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Review

Scenarios for Global Biodiversity in the 21st Century

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Quantitative scenarios are coming of age as a tool for evaluating the impact of future socio-economic development pathways on biodiversity and ecosystem services. We analyze global terrestrial, freshwater and marine biodiversity scenarios using a range of measures including extinctions, changes in species abundance, habitat loss, and distribution shifts, as well as comparing model projections to observations. Scenarios consistently indicate that biodiversity will continue to decline over the 21st century. However, the range of projected changes is much broader than most studies suggest, partly because there are significant opportunities to intervene through better policies, but also because of large uncertainties in projections.

Quantitative estimates of the future trajectories of biodiversity, which we broadly refer to as biodiversity scenarios, are typically based on the coupling of several complex components (Fig. 1). Socio-economic scenarios with trajectories of key indirect drivers of ecological change, such as human population growth and greenhouse gas emissions, are developed under different assumptions regarding society's development, often associated with 'storylines' (*1*). These trajectories are then fed into models that project changes in direct drivers of ecosystem change, such as climate and land-use change, in different regions of the world (*1*, *2*). Finally, the projected drivers are used as inputs to biodiversity models (Table 1). In some cases, associated changes in key ecosystem services are also modeled, although quantifying the link between biodiversity and ecosystem services remains a major scientific challenge (*3*, *4*). Here, we review recent model-based biodiversity scenarios, which have grown rapidly in number over the last few years due to major advances in modeling and data availability.

Biodiversity change has many metrics (*5*). Here we group these metrics into four classes: species extinctions, species abundance and community structure, habitat loss and degradation, and shifts in the distribution of species and biomes. Scenarios of species extinction risk (*6*, *7*) address the irreversible component of biodiversity change, but species

extinctions have weak links to ecosystem services and respond less rapidly to global change than other metrics (e.g. the range of a species can decline shortly after habitat change but that species may not become extinct as a result) (*8*). More-responsive metrics include changes in species abundances and community structure, and, at a higher organizational level, habitat loss or biome changes. At both the species and ecosystem levels, many of the projected changes can best be described as shifts in potential distribution, with their current favorable conditions vanishing in some places, which may cause local extinctions, and appearing in new places, which may result in new colonizations.

Models used to estimate global change impacts on biodiversity vary substantially in complexity and underlying hypotheses (Fig. 1, Table 1), but can be broadly classified into phenomenological or process-based models. Phenomenological models rely on empirical relationships between environmental variables and a biodiversity metric (*9*). One of the simplest phenomenological models is to subtract future land cover changes from a species' current distribution to estimate extinction risk (*6*). Species-area models use the empirical relationship between area and species number to estimate species committed to extinction following habitat loss (*10*). Niche-based models (or bioclimatic envelope models) employ statistical relationships between current species distributions and environmental variables, such as temperature and precipitation, to project the future distribution of a species under climate change (*11*). Dose-response relationships depend on experimental or observational data to estimate the impacts of drivers on biodiversity, e.g., the level of nitrogen deposition on mean species abundance (*12*, *13*). Process-based models simulate processes such as population growth or mechanisms such as ecophysiological responses (*14*). Dynamic global vegetation models (DGVM), which play an important role in many scenarios, are complex ecosystem models integrating processes such as photosynthesis, respiration, plant competition for resources and biogeochemical cycles (*15*). Marine trophic models simulate the biomass dynamics at different levels of the trophic web using mass-balance equations and can be used to assess the population impacts of harvesting (*16*).

Here we review global-scale biodiversity scenarios for each of the four biodiversity metrics outlined above. We analyze sources of variation within and between scenarios, coherence between models and observations, links between biodiversity and ecosystem services and relevance of scenarios to policy.

Species extinctions

Scenarios for terrestrial ecosystems project that future species extinction rates will greatly surpass background rates estimated from the cenozoic fossil record (*17*) and could exceed recent rates of extinction by more than two orders of magnitude (Fig. 2, table S1). There is great variation in projected future extinction rates both within and between studies, with three factors explaining much of this variation. First, the degree of land-use and climate change explains a substantial fraction of the range of projected extinctions within studies [e.g., projected vertebrate extinctions are 11-34% for 0.8-1.7°C global warming vs. 33-58% for >2.0°C warming in (*7*)], indicating that limitation of land-use change, especially in tropical and subtropical regions, and aggressive climate mitigation could substantially reduce extinction risks. Second, an important contribution to the broad range of projections within studies is a lack of understanding of species ecology, especially migration rates [e.g., the highest projected extinction rates are 38% with unlimited migrations rates vs. 58% with no migration in (*7*)] and habitat specificity [e.g. in (*18*) the highest extinction rates are 7% for broad habitat specificity vs. 43% for narrow habitat specificity], emphasizing the need for research on these fundamental aspects of species ecology and their incorporation into global models (*14*). Third, a large fraction of variation between studies appears to arise from differences between modeling approaches [in particular, compare the two studies of global bird extinctions (*6*, *19*)]. The few rigorous inter-model comparisons currently available have also found large differences in model sensitivity (*20*, *21*).

Quantitative scenarios of global extinctions for freshwater and marine organisms are rare. One model for freshwater ecosystems, based on the relationship between fish diversity and river discharge, projects 4-22% (quartile range) fish extinctions by 2070 in about 30% of the world rivers, because of reductions in river discharge from climate change and increasing water withdrawals (*22*). Models of global change impacts on marine organisms have focused on local extinctions, shifts in species distributions and changes in abundance (*23*). The limited amount of extinction scenarios for aquatic ecosystems suggests that quantitative data for global extinctions models are still lacking (*24*), emphasizing the need for improved monitoring of marine and freshwater organisms.

Projections of species extinction rates are controversial because of methodological challenges and because of the lack of agreement with extinction patterns in the recent and distant past (*25*, *26*). First, models project the fraction of species "committed to extinction", primarily resulting from decreases in range size, habitat area or, for freshwater taxa, river flow. However, the lag time between being "committed to extinction" and actually going extinct may range from decades to many millennia (*13*, *25*), so future research must

focus on quantifying these time lags as they constitute windows of opportunity for restoration efforts to prevent future extinctions. Evidence from recent and historical land-use change and the paleontological record suggests that many species can persist for long periods, by exploiting secondary habitats or by surviving in small populations (*25*, *27*). This suggests that the realized extinction rates are likely to be lower and perhaps much lower than the "commited to extinction" rates shown in Fig. 2, and used in other comparisons of past and future extinction rates (*28*, *29*). Second, complex interactions between global change factors are not accounted for in models and these interactions could decrease or increase future extinction risks (*25*). These considerations and the range of projected terrestrial extinctions in Fig. 2 reflect general scientific agreement that uncurtailed rates of climate and land use change will increase extinction risks but that the magnitude of these risks is still uncertain.

Field and laboratory experiments mimicking reductions in species and functional group diversity have shown that species loss at local scales can have negative impacts on ecosystem services such as primary productivity, nutrient cycling, and invasion resistance (*3*). Extinctions of species that play dominant roles in ecosystem functioning, such as large predators and pollinators, could be extremely detrimental for ecosystem services (*30*). However, it has proved difficult to scale these studies up to regional or global scales.

Species abundances and community structure

Models project declines in the population abundances of species in both marine and terrestrial systems (*12*, *23*). Global scenarios for marine fisheries are based on a marine trophic model, Ecosim with Ecopath, which tracks functional groups of species, including multiple groups of primary producers, invertebrates and fish species (*16*). Model parameters are estimated from historic trends of biomass and catches. Future ecosystem dynamics are projected by optimizing fishing effort for a set of criteria, including profit, number of jobs, and ecosystem structure, with the weight given to each criterion depending on the scenario (*23*). The scenarios explored suggest that future increases in landings, partially driven by fisheries subsidies, can only be achieved by intensifying pressure on groups that are not currently fished in large quantities, often at lower trophic levels, leading to a decline in the marine trophic index (*23*, *31*). In contrast, reductions in fishing effort and destructive fishing practices such as trawling would allow rebuilding of a number of major stocks (*31*, *32*).

For terrestrial systems, the GLOBIO model uses dose-response relationships to estimate changes in mean species abundance as a function of land-use change and other drivers

(*12*). For instance, the model uses a matrix of changes in mean local species abundance following conversion between two land-use categories, derived from empirical studies. Scenarios developed using GLOBIO project a decline of 9-17% in mean species abundance by 2050 relative to 2000 (*33*, *34*). The most favorable scenarios involve a doubling of protected areas to 20% of total land area or focusing on sustainability at all levels, with limited human population and consumption growth. The GLOBIO model has also been used to hindcast changes in mean species abundance from 1970 to 2000 (*35*). The modeled decline of 6% over this period is much smaller than the decline of 21% recorded by the Living Planet Index through direct observations of terrestrial species abundance (*5*). However, large differences in how these two indicators are calculated and potential biases in data in the Living Planet Index (*36*) and in the database of GLOBIO make direct comparison impossible and underscore the need to harmonize model and data indices (*35*).

Trade-offs between provisioning services and regulating services are apparent in both marine and terrestrial biodiversity scenarios, and can be a consequence of changes in community structure. For instance, increases in fish provisioning are achieved at the cost of changes in the food web structure with potential impacts on the regulation of trophic cascades (*37*), and often at the cost of sacrificing the long-term sustainability of the service (*32*). Similarly, in Mediterranean ecosystems, modification of forest composition to favor rapid-growth species may lead to decreased fire resilience (*35*).

Habitat loss and degradation

Habitat loss and degradation in terrestrial ecosystems cover a wide range of alteration of natural and semi-natural ecosystems by human activities. Arguably, the conversion of forest to agricultural systems has been the most important of these habitat changes. In most land-use scenarios, global forest area declines slightly over the next few decades (Fig. 3), resulting from extensive deforestation in tropical forests and sub-tropical woodlands, which is partially offset by increased forest cover in the Northern Hemisphere (*38*, *33*, *34*). Therefore, in terms of impacts on biodiversity, the overall picture is worse than the global forest projections indicate, as the habitat losses in the tropics cannot be directly compensated by forest habitat gains in temperate regions, and some of the forest gains in both regions are due to the expansion of species-poor plantations.

A striking characteristic of some studies is that large within-study divergences in socio-economic development pathways lead to relatively small differences in the projected global forest cover (Fig. 3), as well as other measures of global biodiversity change (*12*). The most recent studies, i.e., the Intergovernmental Panel on Climate Change

Representative Concentration Pathways (IPCC RCP) (*2*) scenarios and Wise et al. (*39*), include more favorable trajectories, suggesting that the opportunities for habitat recovery may have been previously underestimated. In particular, Wise et al. (*39*) foresee large increases in global forest cover if global carbon taxes were to include all sources and sinks of carbon, thereby favoring protection of forests and improved agricultural efficiency. However, they also project massive deforestation if carbon taxes were to focus on fossil fuels only, stimulating massive dependence on bioenergy. This study and other recent global scenarios (*40*) emphasize the positive or negative impact that climate mitigation could have on biodiversity depending on how it is implemented. The ongoing land-use harmonization activity for IPCC Assessment Report 5, that connects land-use historical data together with future scenario data from multiple Integrated Assessment Models into a single consistent, spatially gridded set of land-use change scenarios, will open new opportunities for exploring the impacts of a broad range of possible land-use trajectories on biodiversity, and for enhancing the collaboration between the climate, socioeconomic, and biodiversity communities (*41*).

Climate change is projected to cause major changes in marine habitats, through increased water temperature, ocean acidification and expansion of oxygen minimum zones (*42*). Tropical corals are vulnerable to climate change because increases in sea surface temperature of 1ºC for more than eight weeks can lead to severe coral bleaching, with the breakdown of the endosymbiosis between corals and zooxanthellae (*43, but see 44*). Phenomenological models applied to climate change projections foresee that severe tropical coral bleaching may occur on average every two years by 2050 (*43*). In addition, ocean acidification reduces the availability of carbonate for calcification, slowing the growth of corals, and along with bleaching and other stressors, is projected to lead to widespread degradation of coral reefs and the ecosystem services they provide such as fisheries, storm surge protection and income from tourism (*45*).

In freshwater ecosystems, modeling of habitat degradation has focused on the abiotic components of ecosystems, such as river discharge and nutrient loads, and how those changes will directly affect ecosystem services such as water provisioning and regulation of water quality (*1, 46*). In some cases, the same drivers affecting ecosystem services may also affect biodiversity. For example, scenario studies project increased water use as a consequence of population growth and rising water demands by agriculture and industry (*33*), and increase in eutrophication due to agriculture and urban pollution (*46*). This will lead to both water provisioning shortages and declines in biodiversity (*13*).

Shifts in the distribution of species and biomes
DGVMs project large shifts in the distribution of terrestrial biomes, with required velocities to accommodate temperature change reaching more than 1 km yr^{-1} in some biomes (*47, 48*). These shifts are expected to cause the rearrangement of ecosystems, including the creation of novel communities (*49*). For instance, the northern limit of boreal forests is projected to move further north into the arctic tundra, while the southern limit will experience dieback, giving way to temperate conifer and mixed forest (*15, 47*). DGVM projections are in qualitative agreement with the paleontological record, which indicates that climate change has resulted in large shifts in the distribution of vegetation types in the past. However, there is uncertainty in the extent of biome changes simulated by DGVMs, even in analyses using common climate scenarios, with some global vegetation models projecting modest shifts and little vegetation dieback and others projecting large-scale biome shifts over much of the globe during the 21st century, underscoring the pressing need to benchmark models against data (*15*).

DGVMs provide a powerful means to explore the relationship between ecosystem services and shifts in the distribution of biomes or functional groups of plants because vegetation type plays a dominant role in controlling terrestrial provisioning, supporting and regulating services. Recent simulations with DGVMs suggest that the Amazon forest may reach a tipping point due to a combination of deforestation, climate change and fire, leading to drier conditions and an irreversible shift to savannah-like vegetation (*50*). If pushed beyond this point, the Amazonian forest could release large quantities of carbon into the atmosphere and modify rainfall patterns over large areas of South and southern North America (*50*).

Bioclimatic models of the ranges of marine organisms also suggest poleward shifts because of climate change (*47*). Average speeds for demersal species may exceed 4 km yr^{-1} in certain regions (Fig. 4A), consistent with recent trends observed in the North Sea for widespread thermal specialists (*51*). Projected shifts for pelagic species are foreseen to be more rapid than demersal species (Fig. 4B), due to the higher motility of pelagic species and larger changes in ocean conditions in the surface layer. Furthermore, rates of shift can be more than double in a high-range climate change scenario (A1B) compared to a low-range scenario (committed climate change experiment) (*52*), suggesting that limiting greenhouse gas emissions will allow more time for species to adapt. The capacity of freshwater species to move polewards in response to climate change will be more limited due to the linear nature of many freshwater ecosystems. This problem will be particularly acute in river basins with an East-West configuration (*35*). Species may also respond to warming by

migration to higher elevations in terrestrial systems (*19*), and greater depths in marine systems (*53*).

Given the rapidly growing use of bioclimatic models for decision support, such as studies of the impacts of climate change on future costs and efficiency of networks of protected areas (*54*) and development of adaptive forestry management schemes (*55*), it is important that model projections are accurate. Bioclimatic models can, in some cases, predict the direction of range contractions or expansions (*56*) and population increases or declines (*57*) observed in the last few decades. However, insufficient treatment of key mechanisms, such as migration, biotic interactions, and interactions between drivers such as climate and land-use, still limits the accuracy of future range projections from bioclimatic models (*14*).

Challenges in improving biodiversity scenarios

Reducing uncertainty within and among model projections is urgent. More attention must be paid to evaluating model projections using indicators that allow comparisons between models and between models and data. Key components of this effort will be the development of comprehensive biodiversity monitoring through efforts such as the Global Biodiversity Observation Network or GEO BON (*58*), and the harmonization of the biodiversity indicators used by the data and scenarios communities.

The importance of the drivers of biodiversity change differs across realms, with land-use change being a dominant driver in terrestrial systems, overexploitation in marine systems, while climate change is ubiquitous across realms (*28*). Available models reflect these differences, but fail to account for the full set of major drivers of future biodiversity change — for instance, the lack of global models of the impact of dams and pollution on freshwater biodiversity. Modeling climate change impacts on biodiversity is currently tractable and popular, in part because a wide range of climate scenarios and bioclimatic envelope modeling tools are readily available, but it is vital to develop models of other important drivers and their interactions (*59*). This will require the development of mechanistic models linking changes in land use, pollution levels, and biotic competition (e.g. invasive species) to population dynamics of individual species through changes in life-history parameters such as survival and dispersal, using techniques that are scalable across space and across species assemblages (*10*, *14*). This approach has recently been explored to assess how interactions between life history and disturbance regime mediate species extinction risk under climate change (*60*).

To better inform policy, scenarios must move beyond illustrating the potential impacts of global change on biodiversity towards more integrated approaches that account for the feedbacks that link environmental drivers, biodiversity, ecosystem services and socio-economic dynamics. Current global biodiversity models rarely relate estimates of biodiversity loss to ecosystem services, infrequently explore policy options (*but see 12*, *23*) and do not account for the feedbacks from changes in biodiversity and ecosystem services to societal response (Fig 1, dashed arrows). Introducing complex feedbacks to biodiversity scenarios will require moving away from the relatively linear, non-interactive relationships between the social and natural sciences (Fig. 1, thick arrows pointing downwards) towards a more interactive, interdisciplinary association (*61*).

The likely imminent launch of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) opens an opportunity to develop a major effort to improve and evaluate biodiversity scenarios. Improved biodiversity models will strengthen the role of scenarios in testing policies to minimize the impacts of human activities on biodiversity and maxime the ecosystem services provided by biodiversity. As such, scenarios should play a large role in IPBES and in helping to achieve the targets to be set in the new strategic plan of the Convention on Biological Diversity (*62*).

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64. Materials and methods are available as supporting material on *Science* Online.

65. This work was developed in the context of a scenarios synthesis coordinated by DIVERSITAS and UNEP-WCMC for the Secretariat of the Convention on Biological Diversity (*35*), with financial support from the Department of the Environment, Food and Rural Affairs of the UK, the European Commission and UNEP. We thank Lucy Simpson for organizing a workshop. H.M.P. was supported in part by grant PTDC/AMB/73901/2006 from Fundação para a Ciência e Tecnologia.

Supporting Online Material

Fig. 1. Overview of methods and models commonly used for constructing biodiversity scenarios. Some models include several components of this figure, such as the integrated assessment model IMAGE (*1*), or the marine trophic model 'Ecosim with Ecopath' (*23*). Black arrrows indicate key linkages treated in biodiversity scenarios. Dashed grey arrows indicate linkages that are absent in current biodiversity scenarios. In some cases, impacts on ecosystem services may be mediated by changes in the abiotic condition of ecosystems (small arrow from direct drivers to ecosystem services).

Fig. 2. Comparison of recent and distant past extinction rates with rates at which species are 'committed to extinction' during the 21st century (*64*). E/MSY is number of extinctions per million species years. "Fossil record" refers to the extinction rate of mammals in the fossil record (*17*). "20th century" refers to documented extinctions in the 20th century - mammals (upper bound), birds, and amphibians (lower

bound) (*17*). "21st century" refers to projections of species committed to extinction according to different global scenarios: vascular plants (*38*, *18*), plants and animals (*7*), land birds (*6*, *19*) and lizards (*63*). Extinction rate caused by each driver and total extinction rates are discriminated, when possible.
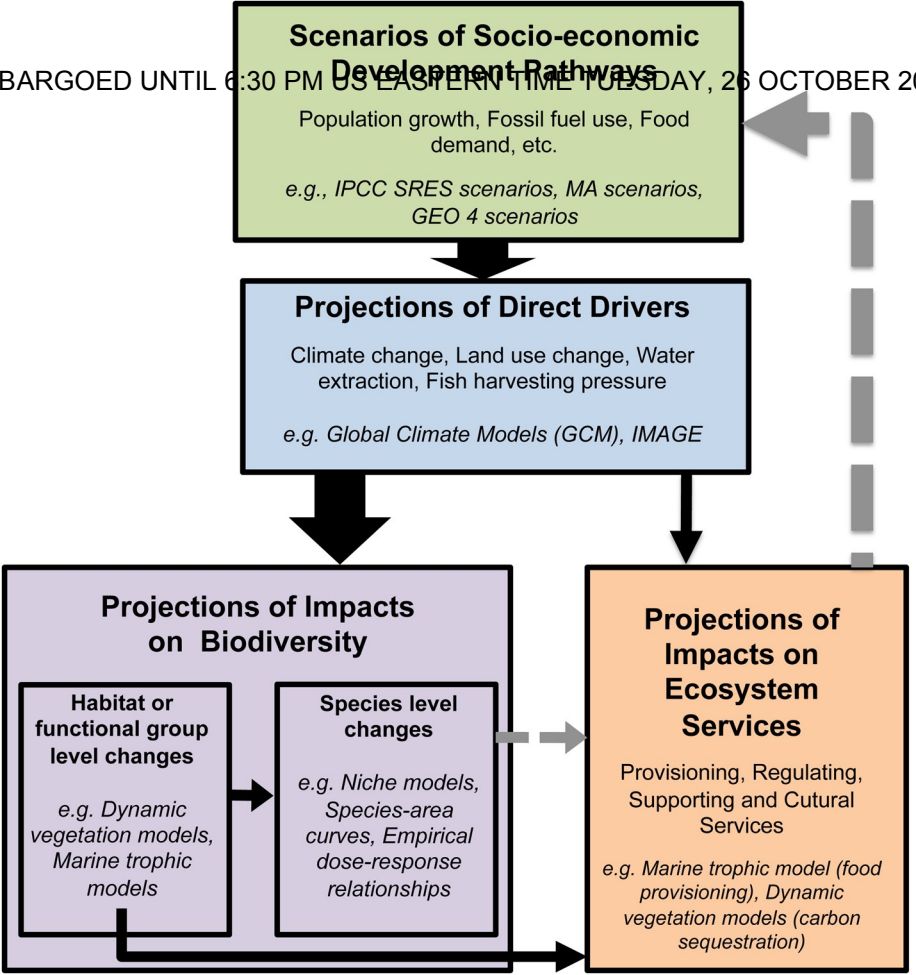
Fig. 3. Change in the extent of forests to 2050 in different global scenarios (*64*): MA scenarios (*1*), GBO2 scenarios (*34*), GEO4 scenarios (*33*), MiniCAM scenarios (*39*), RCP scenarios for IPCC-AR5 (*41*). For each study, trajectories of the two most contrasting scenarios are shown. By 2050, the envelope of scenarios using the IMAGE model (MA, GBO2, GEO4) is narrower than the envelope of scenarios based on the MiniCAM model.

Fig. 4. Projected rate of range shifts in marine organisms caused by climate change from 2005 to 2050 (*52, 64*). (A) Latitudinal shift of demersal species (excluding areas > 2000 m in depth because of under-sampling of the deep sea region). (B) Latitudinal shift of pelagic species. The projections are based on bioclimatic envelope models for 1,066 species of fish and invertebrates, under IPCC SRES A1B. For each map cell, the mean shift of the range centroids of the species currently present in that cell is given.
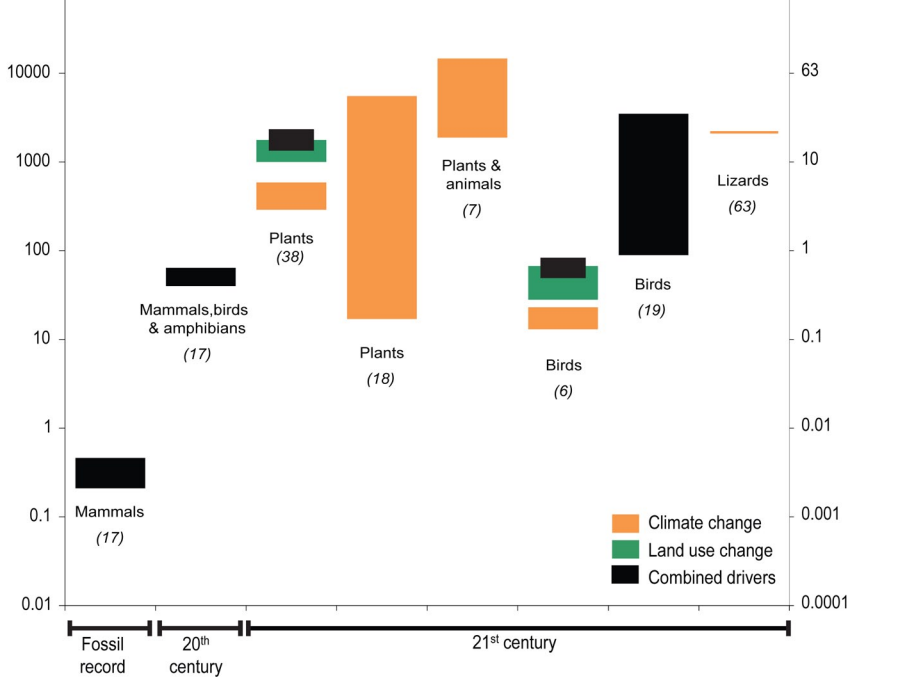
Table 1. Examples of biodiversity scenario studies highlighting methods used to calculate impacts of global change on several biodiversity metrics. Socio-economic scenarios: Millennium Ecosystem Asessment (MA), Global Biodiversity Outlook 2 (GBO2), Global Environmental Outlook 4 (GEO4), IPCC Special Report on Emission Scenarios (IPCC SRES), International Assessment for Agricultural Science, Technology and Development (IAASTD). Direct drivers: land-use change (LUC), climate change (CC), nitrogen deposition (N), water use and fishing effort. Projections of direct drivers: indicates model that was used to simulate future changes in direct drivers (GCM = General Circulation Model with specific climate model indicated in parentheses).
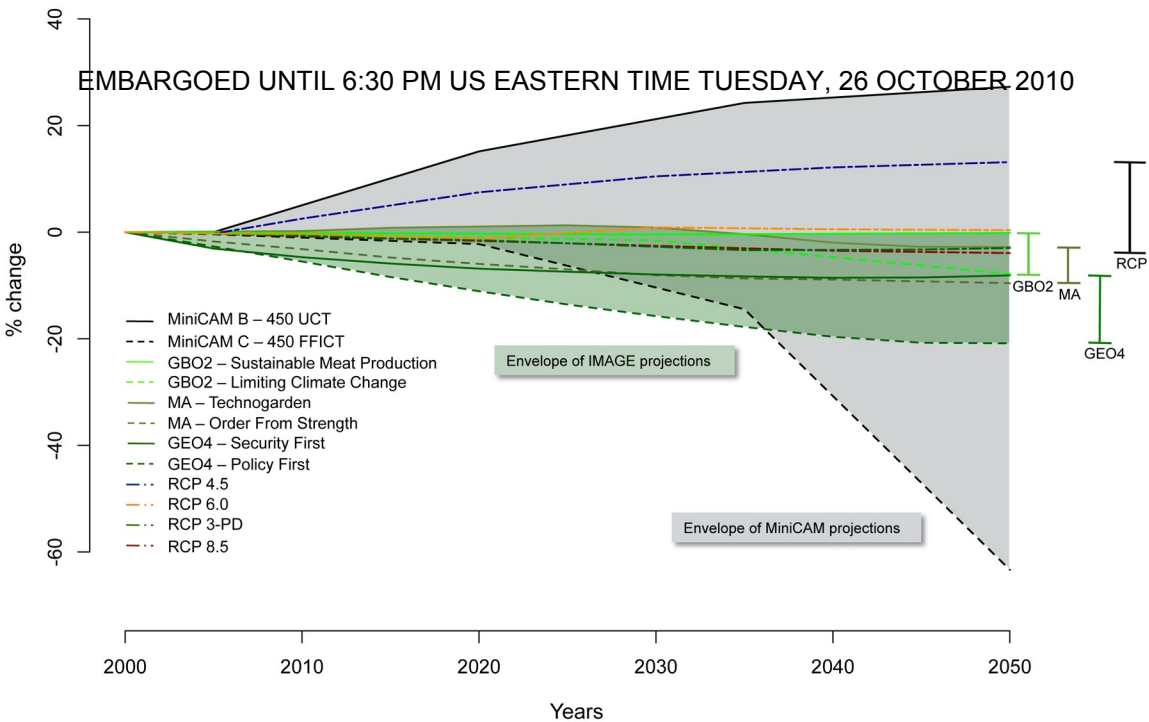
	Study	Socio-economic scenarios	Direct drivers	Projections of direct drivers	Projections of impacts on biodiversity	Metric of biodiversity and ecosystem service	Year
Terrestrial	(*38*)	MA	LUC, CC	IMAGE	Species-area relationships.	Species extinctions (plants) and habitat loss.	2100
	(*7*)	IPCC SRES and others	CC	GCM (HadCM2)	Niche based models. Range changes converted to extinction risk using species-area curves or IUCN status.	Species extinctions (plants and animals)	2050
	(*6*)	MA	LUC, CC	IMAGE	Habitat loss from current species ranges.	Species extinctions (birds)	2100
	(*12*)	GBO2	LUC, CC, N	IMAGE	Dose-response model (GLOBIO).	Species abundance changes	2050
	(*15*)	IPCC SRES	CC	GCM (HadCM3)	Dynamic global vegetation models.	Functional group range shifts (plants) and carbon sequestration	2100
Freshwater	(*22*)	MA	Water use & CC	Water-GAP	Phenomenological model relating river discharge to fish species richness.	Species extinctions (fishes)	2100
Marine	(*23*)	GEO4, IAASTD	Fishing effort	Ecosim	Marine trophic model (Ecosim with Ecopath).	Functional group abundance changes and fish landings	2050
	(*43*)	IPCC SRES	CC	GCMs (HadCM3, PCM)	Phenomenological model relating sea surface temperature to bleaching frequencies.	Habitat loss of tropical coral.	2100
	(*52*)	IPCC SRES	CC	GCMs (GFDL CM 2.1)	Niche based models.	Species range shifts (vertebrate and invertebrates)	2050

E/MSY

% extinctions per century

Mammals
(17)

Mammals, birds & amphibians
(17)

Plants
(38)

Plants
(18)

Plants & animals
(7)

Birds
(6)

Birds
(19)

Lizards
(63)

Climate change
Land use change
Combined drivers

Fossil record

20th century

21st century

EMBARGOED UNTIL 6:30 PM US EASTERN TIME TUESDAY, 26 OCTOBER 2010

Legend:
- MiniCAM B – 450 UCT
- MiniCAM C – 450 FFICT
- GBO2 – Sustainable Meat Production
- GBO2 – Limiting Climate Change
- MA – Technogarden
- MA – Order From Strength
- GEO4 – Security First
- GEO4 – Policy First
- RCP 4.5
- RCP 6.0
- RCP 3-PD
- RCP 8.5

Envelope of IMAGE projections

Envelope of MiniCAM projections

y-axis: % change
x-axis: Years

RCP, GBO2, MA, GEO4
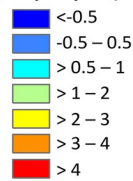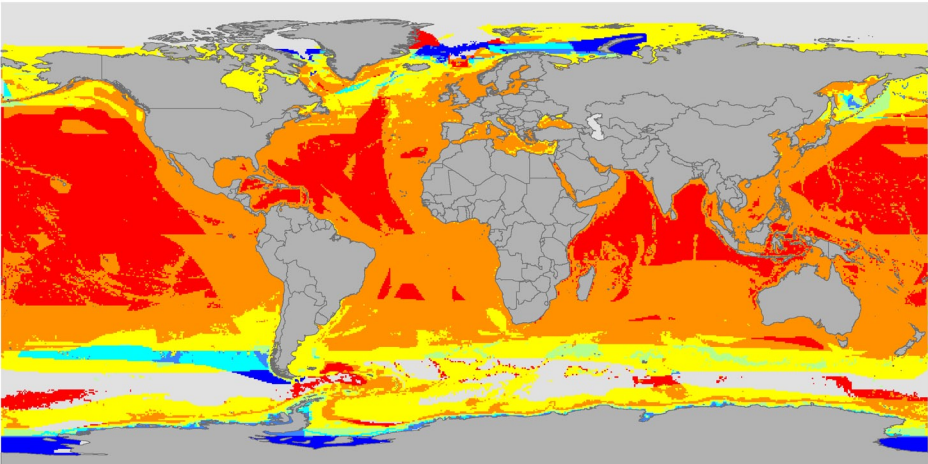
EMBARGOED UNTIL 6:30 PM US EASTERN TIME TUESDAY, 26 OCTOBER 2010
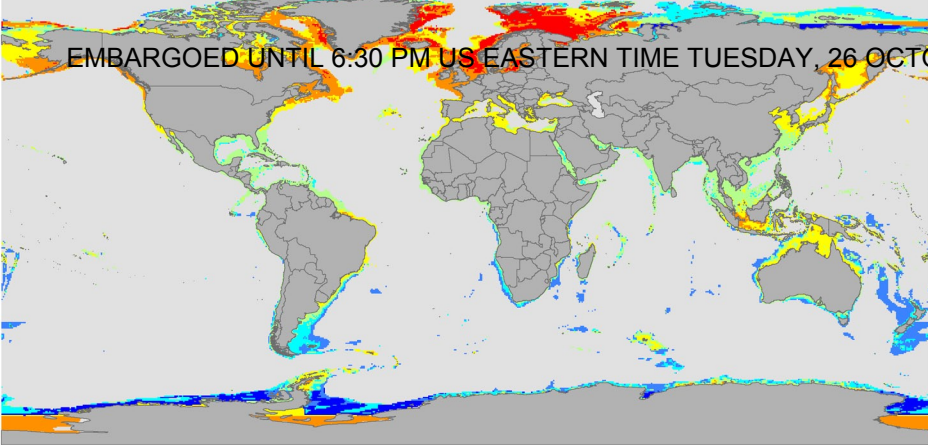
Poleward shift (km per year)

A:
- <-0.5
- -0.5 – 0.5
- > 0.5 – 1
- > 1 – 2
- > 2 – 3
- > 3 – 4
- > 4

B:
- <-0.5
- -0.5 – 0.5
- > 0.5 – 1
- > 1 – 2
- > 2 – 4
- > 4 – 6
- > 6