

Future battlegrounds for conservation under global change

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Global biodiversity is under significant threat from the combined effects of human-induced climate and land-use change. Covering 12% of the Earth's terrestrial surface, protected areas are crucial for conserving biodiversity and supporting ecological processes beneficial to human well-being, but their selection and design are usually uninformed about future global change. Here, we quantify the exposure of the global reserve network to projected climate and land-use change according to the *Millennium Ecosystem Assessment* and set these threats in relation to the conservation value and capacity of biogeographic and geopolitical regions. We find that geographical patterns of past human impact on the land cover only poorly predict those of forecasted change, thus revealing the inadequacy of existing global conservation prioritization templates. Projected conservation risk, measured as regional levels of land-cover change in relation to area protected, is the greatest at high latitudes (due to climate change) and tropics/subtropics (due to land-use change). Only some high-latitude nations prone to high conservation risk are also of high conservation value, but their high relative wealth may facilitate additional conservation efforts. In contrast, most low-latitude nations tend to be of high conservation value, but they often have limited capacity for conservation which may exacerbate the global biodiversity extinction crisis. While our approach will clearly benefit from improved land-cover projections and a thorough understanding of how species range will shift under climate change, our results provide a first global quantitative demonstration of the urgent need to consider future environmental change in reserve-based conservation planning. They further highlight the pressing need for new reserves in target regions and support a much extended 'north-south' transfer of conservation resources that maximizes biodiversity conservation while mitigating global climate change.

Keywords: conservation planning; conservation priorities; protected areas; future land-use and climate change; biodiversity

1. INTRODUCTION

According to the *Millennium Ecosystem Assessment* (MA), the greatest threat facing biodiversity is the combined effect of landscape modification due to agricultural development, urbanization and forestry practices, and accelerated climate change (MA 2005). First studies have assessed the patterns and relative immediacy of future environmental change impacts on biodiversity (Sala *et al.* 2000) and key taxa (e.g. vascular plants, butterflies and birds; Warren *et al.* 2001; van Vuuren *et al.* 2006; Jetz *et al.* 2007), but availability of data has limited scale and generality of results. This may compromise the effective protection of threatened biodiversity and ecosystem services and further exacerbate the current gross disparities between global conservation priorities and funding (James *et al.* 1999; Halpern *et al.* 2006). With approximately 12% of the Earth's terrestrial surface formally protected against direct anthropogenic land-cover conversion (Chape *et al.* 2005), protected areas are crucial for conserving biodiversity and ecosystems, sustaining local livelihoods and supporting natural ecological processes beneficial to human well-being (Balmford *et al.* 2005; Naughton-Treves *et al.* 2005). However, current reserves are unlikely to be effective in buffering against global

climate change impacts as climate and habitat types shift in space. Recent warming has already affected some species' geographical or altitudinal ranges with clear consequences for species' protection (Walther *et al.* 2002; Parmesan & Yohe 2003; Wilson *et al.* 2005). But to date reserve planning has hardly considered the consequences of rapid climate change on biodiversity protection (but see Williams *et al.* 2005). This may jeopardize the long-term persistence of species within reserves, particularly those experiencing range shifts (Lovejoy 2005). The effectiveness of the global reserve network in protecting habitats and maintaining representative species diversity has previously been evaluated in relation to past human land-use change (Rodrigues *et al.* 2004b; Hoekstra *et al.* 2005). However, whether retrospective evaluations of protected area performance will continue to offer guidance about the future effectiveness of biodiversity protection remains untested. This has serious ramifications for effective long-term conservation planning.

Here, we undertake a first global assessment of the impact of future environmental change on the protection of biodiversity. We address the following questions critical to the successful prioritization of future conservation efforts. What is the geography of past and projected environmental change in relation to the existing reserve network? Are patterns of past human land-use change useful indicators of environmental change projected for

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the future? How do patterns of future conservation risk relate to current-day conservation value to determine conservation need? And how is conservation need distributed across regions worldwide and associated with critical national attributes such as governance and wealth? We base this first assessment on projections of future land-cover change, the current-day reserve network and present distribution of terrestrial vertebrates across biomes and nations of the world. This allows us to relate the exposure of current-day biodiversity and its protection to projected change, but it does not address potential shifts in species distribution under climate change, a quandary that is beyond the scope of this study. Potential range shifts—near impossible to quantify with full certainty—would modify our specific results, but unlikely overcome the strong patterns of exposure that emerge or invalidate the conceptual connections we develop.

We use land-cover projections across four socio-economic scenarios as provided by the MA. These scenarios are possible futures devised to compare four possible conditions in 2100 (MA 2005). They use plausible ranges of future greenhouse gas emissions and growth of human populations and economies to estimate the extent to which regions may be affected by anthropogenic climate change and agricultural/urban expansion. Four scenarios were developed that follow two principal development paths, one in which the world becomes initially globalized (*TechnoGarden*, TG; *Global Orchestration*, GO) and the other one in which it becomes increasingly regionalized (*Adapting Mosaic*, AM; *Order from Strength*, OS). These paths were matched by two contrasting approaches to management of environmental problems: reactive (OS, GO) and proactive (TG, AM). We overlay data on dominant current and projected future land-cover type (18 categories; 0.5° resolution) with the biogeographic and geopolitical regions of the world and then evaluate their vulnerability to future change in relation to their existing degree of protection.

2. MATERIAL AND METHODS

We examined the geography of global environmental change (past and future land-cover transformations) in relation to that of the global reserve network across biogeographic and geopolitical regions and 5° latitudinal bands worldwide. We assessed whether the patterns of past human land-use change are useful indicators of future environmental change by correlating the proportion of land impacted in the past with the proportion of land projected to be transformed in the future due to either climate or land-use change across ecological and political units. Furthermore, we defined ‘conservation risk’ as the area subjected to past or future land-cover transformation divided by area currently protected (Hoekstra *et al.* 2005) and evaluated its geographical association with present-day conservation value (here quantified as the endemic and globally threatened terrestrial vertebrate richness) across biogeographic regions and nations. Lastly, we investigated the confounding effects of national governance quality and wealth or conservation means (per capita gross domestic product (GDP) in 2004) on conservation need (defined as a combination of a nation’s global ranks in conservation risk due to land-use change and conservation value) among countries. Further details on the data used in the analyses are provided below.

(a) *Future land-cover transformations*

The MA developed four socio-economic scenarios that we used in this study to examine changes in global land-use and climate under diverse social and political futures (MA 2004; see electronic supplementary material for details). Because the scenarios are simulated under ‘extreme’ but realistically linked to present-day and near-future political decisions it is likely that the ‘actual’ future will be somewhere in between (Alcamo *et al.* 2005). An integral part of the MA scenario evaluations is the IMAGE v. 2.2 model (IMAGE-TEAM 2001), which provides information on current and future distributions for 18 different land-cover types in 0.5° resolution (66 661 terrestrial grid cells; area: approx. 2709 km² at the equator versus approx. 2226 km² at 40° latitude, arithmetic means), three of which indicate direct human impact from agriculture or urbanization. We evaluated the proportion of future transformation in land cover between 2000 (‘now’) and 2050, and 2100 within biogeographic, geopolitical regions and latitudinal bands. Changes from one of the 15 natural to one of the three human-induced land-cover types were regarded as transformation due to land-use change; conversely, changes from one natural to another natural land-cover type without direct human impact were considered as transformation due to climate change (Jetz *et al.* 2007). We acknowledge the relatively low resolution (0.5°, approx. 55 km near the equator) of the land-cover projections, the coarse scale of the land-cover types (18 classes) and the levels of uncertainty associated with climate projections (Intergovernmental Panel on Climate Change 2001) offered by the MA, but emphasize the unique integration of climate and land-use change impacts on the land cover this global modelling effort provides (MA 2005). The proportions of future land-cover transformation (due to climate and land-use change) by 2050 and 2100 are strongly correlated, and only results for changes between 2000 and 2100 are illustrated (electronic supplementary material, figure 5; all scenarios: Spearman rank correlation, $\rho = 0.82\text{--}0.98$; all $p < 0.01$). For the 2000–2050 results, see electronic supplementary material, appendices 3–4.

(b) *Past land-cover transformations*

Past global habitat loss was evaluated using a modified version (Hoekstra *et al.* 2005) of the Global Land Cover 2000 dataset (GLC 2000; European Commission Joint Research Centre 2002). We prefer the GLC 2000 to the MA dataset because the GLC 2000 continental land-cover maps comprise more land-cover classes (23 types) at much higher resolution (1 km) for all land masses except Antarctica. ‘Past land-cover change’ was calculated as the percentage of total land area (excluding areas that are non-terrestrial and with no data) classified as cultivated and managed, mosaics including cropland, and artificial surfaces and associated areas in the modified GLC 2000 in each biogeographic or geopolitical unit.

(c) *Biogeographic regions*

We estimated levels of land-cover transformation across 55 terrestrial biome–realm combinations. Each bio-realm represents a biogeographic region that is ecologically significant (Olson & Dinerstein 1998) and comprises a biome unique to each of the seven main biological realms. For our analyses, we used the classification and delineation of realms and biomes following the Terrestrial Ecoregions of the World (Olson *et al.* 2001). The bio-realms are distinct biogeographic regions with

unique ecosystems and species assemblages (Olson *et al.* 2001) and harbour a range of habitats, ecological interactions and evolutionary forces that support biodiversity, its evolutionary potential and valuable ecosystem services (Olson & Dinerstein 1998; Hoekstra *et al.* 2005). We excluded the mangrove biome due to spatial mismatches with land-cover and protected area data layers (Hoekstra *et al.* 2005), and the Antarctic tundra due to the lack of data from MA land cover. Use of bio-realms instead of, for example, much smaller ecoregions as units of analysis ensured sufficient sample size across all units given that MA land-cover projections were only available in 0.5° resolution.

(d) Geopolitical units and national governance quality and wealth

We estimated the proportion of area potentially transformed in 174 countries where corresponding protected area information is available. In addition, we assessed the relationship between quality of governance and wealth, and anticipated loss of natural habitats to only land-use change among nations. The governance indicators used measure the following six dimensions of governance in 2004: (i) voice and accountability, (ii) political instability and violence, (iii) government effectiveness, (iv) regulatory quality, (v) rule of law, and (vi) control of corruption (Kaufmann *et al.* 2005). These aggregated indicators are derived independently from the MA and are based on several hundred individual variables quantifying perceptions of governance, drawn from 37 separate data sources constructed by 31 different organizations. However, for ease of interpretation, we expressed the six highly correlated indicators as a single principal component (PC) that explained approximately 88% of variation in the data (henceforth governance quality). We use nation's per capita GDP (constant 2000 US dollars) in 2004 (the most recent year for which most data is available) as a surrogate for potential national conservation means (James *et al.* 1999; Bruner *et al.* 2004; <http://www.worldbank.org/data>). National governance quality scores and per capita GDP (log transformed) are strongly positively correlated (electronic supplementary material, figure 6; $Rho = 0.80$; $p < 0.01$, $n = 155$).

(e) Global protected area network

We used the 2005 World Database on Protected Areas (WDPA; WDPA-Consortium 2005), the most detailed global compilation of protected areas to assess the global extent of habitat protection. The WDPA was consolidated by an alliance of organizations with a chief goal to maintain a freely available, accurate, up-to-date and well-endorsed database on reserves. We included protected areas of all IUCN categories (i.e. I–VI; IUCN 1994) but excluded sites that were very small (less than 50 ha; representing less than 0.001% of all protected areas), marine protected areas, and sites lacking location information or permanent designation (Hoekstra *et al.* 2005). This scheme generated a list of 30 965 reserves covering a total of approximately 12 Mkm². Of these, approximately 53% with point location and area data were mapped as circles with suitable radii (approx. 3.4 Mkm²). We then calculated total and per cent area of each biogeographic and geopolitical unit, and latitudinal band, currently protected. We assume that protected areas will buffer against direct land-use change to exemplify the best-case scenario. This assumption, however, may be an unrealistic situation given the growing prevalence of 'paper' parks and deforestation within reserves, particularly across

the tropics (Curran *et al.* 2004). We did not explicitly consider management effectiveness of the reserves for our analyses, but attempt to address this issue by examining conservation risk in relation to national governance quality.

(f) Global endemism and endangerment of terrestrial vertebrates

We derived the numbers of unique and globally threatened terrestrial vertebrate species for each biogeographic and geopolitical unit using the global vertebrate occurrences (WildFinder; World Wildlife Fund 2006) and threat status (IUCN Red List of Threatened Species; IUCN 2006) databases. The WildFinder database contains occurrence data across the World Wildlife Fund's ecoregions for extant vertebrate species (4804 amphibians, 7533 reptiles, 9658 birds and 4716 mammals), was compiled from the primary and secondary scientific literatures, field guides or directly from experts and is based on the natural, historic ranges of species. It excludes species that are introduced, vagrants or migrants or present as human commensals (World Wildlife Fund 2006). We obtained species occurrence estimates for bio-realms (or countries) by assigning terrestrial ecoregions and their respective species occurrences to each of the 54 bio-realms (or 174 countries). Because some ecoregions overlapped with multiple countries, the species occurrence estimate for each country here represents the upper estimate limit. We define globally threatened species as those with critically endangered, endangered or vulnerable red list categories (IUCN 2001). However, due to nomenclature inconsistencies between the two databases, not every species from the WildFinder database has a corresponding IUCN threat status (amphibians: 70% with threat status (Red List $n = 5918$); reptiles: 97% ($n = 664$); birds: 99% ($n = 9934$); and mammals: 98% ($n = 4864$)). While an assessment of per-reserve species representation would be desirable, the spatial resolution of global extent of occurrence data for vertebrates (unless further refined) currently does not support such an analysis (Hurlbert & Jetz 2007). Correlation analyses were performed using the residuals from species-area regression analyses to account for the effect of area on endemic and threatened species richness per region (all variables were log transformed prior to analyses; Balmford & Long 1995).

3. RESULTS AND DISCUSSION

(a) Geography of future global environmental change

Patterns of globally projected environmental change vary markedly with latitude, change type and socio-economic scenario (figure 1). In addition, depending on the scenario choice, the relative effects of change type differ strongly across the world's terrestrial realms, biomes and geopolitical regions (see electronic supplementary material, figure 1). However, these relative differences between transformations due to climate and land-use change inherently stem from the underlying assumptions made during the MA projections. For instance, forecasted land-cover transformations from climate change are the greatest at high latitudes in the Northern Hemisphere (greater than 30°), up to 31% under the AM and GO scenarios (figure 1a), due to the high temperature increases forecasted for temperate and arctic regions. In contrast, future land-use change is projected to have the highest impacts near the equator, particularly under the OS and GO scenarios (up to 32%;

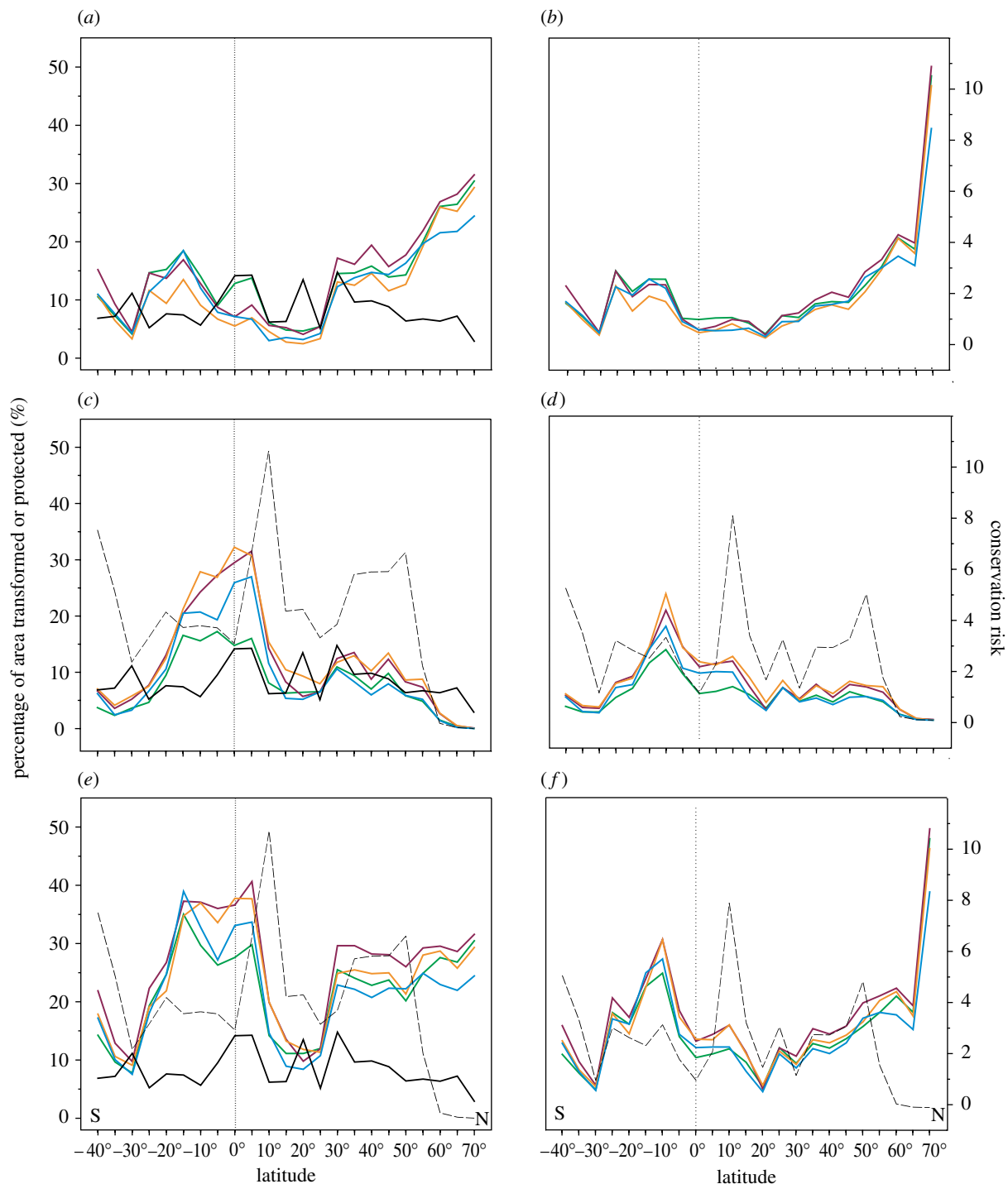


Figure 1. Patterns and interactions of past and future impact of environmental change and protection across latitudes. Projected land-cover transformation due to changes in (a) climate, (c) land-use and (e) combined, by 2100 under the four socio-economic scenarios AM (green line); GO (violet line); OS (orange line); and TG (blue line) generated from the MA (left vertical axis). ‘Past’ (dashed line) and ‘protect’ (black solid line) represent the estimated proportion of past land-cover change (due to past human impact) and protected area per 5° latitudinal band, respectively. The vertical dotted line indicates the equator and separates the Northern and Southern Hemispheres, indicated by N and S. Data at the extreme latitudes ($< -40^\circ$ and $> 70^\circ$) are truncated due to their relatively small land area. Average conservation risk is calculated for each 5° band as ‘past and projected change to current protection ratio’. Past conservation risk is calculated for past land-cover conversion due to land-use change, (d,f), using the GLC 2000 global land-cover dataset; future conservation risk is given for land-cover transformation due to (b) climate, (d) land-use and (f) combined changes in all areas by 2100 under the four socio-economic scenarios.

figure 1c), as a consequence of the high rates of population and economic growth forecasted for these regions (MA 2004; Jetz *et al.* 2007). These impacts then combine to overall future habitat losses that are most intense near the equator and in the north (and extreme south) temperate/polar regions (figure 1e).

(b) Past and future environmental change and conservation risk

Patterns of past change exhibit a contrasting latitudinal gradient with changes highest in the subtropical and south temperate regions of the Northern Hemisphere (figure 1c). The discrepancy between past and future patterns of change

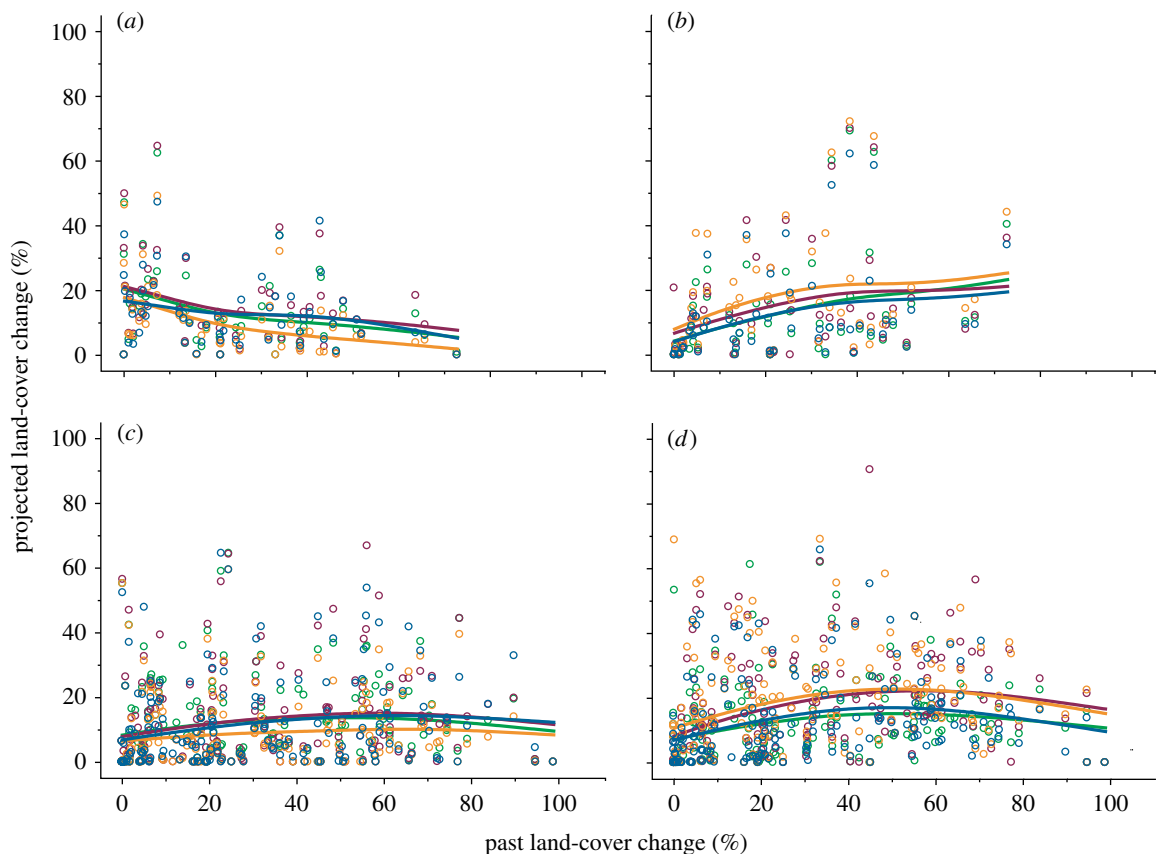


Figure 2. The association between patterns of past and future environmental change: proportion of past land-cover change versus projected land-cover change under the four MA scenarios across (a,b) the world's 55 biome–realm combinations and (c,d) 174 countries. (a,c) Climate and (b,d) land-use. Cubic smoothing spline (3 d.f.) is shown for each plot for illustrative purposes only. Projected land-cover change does not account for past land-cover change. For other details, see the legend of figure 1.

across latitude reflects a general trend across meaningful and representative ecological and geopolitical units: the 55 bio-realms (Olson & Dinerstein 1998) and 174 nations. Bio-realms provide a critical taxon-free perspective in the face of limited knowledge concerning the exact distribution and magnitude of biodiversity. Conversely, countries represent the most fundamental political units to make conservation, management and policy decisions (Chape *et al.* 2005). Across bio-realms, there are weak relationships between past habitat loss and future transformations due to either climate or land-use change (figure 2a,b; all scenarios: Spearman rank correlation, $Rho = -0.20$ to -0.46 and $Rho = 0.31$ – 0.44 , respectively; all $p \leq 0.14$). Across nations, the associations are even weaker (though statistically significant) and appear slightly hump shaped (figure 2c,d; $Rho = 0.26$ – 0.30 and $Rho = 0.36$ – 0.44 for climate and land-use change, respectively; all $p < 0.01$). These disparate impacts of environmental change are exacerbated in the context of current levels of protection. A quantitative measure that integrates this is the conservation risk index, defined as the ratio of area susceptible to land-cover transformation to area currently protected (Hoekstra *et al.* 2005). Climate change conservation risk peaks sharply approximately 60° – 70° North, while for land-use change it peaks in the Southern tropics/subtropics; when combined, critical peaks at both latitudes are produced (figure 1b,d,f). Past conservation risk due to land-use change shows a different pattern with significant peaks in both hemispheres (figure 1d).

Existing broad-scale conservation priority setting approaches, such as ‘biodiversity hotspots’ (Myers *et al.*

2000) and ‘crisis ecoregions’ (Hoekstra *et al.* 2005), have relied largely on impacts of past habitat loss to geographically and/or taxonomically prioritized conservation efforts. However, at our scale of analysis, we find that future land-cover transformation by either type of environmental change is at best weakly correlated to past conversion, casting doubts on the future effectiveness of such an approach. This highlights the need for a rigorous integration of projected future environmental change threats, presently unaccounted for in any major proactive conservation blueprint (Brooks *et al.* 2006), when setting global priorities for conservation to maximize the benefits from finite conservation resources (James *et al.* 1999; Halpern *et al.* 2006).

Regions such as Southeast Asia and the IndoMalaya realm, which were heavily impacted in the past, will probably continue to be threatened (electronic supplementary material, figure 2). But overall, marked shifts of focal battlegrounds for conservation are projected for the twenty-first century. In particular, Africa and many tropical biomes are forecasted to have dramatic increases in conservation risk due to land-use change, while some previously strongly impacted regions now rank much lower (electronic supplementary material, figure 2). The nearctic and palaeartic realms, tundra and boreal forest/taiga biomes and Asia, Europe and North America warrant attention given their high conservation risk due to climate change (electronic supplementary material, figure 2). Much of Africa is likely to be increasingly at risk (figure 3a–d) while bio-realms in Europe are projected to

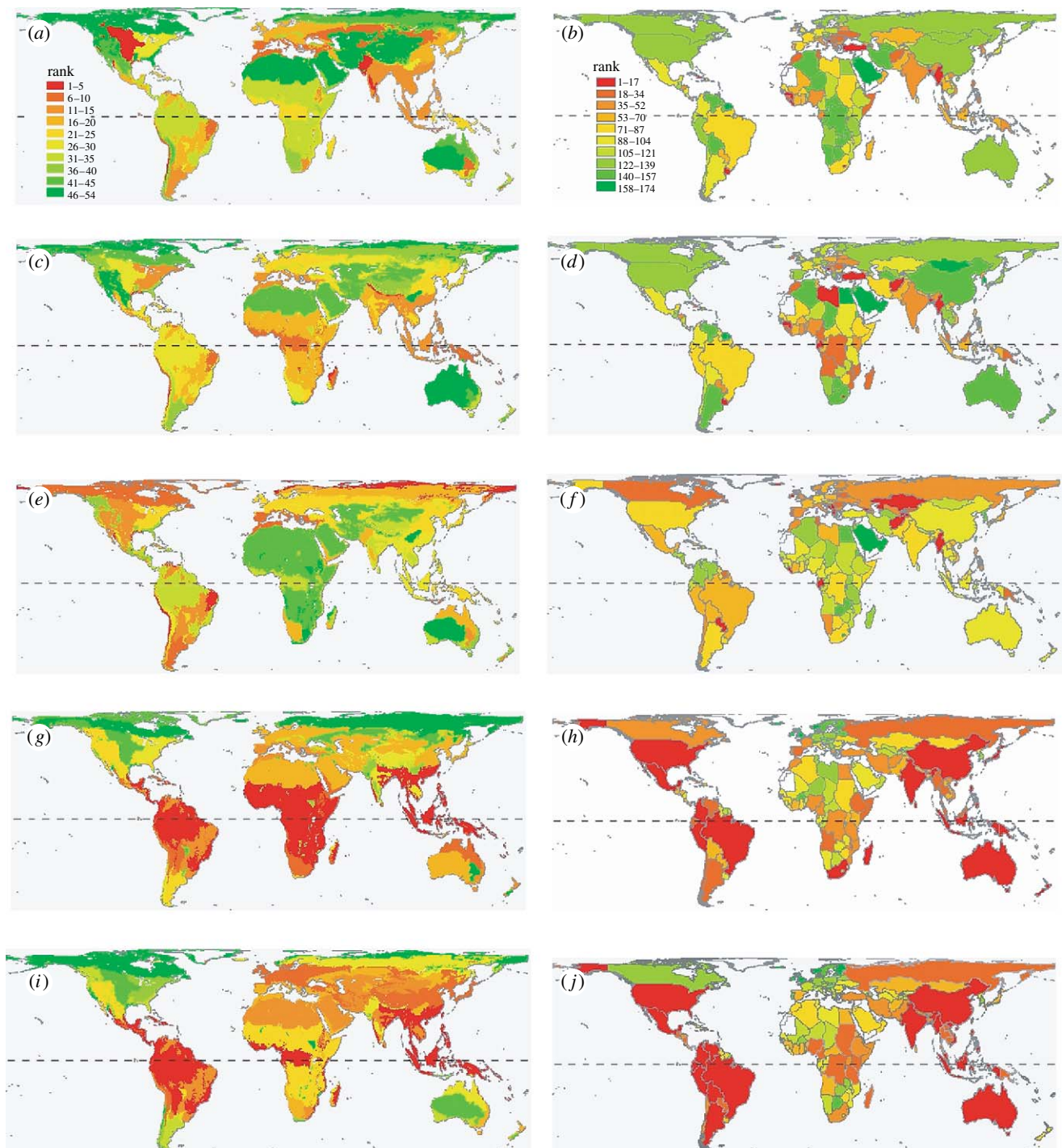


Figure 3. Geographical trends of past and future conservation risk and current conservation value for global terrestrial vertebrates across (a,c,e,g,i) bio-realms and (b,d,f,h,j) countries. Geographical units are ranked by global conservation risk rank due to: (a,b) past land-use change, the total sum of ranks, which is a composite index calculated by adding the global conservation risk ranks across all four socio-economic scenarios, (c,d) future land-use change, or (e,f) climate change. Bio-realms and nations exposed to the greatest environmental change impact are those with the lowest rank or total sum of ranks ($\text{rank}_{\text{total}} = \sum (\text{rank}_i)$, where i represents each MA scenario) and represented in red. Finally, we assessed the geographical distribution of current conservation value using global ranks of richness of (g,h) endemic (unique to either a bio-realm or nation) and (i,j) globally threatened terrestrial vertebrates; units in red have the highest conservation value. Maps are projected using the Behrmann equal-area projections; horizontal dashed line indicates the equator.

be relatively less vulnerable in the future than in the past (figure 3a,c). Geographical patterns of future conservation risk rank are highly disparate between the climate and the land-use change: tropical/sub-tropical bio-realms and countries are generally at greatest risk due to future land-use change, while regions of high conservation risk due to climate change are mostly located near the poles (figure 3c-f).

(c) Future conservation risk and current-day conservation value

Our measure of conservation risk does not consider potential differences between regions in terms of their relative global importance for conservation. Taking on the primary conservation objective of preventing global species extinction, we adopt surrogate measures of conservation value that are useful and straightforward: the absolute number of

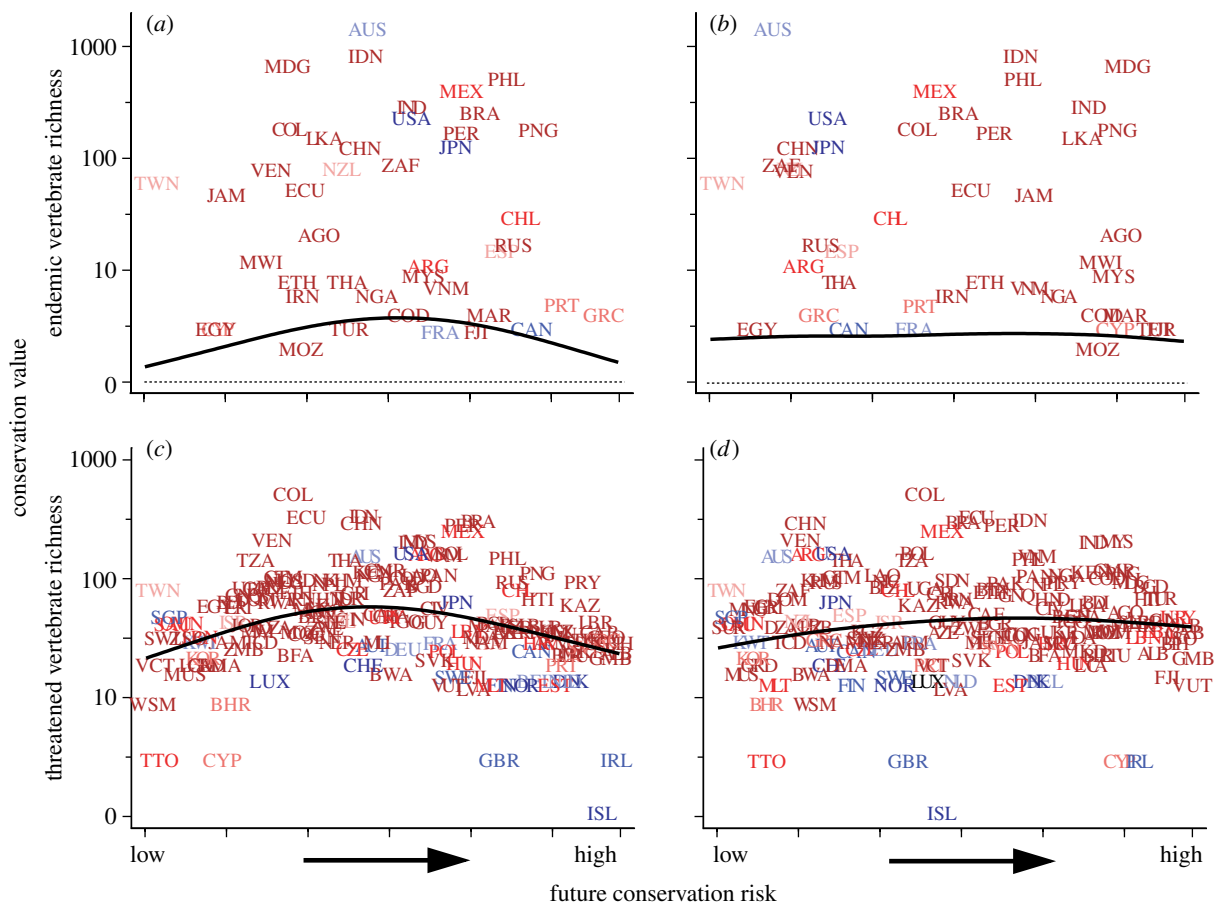


Figure 4. Patterns of conservation need and means across nations based on a combination of future conservation risk and present conservation value. (a,c) Climate change and (b,d) land-use change. (a,b) Countries with no endemic vertebrates are along the horizontal dot-dashed line but are excluded for clarity. For each panel, countries in the top right corner have the highest combined relative future conservation risk and conservation value (most critical), while those in the bottom left corner have the lowest combined relative future conservation risk and conservation value (least critical). Countries are coloured from dark red to dark blue according to per capita gross domestic product (GDP) for 2004 in constant 2000 US dollars (USD) to illustrate their relative financial capacity in carrying out conservation efforts such as setting up new reserves (figure 5). Cubic smoothing spline (3 d.f.) is shown for each plot for illustrative purposes only. See electronic supplementary material, appendix 2 for country abbreviations.

unique (i.e. endemic; Lamoreux *et al.* 2006) and globally threatened (according to World Conservation Union, IUCN) species (Grenyer *et al.* 2006) of all terrestrial vertebrates (26 711 species of amphibians, reptiles, birds and mammals) a region currently harbours. While this measure has obvious limitations (e.g. Orme *et al.* 2005), we emphasize that it is the only one that allows making this important connection at global scale, particularly in the absence of complete and high-resolution global biodiversity knowledge (van Vuuren *et al.* 2006). Across bio-realms the association between both the measures of conservation value and the future conservation risk, though not statistically significant, is positive for future land-use change (electronic supplementary material, figure 3b,d; $Rho=0.18-0.24$; $p>0.08$) and negative for future climate change (electronic supplementary material, figure 3a,c; $Rho=-0.06$ to -0.18 ; $p>0.20$). Separate analyses controlling for the effect of area yield qualitatively similar results (land-use change, $Rho=0.26-0.29$; $p<0.05$; climate change, $Rho=-0.20$ to -0.37 ; $p<0.14$). The same patterns generally hold for nations: land-use change (figure 4b,d; $Rho=-0.01-0.06$; $p>0.44$ (controlled for area: $Rho=0.06-0.12$; $p>0.11$)) and climate change (figure 4a,c; $Rho=-0.15$ to -0.25 ; $p<0.04$ (controlled for area: $Rho=-0.03-0.06$; $p>0.46$)). Overall, regions with high land-use change driven conservation risk are

home to a particularly high richness of threatened and endemic taxa (figure 3g-j). Consistent with other studies (Olson & Dinerstein 2002), many tropical bio-realms such as the Afrotropics and Indomalaya tropical and subtropical moist broadleaf forests (electronic supplementary material, figure 3b,d) and nations within the tropics/subtropics (figure 4b,d) are projected to remain of highest priority for global conservation.

(d) National conservation capacity and conservation need

Nations represent the sovereign authorities that implement and manage conservation efforts (Chape *et al.* 2005). It follows that for successful biodiversity protection factors representing the capacity for conservation, such as the quality of national governance and wealth, are particularly critical. Poor national governance is linked to habitat and biodiversity loss in developing countries (Smith *et al.* 2003), where conservation priorities are often highest (but see Barrett *et al.* 2006). However, because biodiversity conservation is extremely complex, effective reserve governance requires a broad pluralistic approach that entails building a network across institutional levels (Berkes 2007). While governance that begins from the ground up (e.g. community-based

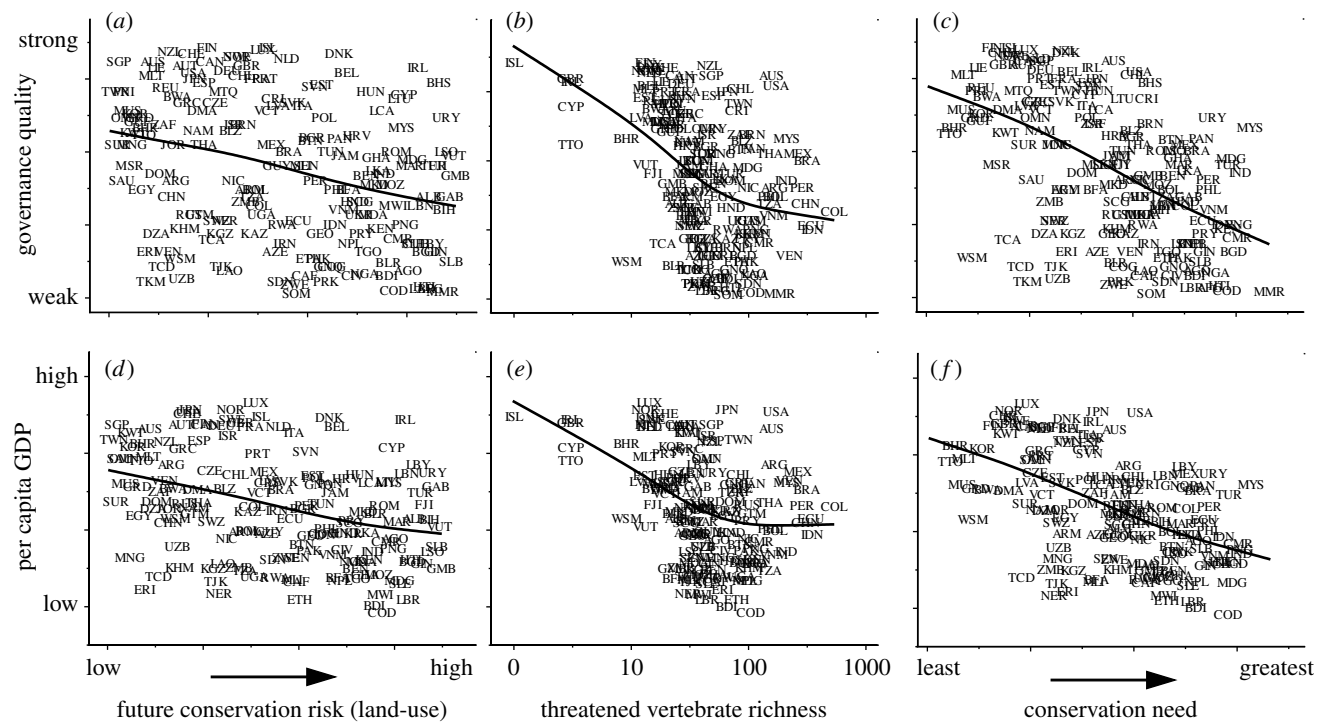


Figure 5. The associations between patterns of (a,d) future conservation risk (due to land-use change), (b,e) current conservation value (threatened vertebrate richness) and (c,f) conservation need, with (a–c) governance quality score and (d–f) conservation means across nations. (d–f) Each unit along the y-axis represents an increment of an order of magnitude ranging from USD 100 (‘Low’) to 100 000 (‘High’). Cubic smoothing spline (3 d.f.) is shown for each plot for illustrative purposes only. See electronic supplementary material, appendix 2 for country abbreviations.

conservation) is increasingly advocated, the vertical interplay between local communities and state suggests that weak national governance may compromise the overall effectiveness of protected areas. Therefore, we argue that in the absence of a more direct measure of reserve governance, our selected proxy (which has clear limitations) appears relevant and useful. The problematic association between conservation risk and low governance quality score holds for the case of future land-use change (figure 5a; $Rho = -0.32$; $p < 0.01$, $n = 170$), but not climate change (electronic supplementary material, figure 4a; $Rho = 0.01$; $p = 0.86$). Africa emerges as home to most nations of particular conservation concern (figure 3d) and remains a region plagued by conservation conflicts between human settlements and areas of high vertebrate richness (Balmford *et al.* 2001). The high land-use change conservation risk of weak-governance nations is further exacerbated by their high conservation value in terms of threatened richness (figure 5b; $Rho = -0.46$; $p < 0.01$ (controlled for area: $Rho = -0.27$; $p < 0.01$)) but not endemic richness (electronic supplementary material, figure 4b; $Rho = 0.02$; $p = 0.79$ (controlled for area: $Rho = 0.22$; $p < 0.01$)). By relating the combined conservation risk and current-day conservation value (particularly threatened richness) to governance quality, we find that countries with the greatest conservation need are also the most poorly governed (figure 5c; $Rho = -0.54$; $p < 0.01$). In particular, countries in sub-Saharan Africa (e.g. Democratic Republic of Congo), South and Southeast Asia (e.g. Sri Lanka and the Philippines) are projected to be regions of particularly high concordance between conservation risk and value (figure 3d,h,j), worsening the existing global disconnect between the conservation efforts and the biological value previously highlighted

(Rodrigues *et al.* 2004b). The double jeopardy facing biodiversity in certain high conservation-need nations compounded by compromised governance quality calls for urgent conservation attention. However, because governance quality may confound future land-use change conservation risk and thus complicate global conservation prioritization, it may be necessary to triage funds according to the projected long-term political stability and conservation commitment.

Clearly, some nations exhibit particularly strong conservation need due to a combination of high conservation value and high projected conservation risk. The mitigation of projected conservation risk through additional protected areas will be costly and not all nations could achieve this without substantial external or international aid (Bruner *et al.* 2004; e.g. recent foreign-aided reserve network expansion in Gabon and Madagascar). To offer a preliminary assessment of this challenge, we follow existing practice (James *et al.* 1999; Bruner *et al.* 2004) and use nation’s per capita GDP as a surrogate for potential national conservation means and relate it to levels of projected conservation need. We acknowledge that this measure is limiting but argue that in the absence of detailed data on national budgets for conservation per capita GDP appears as a useful first proxy. We reveal a clear disparity between national conservation need and means: nations with the greatest conservation risk (due to land-use change (figure 5d; $Rho = -0.35$; $p < 0.01$, $n = 155$) but not climate change (electronic supplementary material, figure 4c; $Rho = 0.11$; $p = 0.19$)) and conservation value (figure 5e; threatened richness: $Rho = -0.38$; $p < 0.01$ (controlled for area: $Rho = -0.27$; $p < 0.01$); figure 4d in the electronic supplementary material; endemic richness: $Rho = 0.08$; $p = 0.32$ (controlled for area: $Rho = 0.23$; $p < 0.01$)) almost

exclusively are the least wealthy. Indeed, nations with the greatest conservation need (calculated as a combination of a nation's global ranks in conservation risk due to land-use change and threatened richness) evidently also have the least conservation means (figure 5f; $Rho = -0.52$; $p < 0.01$; e.g. Cameroon and Indonesia). Barring the dramatic economic turnaround of dozens of nations, the previously noted combination of relative poverty, threatened biodiversity and high levels of habitat loss due to land-use change (Balmford *et al.* 2001) are set to characterize the twenty-first century.

4. CONCLUSIONS

Our results will clearly benefit from overcoming assumptions and issues associated with land-cover projections and species range shifts. Many other additional caveats will also need to be addressed before these insights may be translated to on-the-ground conservation action. For example, as more accurate data become available, finer-scale projections of land-cover transformation between existing protected areas (within and among bio-realms/nations) would reveal the locations and degrees to which connectivity may be disrupted (or restored) in the future (Hannah *et al.* 2002). Reserve-based conservation planning also requires the consideration of trans-boundary migration or potential species shifts (Hannah *et al.* 2005) as biodiversity is not confined within administrative/political boundaries. As it is now, protected areas are unable to buffer against broad-scale shifts in the distribution of species or ecosystems, a conundrum that requires careful deliberation. Furthermore, effective reserve administration and governance, better management of the surrounding matrix and improved regional/national/international coordination (Bruner *et al.* 2004) represent complementary and high-priority conservation actions. Clearly, future land-use and climate change impacts will need to be integrated more prominently in all these components of conservation action over the coming decades (see examples of ongoing works in Lovejoy (2005)).

Overall, our results indicate that future environmental change will lead to dramatic shifts in the battlegrounds for conservation in the twenty-first century. Developing countries in the tropics help mitigate future carbon emissions due to the substantial terrestrial carbon sinks they possess (Intergovernmental Panel on Climate Change 2001), often in the form of primary forests that if adequately protected would greatly reduce their future conservation risk. The complex feedbacks between land-use (e.g. deforestation) and climate change will therefore require a concerted international effort (e.g. United Nations Framework Convention on Climate Change) to successfully combat global climate change (MA 2005; Gullison *et al.* 2007). In essence, the uneven distribution of conservation need and capacity, and the interconnectedness between conservation and climate policies among high-risk nations outlines a clear opportunity for the 'north-south' flow of conservation resources to meet the conservation funding shortfalls for expanding, strengthening and effective management of reserve networks in the tropics (Balmford & Whitten 2003; Bruner *et al.* 2004; Rodrigues *et al.* 2004a). In this process, ongoing integrative assessments (MA 2005) of the effectiveness

of the global reserve network under global change will be paramount to optimizing conservation spending. While future, more detailed and accurate projections of environmental change (e.g. IPCC Fourth Assessment Report 2007; and resulting updated land-cover projections) will be critical in refining and updating our findings, the observed trends are likely to persist and deserve urgent and careful attention.

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REFERENCES

- Alcamo, J., van Vuuren, D. & Cramer, W. 2005 *Changes in ecosystem services and their drivers across the scenarios*. Washington, DC: World Resources Institute.
- Balmford, A. & Long, A. 1995 Across country analyses of biodiversity congruence and current conservation effort in the tropics. *Conserv. Biol.* **9**, 1539–1547. (doi:10.1046/j.1523-1739.1995.09061539.x)
- Balmford, A. & Whitten, T. 2003 Who should pay for tropical conservation, and how could the costs be met? *Oryx* **37**, 238–250. (doi:10.1017/S0030605303000413)
- Balmford, A., Moore, J. L., Brooks, T., Burgess, N., Hansen, L. A., Williams, P. & Rahbek, C. 2001 Conservation conflicts across Africa. *Science* **291**, 2616–2619. (doi:10.1126/science.291.5513.2616)
- Balmford, A. *et al.* 2005 The convention on biological diversity's 2010 target. *Science* **307**, 212–213. (doi:10.1126/science.1106281)
- Barrett, C. B., Gibson, C. C., Hoffman, B. & McCubbins, M. D. 2006 The complex links between governance and biodiversity. *Conserv. Biol.* **20**, 1358–1366. (doi:10.1111/j.1523-1739.2006.00521.x)
- Berkes, F. 2007 Community-based conservation in a globalized world. *Proc. Natl Acad. Sci. USA* **104**, 15 188–15 193. (doi:10.1073/pnas.0702098104)
- Brooks, T. M., Mittermeier, R. A., da Fonseca, G. A. B., Gerlach, J., Hoffmann, M., Lamoreux, J. F., Mittermeier, C. G., Pilgrim, J. D. & Rodrigues, A. S. L. 2006 Global biodiversity conservation priorities. *Science* **313**, 58–61. (doi:10.1126/science.1127609)
- Bruner, A. G., Gullison, R. E. & Balmford, A. 2004 Financial costs and shortfalls of managing and expanding protected-area systems in developing countries. *Bioscience* **54**, 1119–1126. (doi:10.1641/0006-3568(2004)054[1119:FCASOM]2.0.CO;2)
- Chape, S., Harrison, J., Spalding, M. & Lysenko, I. 2005 Measuring the extent and effectiveness of protected areas as an indicator for meeting global biodiversity targets. *Phil. Trans. R. Soc. B* **360**, 443–455. (doi:10.1098/rstb.2004.1592)
- Curran, L. M., Trigg, S. N., McDonald, A. K., Astiani, D., Hardiono, Y. M., Siregar, P., Caniago, I. & Kasischke, E. 2004 Lowland forest loss in protected areas of Indonesian Borneo. *Science* **303**, 1000–1003. (doi:10.1126/science.1091714)
- European Commission Joint Research Centre, I.f.E.a.S. 2002 GLC 2000: global land cover mapping for the year 2000. See www-gym.jrc.it/glc2000.
- Grenyer, R. *et al.* 2006 Global distribution and conservation of rare and threatened vertebrates. *Nature* **444**, 93–96. (doi:10.1038/nature05237)

- Gullison, R. E. *et al.* 2007 Tropical forests and climate policy. *Science* **316**, 985–986. (doi:10.1126/science.1136163)
- Halpern, B. S., Pyke, C. R., Fox, H. E., Haney, J. C., Schlaepfer, M. A. & Zaradic, P. 2006 Gaps and mismatches between global conservation priorities and spending. *Conserv. Biol.* **20**, 56–64. (doi:10.1111/j.1523-1739.2005.00258.x)
- Hannah, L., Midgley, G. F. & Millar, D. 2002 Climate change-integrated conservation strategies. *Global Ecol. Biogeogr.* **11**, 485–495. (doi:10.1046/j.1466-822X.2002.00306.x)
- Hannah, L., Midgley, G., Hughes, G. & Bomhard, B. 2005 The view from the cape. Extinction risk, protected areas, and climate change. *Bioscience* **55**, 231–242. (doi:10.1641/0006-3568(2005)055[0231:TVFTCE]2.0.CO;2)
- Hoekstra, J. M., Boucher, T. M., Ricketts, T. H. & Roberts, C. 2005 Confronting a biome crisis: global disparities of habitat loss and protection. *Ecol. Lett.* **8**, 23–29. (doi:10.1111/j.1461-0248.2004.00686.x)
- Hurlbert, A. H. & Jetz, W. 2007 Species richness, hotspots, and the scale dependence of range maps in ecology and conservation. *Proc. Natl Acad. Sci. USA* **104**, 13 384–13 389. (doi:10.1073/pnas.0704469104)
- IMAGE-TEAM 2001 *The IMAGE 2.2 implementation of the SRES scenarios: a comprehensive analysis of emissions, climate change and impacts in the 21st century*. CD-ROM. Bilthoven, The Netherlands: RIVM (Rijksinstituut voor Volksgezondheid en Milieu/National Institute of Public Health and the Environment).
- Intergovernmental Panel on Climate Change 2001 *Climate change 2001: synthesis report*. Cambridge, UK: Cambridge University Press. Published for the Intergovernmental Panel on Climate Change
- IUCN 1994 *Guidelines for protected areas management categories*. Cambridge, UK; Gland, Switzerland: IUCN.
- IUCN 2001 *IUCN red list categories and criteria: version 3.1*. IUCN species survival commission. Gland, Switzerland; Cambridge, UK: IUCN.
- IUCN 2006 IUCN red list of threatened species. See <http://www.iucnredlist.org/>.
- James, A. N., Gaston, K. J. & Balmford, A. 1999 Balancing the Earth's accounts. *Nature* **401**, 323–324. (doi:10.1038/43774)
- Jetz, W., Wilcove, D. S. & Dobson, A. P. 2007 Projected impacts of climate and land-use change on the global diversity of birds. *Public Libr. Sci. (Biol.)* **5**, 1211–1219. (doi:10.1371/journal.pbio.0050157)
- Kaufmann, D., Kraay, A. & Mastruzzi, M. 2005 Governance matters iv: governance indicators for 1996–2004. World Bank Policy Research Working Paper Series No. 3630. See <http://www.worldbank.org/wbi/governance/pubs/govmatters4.html>.
- Lamoreux, J. F., Morrison, J. C., Ricketts, T. H., Olson, D. M., Dinerstein, E., McKnight, M. W. & Shugart, H. H. 2006 Global tests of biodiversity concordance and the importance of endemism. *Nature* **440**, 212–214. (doi:10.1038/nature04291)
- Lovejoy, T. 2005 Conservation with a changing climate. In *Climate change and biodiversity* (eds T. Lovejoy & L. Hannah), pp. 325–328. New Haven, CT; London, UK: Yale University Press.
- MA 2004 *Scenarios: findings of the scenarios working group*. Washington, DC: Millennium Ecosystem Assessment. Island Press.
- MA 2005 *Ecosystems and human well-being: biodiversity synthesis*. Washington, DC: Millennium Ecosystem Assessment. World Resources Institute.
- Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. & Kents, J. 2000 Biodiversity hotspots for conservation priorities. *Nature* **403**, 853–858. (doi:10.1038/35002501)
- Naughton-Treves, L., Holland, M. B. & Brandon, K. 2005 The role of protected areas in conserving biodiversity and sustaining local livelihoods. *Annu. Rev. Environ. Resour.* **30**, 219–252. (doi:10.1146/annurev.energy.30.050504.164507)
- Olson, D. M. & Dinerstein, E. 1998 The Global 200: a representation approach to conserving the Earth's most biologically valuable ecoregions. *Conserv. Biol.* **12**, 502–512. (doi:10.1046/j.1523-1739.1998.012003502.x)
- Olson, D. M. & Dinerstein, E. 2002 The global 200: priority ecoregions for global conservation. *Ann. Miss. Bot. Gard.* **89**, 199–224. (doi:10.2307/3298564)
- Olson, D. M. *et al.* 2001 Terrestrial ecoregions of the world: a new map of life on earth. *Bioscience* **51**, 933–938. (doi:10.1641/0006-3568(2001)051[0933:TEOTWA]2.0.CO;2) (<http://www.worldwildlife.org/science/data/terreco.cfm>)
- Orme, C. D. L. *et al.* 2005 Global hotspots of species richness are not congruent with endemism or threat. *Nature* **436**, 1016–1019. (doi:10.1038/nature03850)
- Parmesan, C. & Yohe, G. 2003 A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**, 37–42. (doi:10.1038/nature01286)
- Rodrigues, A. S. L. *et al.* 2004a Global gap analysis: priority regions for expanding the global protected-area network. *Bioscience* **54**, 1092–1100. (doi:10.1641/0006-3568(2004)054[1092:GGAPRF]2.0.CO;2)
- Rodrigues, A. S. L. *et al.* 2004b Effectiveness of the global protected area network in representing species diversity. *Nature* **428**, 640–643. (doi:10.1038/nature02422)
- Sala, O. E. *et al.* 2000 Global biodiversity scenarios for the year 2100. *Science* **287**, 1770–1774. (doi:10.1126/science.287.5459.1770)
- Smith, R. J., Muir, R. D. J., Walpole, M. J., Balmford, A. & Leader-Williams, N. 2003 Governance and the loss of biodiversity. *Nature* **426**, 67–70. (doi:10.1038/nature02025)
- van Vuuren, D. P., Sala, O. E. & Pereira, H. M. 2006 The future of vascular plant diversity under four global scenarios. *Ecol. Soc.* **11**, 25.
- Walther, G. R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J. C., Fromentin, J. M., Hoegh-Guldberg, O. & Bairlein, F. 2002 Ecological responses to recent climate change. *Nature* **416**, 389–395. (doi:10.1038/416389a)
- Warren, M. S. D. *et al.* 2001 Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature* **414**, 65–69. (doi:10.1038/35102054)
- WDPA-Consortium 2005 *2005 World database on protected areas*. See <http://sea.unep-wcmc.org/wdpa/>.
- Williams, P. *et al.* 2005 Planning for climate change: identifying minimum-dispersal corridors for the Cape proteaceae. *Conserv. Biol.* **19**, 1063–1074. (doi:10.1111/j.1523-1739.2005.00080.x)
- Wilson, R. J., Gutierrez, D., Gutierrez, J., Martinez, D., Agudo, R. & Monserrat, V. J. 2005 Changes to the elevational limits and extent of species ranges associated with climate change. *Ecol. Lett.* **8**, 1138–1146. (doi:10.1111/j.1461-0248.2005.00824.x)
- World Wildlife Fund 2006 WildFinder: online database of species distributions, v. 6 January. See www.worldwildlife.org/wildfinder.