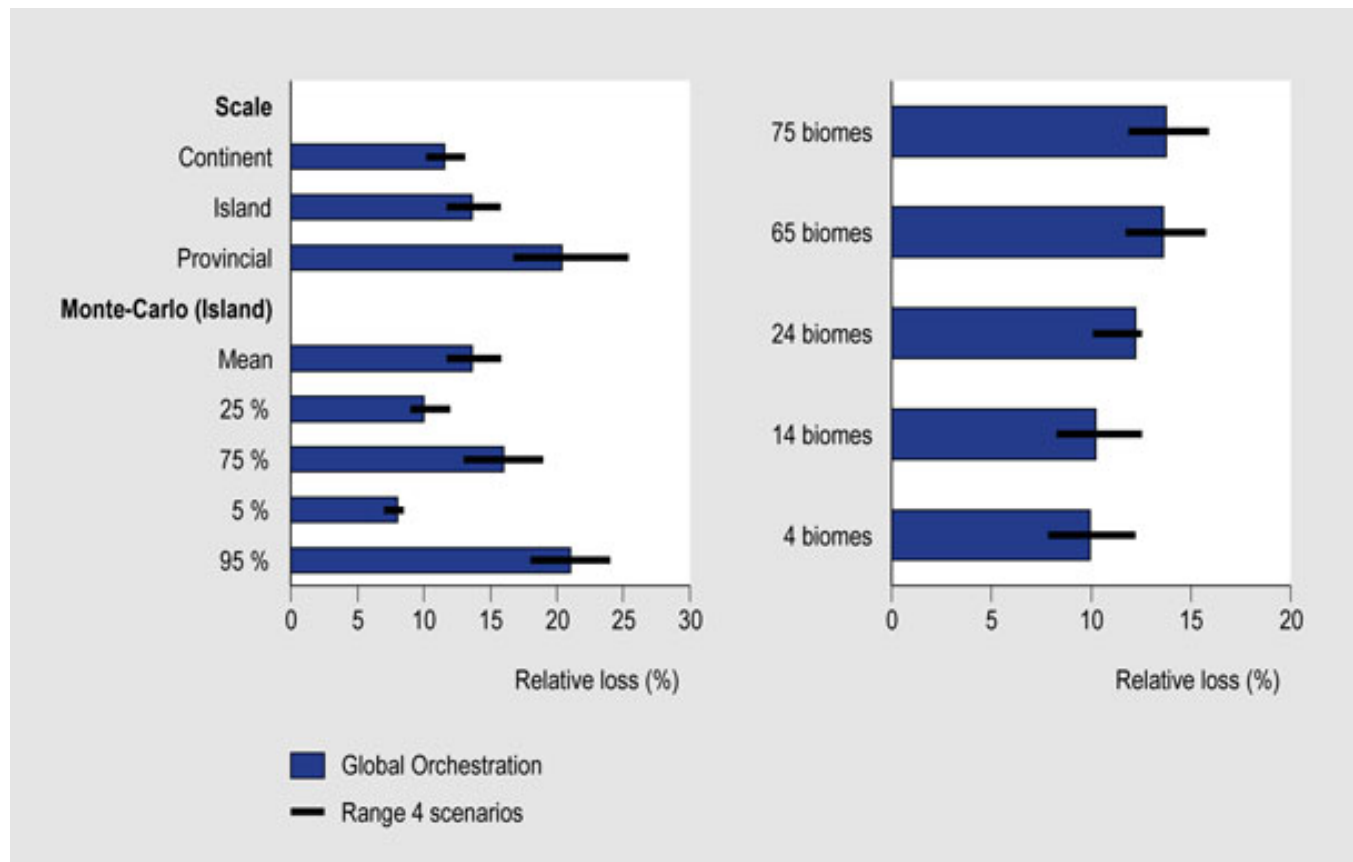
A third formal uncertainty analysis is associated with the number of regions in which the Earth vegetation is disaggregated. If one uses very few regions or units of analysis, then the number of species that are unique to each region, i.e., degree of endemism, is very high, but we may miss more disaggregated impacts of land-use and climate change leading to underestimates of species loss. In contrast, if we use too many regions, then species may occur in more than one region, i.e., the level of endemism is low, and overestimates of species loss

can occur, i.e., species that become extinct in one region may still exist in another region or double counting. This is partially equivalent to the uncertainty analysis using different SAR types above, with the interprovincial z -values corresponding to a world that could be divided in many more regions than the 65 used as our baseline, and the continental z -values corresponding to a world in which 65 units could be aggregated. Two tests, as described below, were performed to determine the possible influence of the number of regions used.

In the first test, we aimed to estimate the number of unique species in each region, as this would allow us to assess the potential impact of nonendemic species on our global loss estimates. Therefore, we studied the distribution of North American plants using the Kartesz and Meacham (1999) database, in which the composition of vascular plants is listed for each state in the United States and for each Canadian province. From this, we selected a set of states for each biome covered by only that biome, based on the 1995 IMAGE land-cover map. Overlaps varied widely, but the general pattern showed that the larger the distance between the biomes, the lesser the species overlap. On average, overlap of these neighboring biomes was about 60%. Thus, assuming the extreme and unlikely case of one biome disappearing and the other remaining intact, we would be predicting a little more than twice the number of extinctions that would, in fact, occur. However, for most of our biomes, the distances between them were much larger, minimizing this problem.

The second test consisted of a direct sensitivity analysis of the influence of the number of regions. We defined regions on the basis of existing classifications of the natural vegetation. The regions chosen are defined in Table 3. The highest level of aggregation collapses all units into only four units based on the highest level of aggregation of the Bailey (1989) ecosystem map, i.e., the IMAGE biome types are aggregated to Artic, temperate, arid, and tropical ecosystems, and the regional classification is ignored. The second level only includes the 14 IMAGE biome types and ignores any regional classification included in Fig. 1. At the next level, we combine the 4r units of the Bailey map and the 6 biogeographic regions of the Olson et al. (2001) map to create 24 distinct units. Finally, in addition to the standard definition of 65 units, a definition was used that includes East Asia and Japan and the Cape Province as additional

Fig. 5. Uncertainty analysis on the relative global losses of vascular plant species at equilibrium. Figure shows the uncertainty to a) the value of z as function of scale and the uncertainty in Island scale z -values (Monte Carlo analysis; 25–75% and 5–95% range are shown) and b) the effect of modifying the number of units distinguished in the analysis. This analysis is based on the Global Orchestration scenario. The uncertainty bars indicate the maximum and minimum values in the total set of scenarios.



biogeographic regions; thus, creating another 10 units. Figure 5 shows that for the *GO* scenario different aggregation levels yielded loss estimates that ranged from 10% at the highest aggregation level to 14% at the lowest.

DISCUSSION

In this paper, a SAR based methodology was used to assess changes in global and local biodiversity under the four Millennium Ecosystem Assessment (MA) scenarios as a result of land-use change and climate change. Our study suggests that, in 2050,

following these scenarios and using the mean island z -values, 10–16% of all vascular plant species would become extinct when reaching equilibrium with reduced habitat in total 30,000–50,000 species. Including not only the different scenarios, but also including the uncertainty in island z -values expands this range to 7–24, reporting the highest and lowest values for the 90% confidence range of each scenario.

It should be noted that although the SAR is a well-established relationship, there are several open issues that could influence its application to estimating the loss of species caused by the conversion of native habitat to agriculture. Some of

Table 3. Regional definitions explored.

Number of regions	Defined as:
4	Highest level of aggregation on the ecosystem map of Bailey et al., i.e., Arctic, temperate, arid, and tropical
14	Fourteen natural biome types defined in IMAGE, i.e., ice, tundra, wooded tundra, boreal forest, mixed conifer, temperate broadleaf forest, temperate mixed forest, warm mixed forest, grasslands, desert, shrubland, savannah, tropical woodland, tropical forest
24	Intersection of the highest level of Bailey's map, i.e., Arctic, temperate, arid, and tropical, with the six biogeographic regions of the Olson map. This roughly corresponds to the second layer of the Bailey map.
65	Intersection of Olson's map of ecosystem realms with the 14 IMAGE natural biomes
75	Based on the previous (65) regional definitions, but now adding two more realms, i.e., the Cape region in South Africa and East Asia and Japan, again intersecting with the 14 IMAGE natural biomes.

these issues may lead to overestimation of potential extinctions such as species that persist after conversion, the use of too many regions resulting in low endemism or the use of a too high value for z . The last two factors have been addressed by formal uncertainty analysis. For the first issue, it should be noted that there are many species that are not restricted to native habitat and can live in the agricultural landscape (Pereira et al. 2004). For simplicity, we have assumed zero diversity for human-dominated vegetation. However, up to 50% of the plant species in a region may occur in human-dominated habitats (Mayfield and Daily 2005). Therefore, our predictions may overestimate extinctions based on this assumption. There are, however, several other issues that could lead to an underestimation of potential extinctions. These include the issue of habitat fragmentation, the use of too few regions leading to a lack of detail, the use of too low values for z , and the method used to estimate losses from climate change. The last factor is discussed in a separate paragraph below. For habitat fragmentation, it should be noted that the SAR, as applied here, could not account for its effect. IMAGE maps were only available at a $0.5^\circ \times 0.5^\circ$ resolution, a level too coarse for dealing with detailed fragmentation issues. Not including fragmentation issues necessarily underestimates biodiversity losses. The uncertainty about the appropriate SAR type and the level of endemism of

each unit of analysis were examined in our formal uncertainty analysis. We searched the literature and established ranges for the slope (z) of the species-area relationship. Using the z -value of different SAR types and the 95% confidence interval for the island z -values suggest an uncertainty range of 12–20% and 8–21%, respectively for the GO scenario. The analysis of different aggregation levels indicated a somewhat smaller range for this factor from 10–14%. It should be noted that although the influence of the z -value and the definition of biogeographical units have been tested separately, the two are partly related as continental z -values correspond to a higher level of aggregation, whereas provincial values correspond to a lower level of aggregation. In all cases, however, the trends across biomes and among scenarios were found to be robust. The overall range of biodiversity losses may be interpreted as a fair representation of the plant biodiversity losses under the MA scenarios because our uncertainty analysis covers the large range of parameter values reported in literature.

We found that land-use change rather than climate change is likely a more dominant driver of biodiversity loss in the next 50 yr, consistent with the qualitative assessment of Sala et al. (2000), but inconsistent with the results of Thomas et al. (2004). A discussion point is whether biodiversity loss associated with climate change is well described by

the current method. Thomas et al. (2004) used a SAR approach to forecast the impact of climate change in case studies of animal and plant species across the world. Here, we applied the SAR approach to make a global assessment, using a simpler but global approach to estimate biodiversity losses. Losses from climate change were estimated to be around 3% in 2050 using the default method and ranged from 2–4% given alternative assumptions. These losses are clearly lower than the total range of 15–37% reported by Thomas et al. (2004), which covered about 20% of all plant species. However, it should be noted that values reported for different case studies such as those reported by Thomas et al. (2004) vary from a maximum extinction rate of 100% for plant species in Amazonia, based on a very unfavorable climate scenario for this area and assuming no dispersal capabilities, and a minimum value of 3% for Europe, assuming full dispersal. One reason for the differences between the two studies is the fact that Thomas et al. (2004) focused on case studies that may not be completely representative of what will happen at the global scale. In addition to the European case study, several other case studies report lower numbers. Another difference is that Thomas et al. (2004) modeled the response of individual species to climate change, whereas we modeled the response of whole biomes. The coarser resolution of our analysis can miss important changes in the climatic conditions inside our large biomes. On the other hand, Thomas et al. (2004) assumed that species could not survive outside their climate space, ignoring that other factors limit the distribution of species. Although in the AM scenario, the biomes in IMAGE are also defined on the basis of climate factors, the coarser resolution of biomes instead of species minimizes this problem.

Overall, the quantitative outcomes of this study compare well to the qualitative assessment made by Sala et al. (2000), not only with respect to the relative importance of land-use change and climate change in terms of their impacts on global biodiversity, but also in terms of the biomes that will suffer the largest losses, i.e., warm mixed forests, some of the tropical biomes, and temperate forests outside the developed regions. The index used by UNEP's Global Environment Outlook focuses on intactness of ecosystems instead of biodiversity. Using a different set of scenarios, the present study found a similar position of the drivers land use and climate change in 2030, and a decline of intactness that

seems to be consistent with the figures presented here, i.e., 5–13% for 2030 (UNEP 2002). Leemans and Eickhout (2004) found a similar pattern for most of the biomes affected by climate change. Thuiller et al. (2005) studied the impact of climate on plant diversity in Europe. They found that an average loss of local species ranging from 27–42% for different IPCC scenarios by 2080, measured as percentage species loss per pixel averaged over space. Their metric is more similar to the local biodiversity indicator that we introduced in this paper, but given the different weighting method, the results cannot directly be compared. The reported losses seem to be somewhat higher than those reported here, but as in the Thomas et al. (2004) study, they used climatic models for individual species.

Improvement of the current methodology

To improve future assessments of biodiversity change, we need a better understanding of the type of SAR that best describes the response of biodiversity to land-use change. We also need the classic SAR to be extended to account for species that use human-dominated habitat. There are now a couple of proposals for modifying the SAR to account for the distribution of species across different habitats (Tjorve 2002, Pereira and Daily 2006, but empirical tests are lacking. Others have also suggested improved SAR methods, which may be used in the future, to account for loss of endemics or more detailed spatial patterns, but only if more detailed scenario information becomes available (Kinzig and Harte 2000, Seabloom et al. 2002).

Other methods besides the SAR can be used to analyze the response of biodiversity to drivers of ecosystem change (Kareiva et al. 2006). For instance, population viability analysis (Beissinger and Westphal 1998) can be used to study the effects of change in harvest pressure or habitat loss and fragmentation in a species population. Species climate-envelope models allow the study of the potential impact of climate change on each species range (Thomas et al. 2004, Thuiller et al. 2005). However, to use these types of models at the global level, we need to know the global distribution of species. For selected taxa, this is now becoming possible with the ongoing development of global distribution databases for terrestrial vertebrates (Brooks et al. 2004, Pereira and Cooper 2006). Finally, we need more global monitoring data that shows how species are responding to the different

drivers of ecosystem change so that we can test and improve the models (Pereira and Cooper 2006).

Overall assessment

Our estimate of biodiversity loss includes assumptions that could result in both underestimates, e.g., not including fragmentation, conservative climate change impacts, and overestimates, e.g., no overlap in species between units, in biodiversity loss. However, overall, our assessment is likely to be conservative because we considered only habitat and climate change as drivers of biodiversity loss. If other drivers such as overharvesting, pollution, and invasive species were included, then biodiversity loss estimates would likely increase.

CONCLUSION

In this study, we presented a SAR-based method to estimate the loss of vascular plant species under the four scenarios of the Millennium Ecosystem Assessment (MA). Our study suggests that, in 2050, following these scenarios, 7% to almost 25% of all vascular plant species would be extinct when populations reach equilibrium, when habitat is reduced, i.e., in total 20,000–70,000 species. The range indicated above is based on the results of different scenarios and the influence of uncertainty in z -values, reporting the highest and lowest values for the 90% confidence range for each scenario. For the default values, the *OS* scenario of the MA leads to the highest loss of equilibrium biodiversity, i.e., 16% in 2050 and 23% in 2100, whereas the *TG* scenario leads to the lowest loss, i.e., 10% in 2050 and 13% in 2100. This implies that the assumed differences in driving forces among these scenarios can have a major impact on future biodiversity loss. More specifically, the lower population growth and the proactive environmental attitude, leading to ambitious climate policies and lower meat consumption in the *TG* scenario, are shown to lead to a stabilization in equilibrium biodiversity loss in the second half of the century, thereby reducing losses from 23–13% compared to the worst scenario. Our results also indicate that in the next two decades, equilibrium-extinction rates are likely to be similar to those experienced in the recent past; and thus, not substantially reduced as called for under the Convention of Biodiversity. The most important driver of biodiversity loss is land-use change. In time, climate change is likely to become

an additional threat. Given the important role of biodiversity in the provision of several ecosystem services, further efforts for protection should be considered. Such measures could focus on reducing habitat conversion, both by controlling direct drivers such as agricultural expansion, and by controlling indirect drivers such as population growth and consumption. Limiting climate change to the extent possible by minimizing emissions and sequestering carbon will also reduce biodiversity losses.

Responses to this article can be read online at:
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Appendix. Including climate change in the SAR calculations as applied in this paper.

In the main text, three different simple algorithms for assessing the biodiversity loss of climate change using the available information of the IMAGE 2.2 model are proposed. These are (equations are given in the main text):

1. Biodiversity adapts on the basis of the adaptation speed in IMAGE; some of the biodiversity in the areas where potential vegetation and actual vegetation are out of phase is lost
2. Biodiversity does not adapt, causing all changes from the original potential vegetation to be marked as losses;
3. Biodiversity adapts immediately to climate change, which means that only where the total biome area of potential vegetation declines, will biodiversity loss occur;

Figure A1.1 shows the results of each of these methods in terms of equilibrium biodiversity loss for the TechnoGarden (TG) (relatively weak climate change) and Order from Strength (OS) (strong climate change) scenarios in 2050 and 2100 compared to 1995.

The default method (M1) gives results within the two extreme assumptions of no adaptation (M2) and immediate full adaptation (M3). For the strong climate change scenario (OS), 2050 losses range from 2% with full adaptation to 4% without adaptation. By 2100, the differences between these methods become more pronounced: 3% with adaptation and 10% without adaptation. Based on their definitions (but subject to the limitations of the overall method) assuming no adaptation or full adaptation are clearly unlikely extremes. The numbers for the default method (M1) are 3% and slightly more than 6%. A discussion of the interpretation of these results vis-à-vis other studies that estimate loss of plant diversity as a result of climate change is given in the discussion section of the main text.

Figure A1.1. Biodiversity loss at equilibrium in 2050 and 2100 for the TechnoGarden (TG) and Order from Strength (OS) Scenario three different methods explored for assessing the impacts of climate change. M1 represents our default method, while M2 assumes no adaptation and M3 full adaptation.

