Developed and developing countries will suffer the consequences of climate change, but differ in both their responsibility and how badly it will affect their ecosystems.

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Global anthropogenic climate change is contributing to the considerable economic imbalance between rich and poor nations. The changing climate will inevitably influence natural resources, but it is the poorest countries—where humans rely most directly on natural systems for their livelihoods—that are expected to experience the greatest changes. Accordingly, the resources, economies and societies of these nations are likely to be most severely affected, despite the fact that they are least able to cope with—and are least responsible for—climate change itself. Here, we analyse which countries and regions will suffer the most severe changes to their natural ecosystems and biodiversity, and how the responsibility for those changes is distributed across the world.

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On a broad scale, geographic variations in temperature, rainfall and seasonality determine ecosystem productivity and species diversity. Ecosystems therefore respond to changes in temperature and precipitation, which inevitably have an impact on biodiversity. Recent shifts in the distributions of various species towards the poles and to higher altitudes (Parmesan & Yohe, 2003; Root et al, 2003; Walther et al, 2005; Wilson et al, 2005; Franco et al, 2006; Hickling et al, 2006), and the extinction of more than 1% of all amphibian species (Pounds et al, 2006), indicate that climate change is already having a major impact on biodiversity. Climatic changes are also expected to alter the distributions of most types of vegetation (Cramer et al, 2001; Scholze et al, 2006) and there is already evidence of a shift from deciduous woodland to evergreen forest in part of southern Europe (Walther et al, 2002). Such changes will have implications both for biodiversity (Malcolm et al, 2006) and for the humans that rely on natural ecosystems to survive.

Indeed, vegetation change is one of the most important results of a changing climate because it affects the habitats of most terrestrial species. Dynamic global vegetation models (DGVMs) have been developed to simulate how various climates and atmospheric carbon dioxide (CO₂) concentrations could affect vegetation around the world (Cramer et al, 2001; Prentice et al, 2007). We used the empirically tested Lund–Potsdam–Jena (LPJ)-DGVM (Sitch et al, 2003) to calculate how temperature, precipitation and atmospheric CO₂ might affect the growth of various plant types between two periods, 1931–1960 (hereafter referred to as ‘1945’) and 2041–2050 (hereafter referred to as ‘2045’), in a moderate climate-warming scenario (see below). On the basis of the distribution of plant types, we categorized each 0.5° cell of land surface into one of 18 major vegetation categories—such as tropical seasonal forest or dry grassland (Hickler et al, 2006)—and considered a change between any two categories (or ‘biomes’) to be a major vegetation shift (Fig 1A).

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Our simulation showed that by 2045, the most extensive changes are likely to occur in the parts of the world that are already dry—such as central Asia—and along the existing boundaries of major vegetation types (Fig 1A). The model predicts increases in the amount of vegetation and woody cover in many dry areas because an increase in atmospheric CO₂ will allow plants to survive increased levels of drought. Furthermore, the boundaries of major vegetation types will shift along both moisture and temperature gradients.

However, the major changes will not be restricted to regions where the vegetation is projected to shift from one biome to another. In many places, the total amount of vegetation will change considerably, but not necessarily enough to be placed into a different vegetation category. It is useful, therefore, to calculate changes in vegetation as a continuous variable. Hence, we expressed the LPJ-DGVM output as the predicted area of woody plant leaves per unit
ground area—as woody plants are important structural components of vegetation and a habitat for many species—in response to climate change. In this case, the simulation predicted vegetation change to be widespread and not just in regions where a change in biome is expected (Fig 1B).

We then correlated the predicted changes in vegetation—which will affect most animals and plants—with the number of species in each country to establish whether the changes are greatest in countries that contain relatively large or small numbers of species. We analysed three categories: the total number of species per country, the number of endemic species per country—that is, those with global distributions restricted to a single country—and the number of species that are already listed as threatened. As the data relating to global biodiversity are far from complete, we had to analyse relatively well-known groups. For total and endemic species, we considered the number of mammal, bird, reptile, amphibian and plant species recorded in each country (http://earthtrends.wri.org). For threatened species, we analysed the number of mammal, bird, reptile and amphibian species that are listed as critically endangered, endangered or vulnerable by the World Conservation Union (http://www.iucn.org).

Overall, vegetation change will disproportionately affect countries with high biodiversity. The proportion of land surface expected to change from one vegetation class to another (Fig 1A) within each country is positively correlated with the total number of species and the number of threatened species currently within those countries, but is not significantly correlated with the number of endemic species (the Spearman correlation coefficients and \( P \) values for \( n = 163 \) countries were: \( \rho = 0.298 \) and \( P < 0.01 \); \( \rho = 0.187 \) and \( P < 0.05 \); and \( \rho = 0.059 \) and non-significant, respectively). Similarly, the average woody plant cover change predicted by 2045 is positively correlated with the total number of species, the number of endemic species and the number of threatened species currently present (\( \rho = 0.277 \) and \( P < 0.01 \); \( \rho = 0.234 \) and \( P < 0.01 \); and \( \rho = 0.235 \) and \( P < 0.01 \), respectively). Therefore, most vegetation change is predicted to take place in countries that currently support high levels of biodiversity.

An alternative approach to modelling future vegetation changes is to analyse...
the changing climate directly—that is, whether the animal and plant populations in a particular location are likely to experience unprecedented new climatic conditions (Williams et al., 2007). For each 0.5° grid cell, we divided the expected average change in climate (from 1945 to 2045) by the 1931–1960 year-to-year climatic variability (standard deviation). We weighted four climate variables (December–January–February and June–July–August mean temperature, and December–January–February and June–July–August mean precipitation) equally to produce a standardized Euclidean distance (SED) as a single measure of change (Overpeck et al., 1985). SED values greater than 3.2 might be expected to cause major vegetation changes (Williams et al., 2007).

According to this model, the greatest potential changes will take place in parts of the tropics, where animals and plants will be exposed to climatic conditions far outside the range of conditions experienced between 1931 and 1960 (Fig 1C). Although the absolute magnitude of the projected temperature change is larger at high latitudes, the relatively high annual variation in the climate at high latitudes means that the species there have already experienced and survived a wide range of conditions around the historical mean, including occasional warm years. However, many of the predicted tropical climates will be new—that is, not experienced anywhere in the world before—and it is unclear exactly which species will be able to inhabit these areas (Williams et al., 2007). This index of change is positively correlated with total, endemic and threatened species numbers (the Spearman correlation coefficients and P values for n = 163 countries were: ρ = 0.194 and P < 0.05; ρ = 0.255 and P < 0.01; and ρ = 0.206 and P < 0.01, respectively). Hence, historically unprecedented climatic conditions are more likely to occur in countries with relatively high levels of biodiversity.

The other main approach used to assess biodiversity change is to match the geographic variation in the distribution of climate variables with the distribution of individual species, and to evaluate where these conditions might be found in the future (Williams et al., 2003; Thomas et al., 2004; McClean et al., 2005). We did not use this approach because we lacked detailed data on every species, but we used an analogue based on the observation that the ranges of many species change in response to climate change (Parmesan & Yohe, 2003; Root et al., 2003; Walther et al., 2005). The species that are most at risk of extinction through climate change are therefore those that are restricted to shrinking climates (Williams et al., 2003; Thomas et al., 2004; McClean et al., 2005). We can define areas of high risk as places where the existing local climate is shrinking markedly or has disappeared (Ohlemüller et al., 2006; Williams et al., 2007) using the same four climate variables as described above. Low-risk areas are those where the current climate is expected to become more widespread in the future.

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Most parts of the world are expected to exhibit changes to the 1945 climate by 2045 (Fig 1D). Some particular climates will disappear entirely, whereas others will still exist, but species will need to travel more than 1,000 km to reach them. Climate shrinkage is not correlated with numbers of species, endemic species or threatened species per country, so those with high biodiversity are no better or worse off than those with low diversity.

The magnitudes of the projected changes are large. Fig 1 shows that vast areas of the surface of the Earth will undergo one or more of the following: biome change, at least a doubling of foliage cover by woody plants, substantial alterations to climatic conditions and/or more than 80% reduction in analogous climate space within 1,000 km. As SED values are measured in units of standard deviations, an SED value of more than 4 in Fig 1C corresponds to the new average climatic conditions being equivalent to those historically expected based on the 1931–1960 climate only once in 15,000 years. Many species might need several centuries or even a millennium to move up to 1,000 km (Fig 1D; Parmesan & Yohe, 2003; Hickling et al., 2006), which implies that the range boundaries of many species will fail to keep up with the rate of climate change.

All eight of the significant relationships described above indicate that climate change will cause more severe alterations to ecological systems in high-biodiversity countries than in low-biodiversity countries.

This is of particular concern for threatened species, for which even a slight reduction in survival or reproductive success could lead to extinction. Species with small geographic ranges—endemic species—are also at risk because few are able to reach new countries or regions where the climate might be more suitable in the future (Williams et al., 2003; Malcolm et al., 2006).

Two of the four indices of biodiversity change show significant correlations with national wealth and CO₂ emissions (http://www.worldbank.org; http://www.eia.doe.gov). Greater changes in the cover of woody plants (Fig 1B) are expected in countries with low per capita and national gross domestic product (GDP), and with low per capita and total CO₂ emissions (the Spearman correlation coefficients and P values for n = 163 countries were: ρ = −0.161 and P < 0.05; ρ = −0.175 and P < 0.05; ρ = −0.210 and P < 0.01; and ρ = −0.233 and P < 0.01, respectively). The future climate is also expected to change most strongly—in terms of SED units (Fig 1C)—in countries with low per capita and total GDP, and low per capita and total CO₂ emissions (ρ = −0.432 and P < 0.001; ρ = −0.393 and P < 0.001; ρ = −0.447 and P < 0.001; and ρ = −0.388 and P < 0.001, respectively). This shows that those countries that are least responsible for climate change—and that do not have the economic means to develop and adopt adaptive strategies—will experience the greatest changes, which will severely affect their biodiversity. Although the other two measures of biodiversity impact do not correlate with wealth and emissions, they still reveal a mismatch between the origins of the problem and its consequences. Emissions will increase most rapidly in emerging economies between now and 2045, and, although they might fall in the richest countries (Kintisch, 2006), it will not be sufficient to change the overall conclusion.

The mismatch between the responsibility for, and the consequences of, climate change implies that some countries are in fact exporting the biological effects of climate change to others. To calculate whether each country is a net exporter or importer of change to biological systems—which is equivalent to a climate-change ecological footprint—we estimated the difference between its contribution to global climate change (in terms of 2004 fossil fuel CO₂ emissions) and the percentage of the total global impact on biological systems.
that is taking place in that country. We combined four change metrics—proportion of land surface with biome change, change in woody plant leaf area index, climatic deviation and proportional climate shrinkage or expansion (Fig 1)—with four risk types—basic risk, and risk multiplied by number of species, endemic species and threatened species—per country, to estimate the potential biodiversity impact in 16 ways. For example, the total impact of biome changes on species in Argentina was estimated to be the proportion of its 0.5° grid cells predicted to change from one biome category to another multiplied by the total number of species in Argentina. This was divided by the expected sum of these values for all countries, to estimate the proportion of the worldwide impact taking place within Argentina. This type of analysis was repeated for the 16 combinations of change metrics and risk types.

The emissions percentage minus the impact percentage allowed us to calculate 16 export/import ratings for each country, the average of which is shown in Fig 2. We found that 48 countries export biodiversity change through emissions, and the remaining 115 countries import changes. In total, 75% of the exported changes to biodiversity originate from just seven countries, and 90% originate from 16 countries. The net contribution of each country is significantly correlated with both its total and per capita GDP (the Spearman correlation coefficients and P values for n = 159 countries were: ρ = 0.423 and P < 0.001; and ρ = 0.512 and P < 0.001, respectively). Hence, the richest countries are responsible for the greatest change to global ecosystems elsewhere.

Given that it is ultimately impossible to predict the global climate in 2045, we deliberated as to whether our general conclusions are likely to hold true under various scenarios based on the possible development of the world economy and greenhouse gas emissions during the twenty-first century. Various general circulation models (GCMs) can be used to assess how CO2 emissions will affect the climate. We used two models and two ‘storylines’ to assess whether ‘optimistic’ and ‘pessimistic’ views of future climate change would alter our predictions of biodiversity change. In the results described above, we used the Special Report on Emissions Scenarios (SRES) B1 storyline—one of the lowest emissions scenarios that describes a future moving rapidly towards a service and information economy with clean and energy-efficient technologies (IPCC, 2001, 2007). To assess the climatic effects of this storyline, we used data generated by the UK Hadley Centre model of climate change (HadCM3), which produces relatively high levels of warming. When combined with the optimistic SRES B1 storyline, the HadCM3 model represents a medium projection of future global warming (IPCC, 2001).
Although it is clear which countries are most responsible for these changes, alleviating the situation is far more difficult. Ecosystems support the livelihoods of humans across the globe, but this link is often closest in relatively poor countries. Changes in the distributions of plant species might affect cultural knowledge about traditional medicines, crop cultivation, livestock husbandry, and the management of pests and diseases. Finding a mechanism to recompense countries for the human and economic suffering caused by biodiversity changes is problematic.

Major CO₂-emitting countries now recognize the need for climate ‘mitigation’, some countries are in fact exporting the biological effects of climate change to others. which is the term used for measures that limit the amount of climate change—principally, limiting emissions and removing greenhouse gasses from the atmosphere (United Nations Framework Convention on Climate Change, 1997). However, getting all relevant parties, including the USA, China and India, to agree to binding targets in a post-Kyoto treaty is another matter. In the absence of a global treaty, most of these countries will still take some steps to reduce their global carbon footprint, relative to what it would have been in the absence of such measures, even if their total carbon footprint is actually still increasing.

Countries are also starting to develop adaptive strategies to deal with the effects of climate change. However, adaptive measures have limited global reach. If high-emissions countries with relatively low biodiversity are truly worried about the impact of climate change on biodiversity, the most appropriate location for action will be in countries where the most change will take place. ‘Carbon-off-setting’ measures are one possible strategy to allow a polluting person, organization or country to make payments that are used to sequester the carbon they are releasing. Various options are available and relevant to biodiversity, such as replanting forests and supporting countries to protect and maintain existing natural vegetation. Avoiding deforestation is potentially more effective than replanting because carbon is released from the vegetation and soil more rapidly when a forest is destroyed, and because long-established forests support much higher levels of biodiversity. If avoiding deforestation and devegetation in general could be targeted towards high-biodiversity regions, it could potentially lead to a substantial increase in the finances available to maintain global biodiversity and ecosystems. However, great care must be taken that our responses to climate change do not create more problems than they solve. For example, massive increases in bioturf production might increase competition for land, possibly displacing food production and increasing the destruction of natural habitats.

In conclusion, potential ecosystem changes are likely to be largest in the countries that have the highest levels of biodiversity. Vegetation changes and the extent to which the future climate will lie outside historical bounds are predicted to be greatest in countries that contain large numbers of species overall, as well as large numbers of endemic and threatened species. The impacts will be felt disproportionately by countries with relatively low fossil fuel-based CO₂ emissions and low GDPS. Finding ways to direct resources to help such countries adapt to climate change is a daunting task.

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