Title: Climate change modifies risk of global biodiversity loss due to land-cover change

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Running Title: Interactions of future stressors on global biodiversity

Word count: 8,511

Number of References: 55

ABSTRACT

Climate change and land-cover change will have major impacts on biodiversity persistence worldwide. These two stressors are likely to interact, but how climate change will mediate the effects of land-cover change remains poorly understood. Here we use an empirically-derived model of the interaction between habitat loss and climate to predict the implications of this for biodiversity loss and conservation priorities at a global scale. Risk analysis was used to estimate the risk of biodiversity loss due to alternative future land-cover change scenarios and to quantify how climate change mediates this risk. We demonstrate that the interaction of climate change with land-cover change could increase the impact of land-cover change on birds and mammals by up to 43% and 24% respectively and alter the spatial distribution of threats. Additionally, we show that the ranking of global biodiversity hotspots by threat depends critically on the interaction between climate change and habitat loss. Our study suggests that the investment of conservation resources will likely change once the interaction between climate change and land-cover change is taken into account. We argue that global conservation efforts must take this into account if we are to develop cost-effective conservation policies and strategies under global change.

Keywords: habitat loss, climate change, interactions, biodiversity hotspots, conservation planning, prioritisation

1. INTRODUCTION

Over the past 400 years, human pressures including habitat conversion, hunting, and alien species introductions have increased species extinction rates to as much as 1,000 times historical rates (Barnosky et al. 2011; Turvey 2009), and one quarter of the species assessed so far are at risk of extinction (Hoffmann et al. 2010). In the 21st century, conservationists are becoming increasingly concerned about biodiversity disruption and loss as climate change emerges as another major threat, with impacts at the genetic, species, community and ecosystem levels (Foden et al. 2013; Lawler et al. 2009; Pacifici et al. 2015; Pounds et al. 2006; Thomas et al. 2006). As climate change and land-cover change impacts intensify and interact in the coming decades, the threat to biodiversity may be amplified (Jetz et al. 2007; Sala et al. 2000; Visconti et al. 2015). At present, our understanding of the implications of these interactions for ecological systems are limited, and have generally been based on broad assumptions about what the interaction might look like, rather than empirical data about interactions (Brook et al. 2008; Felton et al. 2009; Oliver and Morecroft 2014; Vinebrooke et al. 2004).

Climate change can interact with land-cover change by exacerbating the impact of habitat loss and fragmentation on biodiversity through increasing the susceptibility of fragmented biological populations to stochastic extinction risk (de Chazal and Rounsevell 2009; Jetz et al. 2007; Sala et al. 2000). Climate change can also hinder the ability of species to cope with modified land-cover (Opdam and Wascher 2004). If climate change depresses population sizes or causes increased stochasticity in population dynamics, for example as a consequence of increased incidents of extreme events (Van De Pol et al. 2010), then habitat networks may require larger patches and improved connectivity to maintain populations (Verboom et al. 2010). Loss and fragmentation of habitat may also severely hinder the movement of species and their ability to cope with climate change through tracking of suitable climatic conditions (Brook et al. 2009; Keith et al. 2008; Thomas et al. 2004). Even relatively intact landscapes are at risk, particularly where landscape heterogeneity is low, forcing species to move potentially large distances to track suitable climatic conditions. Spatial heterogeneity may help buffer the impact for some species, however the buffering will vary regionally (Dunlop et al. 2012). Population responses to extreme climatic events, such as fire and flooding, are also likely to be affected by habitat quality, area and heterogeneity (Cochrane and Laurance 2008; Fischer et al. 2006). Interactions between climate change and land-cover change may therefore be widespread phenomena and have the potential to fundamentally alter the magnitude and spatial patterns of declines in biodiversity (Jetz et al. 2007; Sala et al. 2000). However the degree to which these interactions influence biodiversity is likely to vary regionally (e.g. Cochrane and Laurance 2008) and by taxon (e.g. Jetz et al. 2007). Not all species will be negatively affected; some will adapt and even benefit from the changes (Warren et al. 2001). But others are likely to suffer catastrophic declines without effective conservation planning and intervention. It is therefore imperative that we assess the consequences of these interactions for declines in biodiversity and identify the implications for conservation priorities.

Here we quantify the degree to which interactions between climate change and land-cover change will drive the extent and patterns of biodiversity loss due to future land-cover change at the global scale. We used a form of risk analysis (Dawson et al. 2011; McCarthy et al. 2001; Turner et al. 2003) to estimate the risk of biodiversity loss from habitat loss while accounting for its interaction with climate change. Our approach allows us to quantify the effect of climate on the probability that habitat loss has a negative effect on a species. This therefore captures the implications of the interaction between climate and habitat loss for species vulnerability to habitat loss. We applied this model globally to map estimates of the risk of terrestrial birds and mammals to future land-cover change across a range of future climate and land-cover change projections. We also assessed the risk to global biodiversity hotspots and demonstrate that conservation priorities may depend critically on the interactions between climate and land-cover change.

2. MATERIALS AND METHODS

We developed a model of the risk of species being impacted by habitat loss as

$$\mathit{Risk} = [\mathit{Exposure} * \mathit{Vulnerability}] * \mathit{Hazard}, \tag{1}$$

where *Risk* was an index of the expected number of species of terrestrial birds and mammals negatively impacted by habitat loss from future land-cover change, *Exposure* was defined as the number of terrestrial birds and mammals that are exposed to the effect of habitat loss, *Hazard* was defined as the percent change in natural vegetation through anthropogenic land-cover change, projected for a range of land-cover change scenarios, and *Vulnerability* was defined as the probability that anthropogenic land-cover change has a negative impact on bird or mammal species and it explicitly incorporated how climate influences this probability (Fig. 1). We estimated the dependence of *Vulnerability* on climate using an existing empirical model derived from a global meta-analysis of habitat loss effects (Mantyka-Pringle et al. 2012). The *Vulnerability* model was mapped for the entire globe and then projected under a range of climate and land-cover change scenarios.

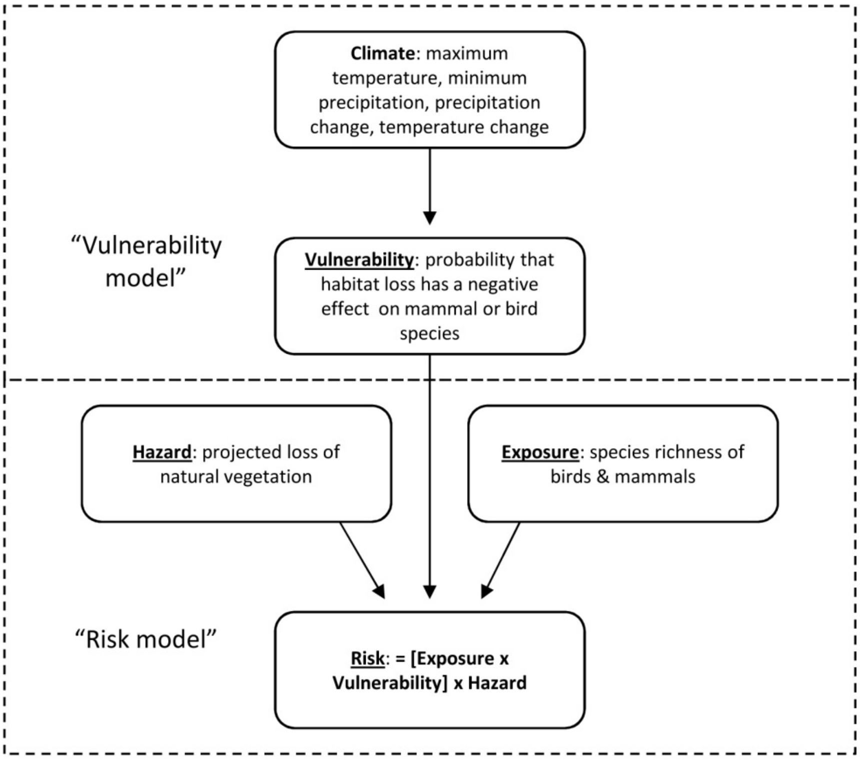

Figure 1. Schematic representation of the steps taken to calculate the risk of biodiversity loss from habitat loss. The dotted-line boxes indicate the division of the analysis into the two separate components of "Risk" and "Vulnerability" taken from Mantyka-Pringle et al. (2012).

2.1 Future climate projections

Climate projections were downloaded from the Climate Change, Agriculture and Food Security (CCAFS) database (http://www.ccafs-climate.org/) in 2012 by statistically downscaling the outputs of three SRES (Special Report on Emissions Scenarios) climate scenarios for the fourth assessment report of the intergovernmental panel on climate change (IPCC) (IPCC 2007), A2A, A1B, and B1 (see Table 1 for a description of these scenarios). Based on the data and model availability, three different climate models were selected to downscale the data (delta method) for the period 2050s (1x1 km), MK3.0 (for A1B), HadCM3 (for A2A) and CNRM-CM3 (for B1). For each climate scenario, five variables were obtained that correspond with those used in the meta-analysis modelling the relationship between habitat loss effects, current climate (1950-2000) and climatic change (1977-2006 minus 1901-1930) (Mantyka-Pringle et al. 2012). For mean maximum temperature of warmest month (mtwm), we used the variable mtwm (BIO5) from CCAFS. For mean precipitation of driest month (podm), we used the variable podm (BIO14) from CCAFS. For mean precipitation change (precdiff), we used the variable mean annual precipitation (BIO12) from CCAFS, and the mean annual precipitation and the monthly average precipitation for the years 1901-1930 (0.5 degree) from the Climatic Research Unit (CRU) at the University of East Anglia (Mitchell and Jones 2005). For mean temperature change (tmxdiff), we used two variables from CCAFS, annual mean temperature (BIO1) and mean diurnal range (BIO2) (BIO1 + 0.5 x BIO2), and the monthly average daily maximum temperature for the years 1901-1930 (0.5 degree) from CRU. We calculated the change in precipitation (precdiff) and temperature (tmxdiff) over time for each grid cell, as the difference in mean values between the periods 2050s (from CCAFS) and 1901-1930 (from CRU) (2050s minus 1901-1930). Time periods were chosen based on the latest and earliest available years from CCAFS and CRU data at the time of analysis (2012). A thirty year period was also chosen as a period long enough to eliminate year-to year variation – consistent with Mantyka-Pringle et al. (2012). All Geographical Information System (GIS) processing was undertaken using ArcGIS version 10.0 (Environmental Systems Research Institute, Redlands, CA, U.S.A.).

Table 1 Characteristics of the six scenarios used in our analysis. More specific details regarding these scenarios can be found elsewhere (IPCC 2007; Visconti et al. 2011)

Scenario	Main characteristics regarding environmental sustainability
Land-cover change (MEA[a])	
Order from Strength	regionalized and fragmented world; reactive approach to ecosystem management (reserves, parks, national-level policies, conservation)
Global Orchestration	integrated world; reactive approach to ecosystem management (sustainable development, economic growth, public goods)
TechnoGarden	integrated world; proactive approach to ecosystem management (green technology; eco-efficiency; tradable ecological property rights)
Climate change (SRES[b])	
SRES A2A	divided world; continuously increasing population; regionally orientated economic growth that is more fragmented and slower than other scenarios
SRES A1B	integrated world; population threshold of 9 billion; rapid economic growth; rapid introduction of new and more efficient technologies; a balanced emphasis on all energy sources
SRES B1	convergent world; population threshold of 9 billion; rapid economic growth with reductions in material intensity; introduction of clean & resource efficient technologies

[a]MEA, Millennium Ecosystem Assessment (MEA 2005); [b]SRES, Special Report on Emissions Scenarios (IPCC 2007).

2.2 Hazard

We projected land-cover change using three global scenarios of human development from the Millennium Ecosystem Assessment (MEA) (MEA 2005) (Table 1). These global scenarios were selected to correspond with those of the IPCC climate scenarios used by the MEA to ensure internal consistency because the emissions and land-use change scenarios are coupled. For each scenario, we used the GLOBIO/Hyde land-cover change model (Bartholomé and Belward 2005) and calculated land-cover change as the % change in natural vegetation (not including any cultivated or built up areas or any mosaic environments containing them) from 2000 to 2050 (11x11 km), Fig. A1.

2.3 Vulnerability

To calculate vulnerability to habitat loss, we used a published model that identified relationships between the vulnerability of species to habitat loss and current climate and climate change (Mantyka-Pringle et al. 2012). This model was based on a meta-analysis of 168 studies on the effects of habitat loss and fragmentation (1,779 individual data points for determining effect sizes; 1,017 for birds and 166 for mammals). These were systematically identified from the past 20 years to represent a range of taxa, landscapes, land-uses, geographical locations and climatic conditions. The location of each study site was spatially mapped and overlayed on high-resolution global climate data. Mixed-effects logistic-regression models were then used to model the relationship between the habitat loss effects and climate, while accounting for variation among studies, taxonomic groups, habitat and land-uses. The model is relatively robust (see Goodness-of-fit test in Mantyka-Pringle et al. 2012), and quantifies the amount by which climate modifies the effect of a given unit of habitat loss on species. Current climate and climate change were both found to be important factors determining the negative effects of habitat loss on species presence, density and/or diversity. The most important determinant of habitat loss and fragmentation effects, averaged across species and geographic regions, was current maximum temperature and mean precipitation change over the past 100 years. Habitat loss and fragmentation effects were greatest in areas with high maximum temperatures. Conversely, they were lowest in areas where rainfall has increased over time.

Based on this model, we made global predictions based on the model-averaged coefficients using current climate and the three future IPCC climate scenarios (IPCC 2007) (Table 1). *Vulnerability* was measured as the climate-mediated probability of a negative habitat loss effect on species and calculated separately for mammals and birds as

$$V = \frac{\exp\left(\mathrm{a} + \mathrm{bx}_{\mathrm{mtwm}} + \mathrm{cx}_{\mathrm{podm}} + \mathrm{dx}_{\mathrm{precdiff}} + \mathrm{ex}_{\mathrm{tmxdiff}}\right)}{1 + \exp\left(\mathrm{a} + \mathrm{bx}_{\mathrm{mtwm}} + \mathrm{cx}_{\mathrm{podm}} + \mathrm{dx}_{\mathrm{precdiff}} + \mathrm{ex}_{\mathrm{tmxdiff}}\right)} \tag{2}$$

where a is the intercept (-0.28), x_{mtwm} is the current or projected mean maximum temperature of warmest month, b is the marginal coefficient for mtwm + the random effect for mammals (= 0.38) or birds (= 0.58) drawn from Mantyka-Pringle et al. (2012), x_{podm} is the current or projected mean precipitation of driest month, c is the marginal coefficient for podm + the random effect for mammals (= -0.03) or birds (= 0.02), $x_{precdiff}$ is the past or projected mean precipitation change, d is the marginal coefficient for precdiff + the random effect for mammals (= -0.23) or birds (= -0.19), $x_{tmxdiff}$ is the past or projected mean temperature change, e is the marginal coefficient for tmxdiff + the random effect for mammals (= 0.04) or birds (= 0.08). Habitat amount (the proportion of the area covered by suitable habitat) was removed from the model because its coefficient average was essentially zero. Two other random effects, habitat type and the response variable measured, were also excluded from the model because we were interested in the average effects across habitat types and studies. All datasets were standardized to have a mean of zero and standard deviation of one prior to analysis.

2.4 Exposure

We used species richness of terrestrial birds and mammals as an exposure indicator (a component of global biodiversity that is exposed to land-cover and climate change). Global richness of birds was compiled from species range maps (≈ 28x28 km) by Birdlife International (http://www.birdlife.org/). Global richness of mammals (10x10 km) was compiled from the distribution of species' suitable habitat, based on the habitat suitability models described in Rondinini *et al*. (2011) (Fig. A2).

2.5 Risk

We used three IPCC and MEA scenario combinations (A2A + Order from Strength, A1B + Global Orchestration, and B1 + TechnoGarden) to calculate, in each grid cell, the risk of terrestrial mammals and birds from habitat loss using Eq. (1).

The scenario combinations represent a wide range of likely climatic and land-cover changes that could occur in the future, and were selected to align with the MEA scenario assumptions regarding greenhouse emissions, population demography, and per-capita consumption (MEA 2005). All maps were resampled to the same resolution as the species richness maps using the nearest neighbour method prior to analysis.

We mapped risk from future vegetation loss for each land-cover change scenario both with (R_a) and without (R_b) the interaction in the calculation of vulnerability (i.e. assuming climate changes according to each scenario versus assuming climate does not change). An estimate of the consequences of the interaction between climate change and habitat loss for the risk of terrestrial birds and mammals being impacted by land-cover change was then calculated for each cell as

$$I = \frac{100 \times (R_a - R_b)}{R_b} \qquad (3)$$

Finally, we performed a sensitivity analysis of our risk model, to determine the relative importance of each climate variable. This was done by mapping the change in risk while isolating each climate variable separately (i.e. assuming that the climate variable changes according to each scenario whilst the other variables stay the same) (Fig. A3-A5). We also quantified uncertainty in risk based on the standard errors of the vulnerability model parameter estimates (see Appendix B). Finally, risk maps, with (R^a) and without the interaction (R^b), were overlaid on top of global biodiversity hotspots (shapefile downloaded from http://sp10.conservation.org/) (Myers et al. 2000) to calculate the mean risk of species impacted per hotspot using zonal statistics. The mean risks were then used to quantify the extent to which the interaction changes the rank of each hotspot in terms of risk.

3. RESULTS

Future climate change was predicted to exacerbate the risk of terrestrial mammal and bird species being impacted from future land-cover change in large parts of the globe, but effects were highly spatially variable (Fig. 2). Under the Order from Strength + A2A scenario, risk was exacerbated by 24% for mammals and 43% for birds. Under the Global Orchestration + A1B scenario, risk was exacerbated by 17% for mammals and 28% for birds. Under the TechnoGarden + B1 scenario, risk was exacerbated by 9% for mammals and 28% for birds. The regions where the interaction has the greatest impacts are in East and South Africa, and Central America. However, areas throughout North and South America, Caribbean, South and West Europe, West and South Asia, East Asia, Australia, and parts of Southeast Asia and North

Europe are also predicted to be at increased risk from land-cover change as a result of the interaction (Fig. 2). In contrast, scattered areas throughout North America, Middle and West Africa, East Europe, South and Central Asia, and Southeast Asia are predicted to have reduced risk from land-cover change as a result of the interaction under all three scenario combinations (Fig. 2). Risk for mammals and birds increases the most in areas where temperature change is predicted to increase the most (Fig. A3-A5). In contrast, risk declines most in areas where mean precipitation is expected to increase the most. Prediction uncertainties showed that the confidence interval size is highest in areas of high habitat loss and lowest in areas of low habitat loss (Fig. A2 & A6).

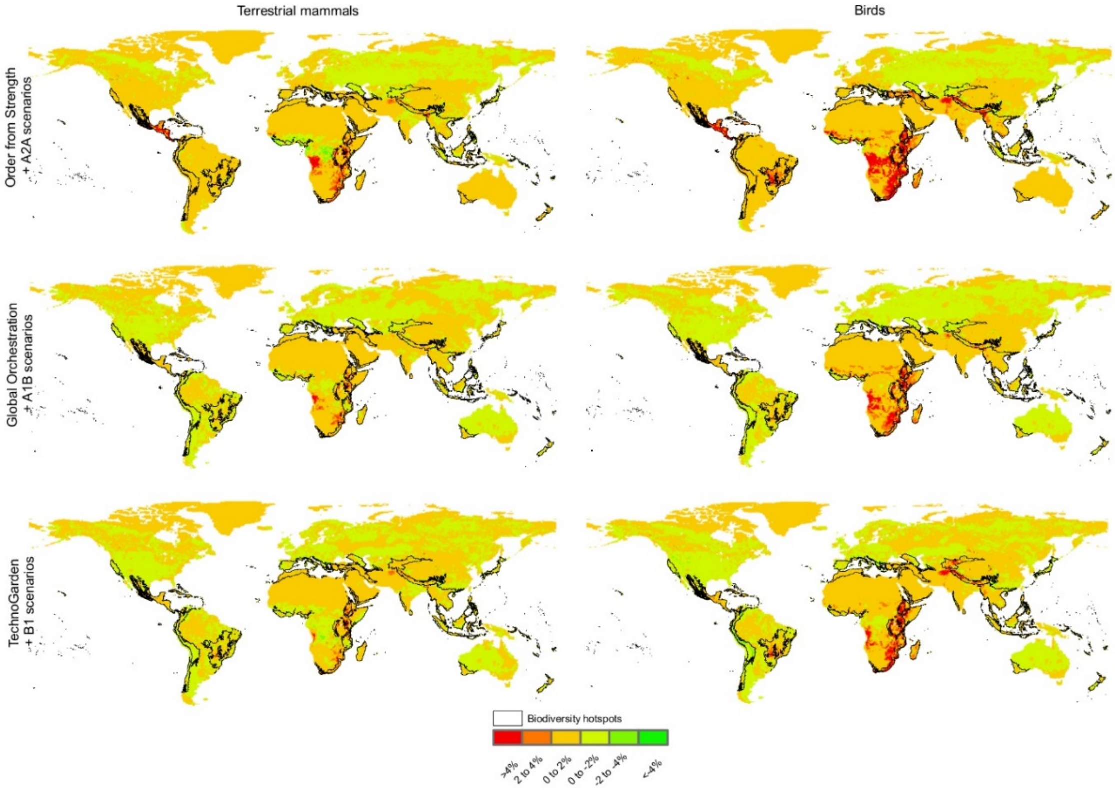

Figure 2. The effect of the interaction between climate change and habitat loss on the risk of species being impacted from future land-cover change for terrestrial mammals, birds, and across biodiversity hotspots. Values represent the percent change in the number of species affected after considering the interaction with climate based on Eq. (3). Land-cover and climate change scenarios are described in Table 1 (MEA 2005, IPCC 2007). Biodiversity hotspots were downloaded from http://sp10.conservation.org/ (Myers et al. 2000). Global richness of birds and terrestrial mammals were compiled by Birdlife International (http://www.birdlife.org/) and Rondinini et al. (2011). Orange and dark red indicate areas where the interaction between climate change and habitat loss increases risk due to future land-cover change, whereas light to dark green indicate areas where the interaction between climate change and habitat loss either reduces or does not affect risk due to future land-cover change.

Future climate change exacerbates vulnerability to habitat loss across large areas of the globe and is the primary driver of the detrimental effect of the interaction between climate change and habitat loss on the risk of species being impacted by land-cover change (Fig. 3). Under high rates of climate change (A2A scenario), vulnerability is exacerbated by 30% for mammals and 52% for birds (Fig. 3a & 3d). Under moderate (A1B scenario) and low climate change (B1 scenario), vulnerability increases by 15-17% for mammals and 30-34% for birds (Fig 3b-c & 3e-f). Regions including Central America, Caribbean, North America (particularly the western side), North and West Coast of South America, East Africa, South and East Europe (particularly the eastern side), Central and West Asia, East Asia, and Australia (particularly the eastern side) are predicted to be most heavily impacted by the interaction (Fig. 3). Small sections throughout Southeast Asia, Melanesia, Middle and West Africa, North America, and South America are predicted to show a decline in vulnerability due to the interaction under all three scenarios (Fig. 3).

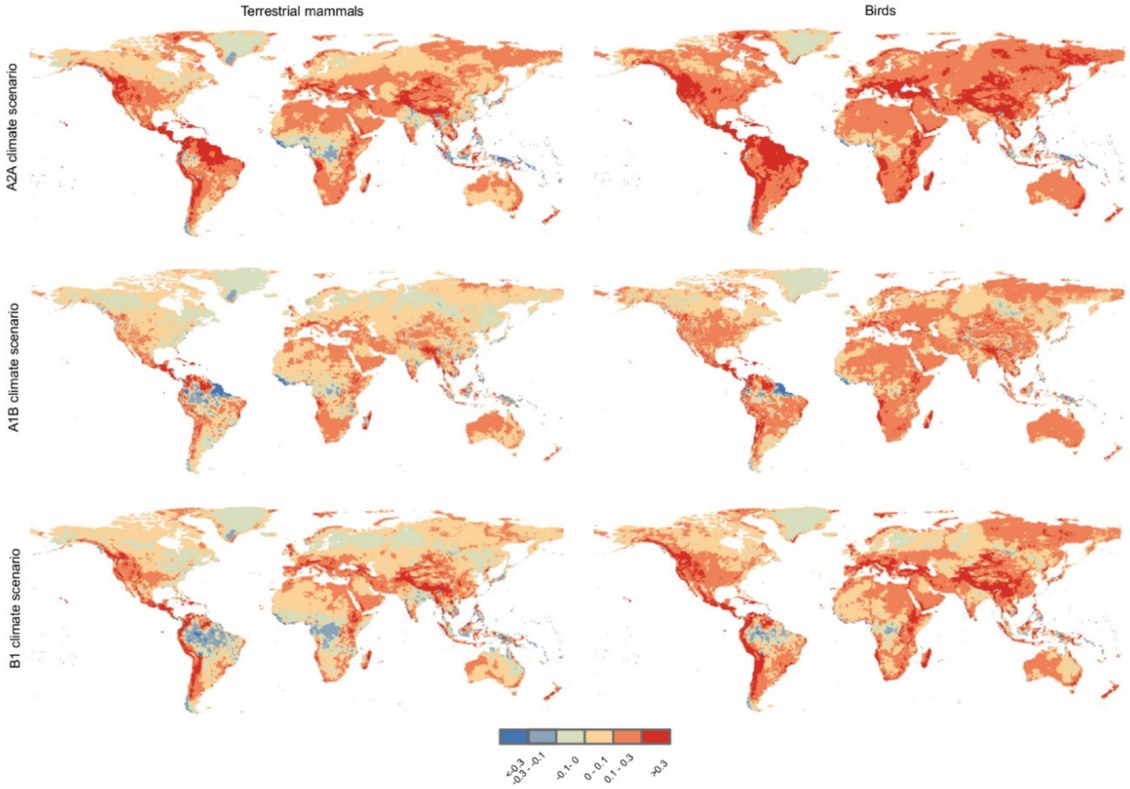

Figure 3. The difference in vulnerability to habitat loss under current versus future climatic conditions (measuring the impact of the interaction between climate change and habitat loss on vulnerability) for terrestrial mammals and birds. Values are calculated for three different 2050 emission scenarios (IPCC 2007). Red indicates areas where vulnerability is predicted to increase as a result of the interaction, while blue indicates areas where vulnerability is predicted to decline as a result of the interaction.

The interaction between climate and habitat loss is likely to modify conservation priorities. When we rank biodiversity hotspots (Myers et al. 2000) according to their risk of species impacted with (R^a) and without interactions (R^b), we discover that 15-32% of terrestrial biodiversity hotspots change by two or more ranks for both birds and mammals (Table 2-3; Fig. 2). For example, for birds, the West African Forests, Cerrado and Indo-Burma become less of a priority, whereas Mesoamerica, Himalaya and the Madrean Pine-Oak Woodlands become more of a priority (Table 2). For mammals, the West African Forests, Indo-Burma and the Atlantic Forest become less of a priority in terms of risk, whereas Mesoamerica, Madagascar and Tumbes-Choco-Magdalena become more of a priority (Table 3).

Table 2 Biodiversity hotspots ranked according to the expected risk for terrestrial bird species under current climate and future land-cover (a) and future climate and future land-cover (b). Lower numbers indicate higher risk. Bold indicates a difference in rankings between a and b of two or more places.

	Order from Strength[a]		Global Orchestration[a]		TechnoGarden[a]	
Hotspot region	a	b	a	b	a	b
Maputaland-Pondoland-Albany	1	1	1	1	1	1
Coastal Forests of Eastern Africa	2	3	2	2	2	2
Eastern Afromontane	3	2	4	3	4	4
West Africa Forests	4	**7**	12	**14**	14	15
Cape Floristic Region	5	5	3	4	3	3
Mesoamerica	6	**4**	14	**12**	15	14
Madrean Pine-Oak Woodlands	7	6	17	17	21	**19**
Horn of Africa	8	8	5	5	5	5
Cerrado	9	9	8	**10**	6	6
Madagascar	10	10	6	6	7	7
Indo-Burma	11	**14**	7	8	8	**12**
Irano-Anatolian	12	12	10	11	13	13
Caribbean Islands	13	13	15	**13**	17	17
Western Ghats and Sri Lanka	14	**16**	13	**15**	16	16
Himalaya	15	**11**	9	**7**	12	**8**
Atlantic Forest	16	15	16	16	9	**11**
Southwest Australia	17	**19**	23	23	19	**21**
Tumbes-Choco-Magdalena	18	17	24	24	20	20
Succulent Karoo	19	18	10	9	10	10
Mediterranean Basin	20	20	19	20	18	18
Tropical Andes	21	21	30	31	32	33
Wallacea	22	22	20	19	24	**22**
Sundaland	23	**26**	21	21	22	23
Philippines	24	**27**	22	22	23	24
California Floristic Province	25	24	33	33	34	34
New Zealand	26	25	25	25	25	25
Chilean Forests	27	**23**	29	29	29	30
Polynesia-Micronesia	28	29	28	28	28	29
Mountains of Southwest China	29	28	18	18	30	**32**
East Melanesian Islands	30	31	26	27	27	27
New Caledonia	31	32	27	26	26	26
Mountains of Central Asia	32	**30**	34	34	11	**9**
Japan	33	33	31	30	33	**31**
Caucasus	34	34	32	32	31	**28**

[a] Scenario combinations are described in *Materials and Methods*. Rankings are based on the average risk across each biodiversity hotspot (Fig. 2).

Table 3 Biodiversity hotspots ranked according to the expected risk for terrestrial mammal species under current climate and future land-cover (a) and future climate and future land-cover (b). Lower numbers indicate higher risk. Bold indicates a difference in rankings between a and b of two or more places.

	Order from Strength[a]		Global Orchestration[a]		TechnoGarden[a]	
Hotspot region	a	b	a	b	a	b
Maputaland-Pondoland-Albany	1	1	1	1	1	1
West Africa Forests	2	**7**	11	**13**	10	**15**
Coastal Forests of Eastern Africa	3	4	2	2	2	3
Eastern Afromontane	4	3	4	4	4	4
Mesoamerica	5	**2**	12	**9**	13	**11**
Cape Floristic Region	6	5	3	3	3	2
Madrean Pine-Oak Woodlands	7	6	16	17	21	**19**
Cerrado	8	8	6	7	5	5
Horn of Africa	9	9	5	5	6	6
Irano-Anatolian	10	10	10	11	9	10
Indo-Burma	11	11	9	10	12	**14**
Atlantic Forest	12	**14**	14	14	7	8
Madagascar	13	13	7	6	11	**9**
Tumbes-Choco-Magdalena	14	**12**	22	22	17	17
Western Ghats and Sri Lanka	15	**17**	15	15	16	**18**
Succulent Karoo	16	16	8	8	8	7
Himalaya	17	**15**	13	12	15	**13**
Mediterranean Basin	18	19	19	19	18	**16**
Caribbean Islands	19	18	18	**16**	19	20
Southwest Australia	20	21	24	24	23	23
Tropical Andes	21	20	31	31	33	33
Sundaland	22	**25**	20	21	20	21
California Floristic Province	23	22	34	34	34	34
Wallacea	24	24	21	20	22	22
Chilean Forests	25	**23**	29	29	29	30
Philippines	26	27	23	23	24	24
Mountains of Southwest China	27	26	17	18	32	32
Polynesia-Micronesia	28	28	28	27	25	**28**
East Melanesian Islands	29	**31**	26	**28**	27	**25**
New Zealand	30	30	25	26	26	26
New Caledonia	31	32	27	**25**	28	27
Mountains of Central Asia	32	**29**	33	33	14	**12**
Japan	33	33	30	30	31	31
Caucasus	34	34	32	32	30	29

[a] Scenario combinations are described in *Materials and Methods*. Rankings are based on the average risk across each biodiversity hotspot (Fig. 2).

4. DISCUSSIONS & CONCLUSIONS

Interactions between stressors may be a critical driver of future global change impacts on biodiversity. Here we have shown that the interaction between climate and habitat loss on the risk of terrestrial mammal and bird species being impacted by land-cover change has critical bearing on both impacts and conservation priorities. If temperatures continue to increase and rainfall continues to decline, as projected in many areas across the globe (Stocker et al. 2013), the impact of habitat loss could be much greater than originally projected. In general, under predictions of substantial climate change (A2A scenario), the effect of the interaction between climate and land-cover was higher than it was under lower (B1 scenario) and moderate (A1B scenario) climate change scenarios for both mammals and birds. However, although the effect of the interaction for mammals increased successively with higher levels of climate change, the effect for birds did not change from low to moderate climate change (B1 to A1B). This was due to the differences in the global distribution of mammals versus birds relative to the locations of climate change and habitat loss. Mammal richness is patchier than bird richness (Fig. A2), resulting in a greater change in vulnerability between the TechnoGarden + B1 scenario and the Global Orchestration + A1B scenario. Bird richness is higher in areas where there is less of an increase in the interaction than compared to mammals. Overall, birds were systematically more impacted by the interaction because the effect of the interaction was larger than for mammals (Mantyka-Pringle et al. 2012). However, this was most apparent under the Order from Strength + A2A scenario and the TechnoGarden + B1 scenario and less apparent under the Global Orchestration + A1B scenario. Once again this occurs because of differences in the locations of habitat loss and climate change effects relative to the distribution of mammals and birds. This points to complex spatial interactions between climate change and land-cover change driving differences between birds and mammals. Nevertheless, overall trends were maintained across scenarios implying that general insights about interactions between climate change and habitat loss are possible for understanding global change impacts.

A prerequisite for conservation planning is to identify areas of high conservation value (i.e. high biodiversity or irreplaceability value; Myers et al. 2000; Olson and Dinerstein 1998) and those subject to high threat or vulnerability (Mittermeier et al. 2004; Rodrigues et al. 2004). Areas that combine both important biodiversity features and high current or future threats are considered conservation priorities. Our analysis suggests that these areas may include East and South Africa, Central America, North and South America, Caribbean, South and West Europe, West and South Asia, East Asia, Australia, and parts of Southeast Asia and North Europe. These areas are where temperatures will increase the most and average rainfall will continue to decline. In comparison to other global assessments based on habitat suitability (e.g. Jetz et al. 2007; Visconti et al. 2011), sharp contrasts exist in that fewer regions are considered to be vulnerable and generally concentrated in Central Africa, Brazil, Central America or North America. Yet, when climate stability is combined with vegetation intactness, similar regions were found to be vulnerable in southwest Europe, India, China and Mongolia, eastern Australia, and eastern South America (Watson et al. 2013). However, notable differences were found in southeast and central Europe, southeast Asia, and central North America (Watson et al. 2013). These differences indicate that if you consider how vulnerability to habitat loss is affected by climate, rather than considering the combined or independent effects of climate change and habitat loss, very different results are obtained.

We show that the incorporation of the interaction between climate change and habitat loss into conservation assessments can affect the ranking of priority areas. Between 15 and 32% of global biodiversity hotspots (regions of exceptional biodiversity value) change their ranking based on threat from land-cover change by two or more ranks when the interaction between climate change and habitat loss is incorporated. TechnoGarden + B1 and Order from Strength + A2A scenarios provided the highest change in rankings as a result of where the biodiversity hotspots overlapped with predicted land clearing relative to climate change and the species distributions. Thus, if we ignore the role of interactions during the prioritisation of conservation areas, we risk substantially under or overestimating threats in many regions and ultimately making conservation prioritisation decisions that are highly sub-optimal. New management strategies or prioritisation approaches may therefore be needed to cope with climate change interactions in order to prevent further biodiversity loss. For instance, habitat protection and restoration efforts can mitigate the risk of biodiversity loss to climate change and habitat loss interactions. Proactive approaches to ecosystem management such as green technology, eco-efficiency, and tradable ecological property rights, and increasing the use of clean and resource efficient technologies can also mediate the interacting effect by minimising the damage on ecosystems. Although, protecting the weak may not always be the best strategy for conservation planning in some regions (Game et al. 2008), in the case of biodiversity hotspots, we argue that investing in habitat protection and/or restoration within highest-risk sites can ameliorate the impacts of climate change on global biodiversity (Malcolm et al. 2006).

Areas identified as being strongly impacted by the interaction between climate change and habitat loss should be a priority for preventing further habitat loss. Preventing habitat loss will require a multifaceted approach including land-use planning and regulation, introduction of incentive programs and managing human population growth (ten Brink et al. 2010). Where these actions are not socially or economically feasible, adopting alternative climate adaptation and biodiversity conservation approaches will be necessary. For example, recent work indicates that incentivising targeted habitat restoration could increase the resilience of some ecosystems in the face of climate change by allowing species to migrate with changing climate (Prober et al. 2012; Renton et al. 2012). For communities that are unlikely to be able to migrate to suitable environments elsewhere (e.g. alpine and freshwater communities), it may be possible to minimize interactions through the protection or installation of climate refuges or buffer strips (Mantyka-Pringle et al. 2014; Shoo et al. 2011) or by manipulating vegetation structure, composition, or disturbance regimes (Hansen et al. 2001). Other adaptation strategies may include translocating vulnerable species to novel habitats (Schwartz and Martin 2013), altering fire regimes, or mitigating other threats such as invasive species, habitat fragmentation and pollution. Policy-makers and planners should therefore optimize management actions as well as protected area placement in areas where biodiversity and endangered species are most at risk.

We considered future habitat loss only through the expansion of agricultural land because other land-cover conversions were not available as global maps (Bartholomé and Belward 2005). In addition, the focus of this study was on the interaction between climate change and land-cover change, so we did not consider the interacting effects of other stressors (Crain et al. 2008) (e.g. hunting, poaching, illegal wildlife trading), or those between interacting species (Bascompte et al. 2006) (e.g. competition, predation, parasitism, food chains). The next challenge will be to apply the *Risk* model to a broader range of stressors, taxa, and global land-cover changes. The global meta-analysis that we used to calculate *Vulnerability* was based on a diversity of response variables, including species density (n = 266), species richness (n = 36), probability of occurrence (n = 13) and species diversity (n = 6) (Mantyka-Pringle et al. 2012). Ideally we would have used a model based solely on species richness to match that of the exposure indicator (global richness of birds and mammals). Nevertheless, our model only requires information on the probability that each species is affected by habitat loss, not an effect on species richness, and this is represented by the expected probability of an impact on each species. As with any predictive model, we assume that the present relationship holds when extrapolated to future conditions outside the period for which the model was fitted. We also assumed that all species in a given location would be equally influenced by or have the same ability to adapt to land-cover change or climate change (Hof et al. 2011) (e.g. through dispersal, behaviour, physiology) in determining impacts on biodiversity. However, the aim of this study was to examine the extent to which interactions influence impacts and conservation priorities across species, rather than saying something definitive about absolute impacts on individual species. Finally, we found highest uncertainty in areas of high habitat loss (East and South Africa, Central America, South Asia), but lowest uncertainty in the world's tropical forests (Amazon, Congo, Borneo). More research is therefore needed in understanding the mechanistic drivers of interactions considered here that can inform the prioritization of multiple conservation actions. Future studies should also incorporate the impacts of extreme events in the 'Vulnerability model' and determine which species will be adversely affected, so that managers can plan for recovery or reduce the threat to threatened species (Ameca y Juárez et al. 2014).

Taking a predictive approach based on an interaction effect that was empirically derived is a major advance. Our results highlight the need for more global biodiversity response studies to consider climate change interactions if we are to develop and improve conservation policies and strategies. Should such predictions continue to be refined then there is every prospect that they can form the basis of management decisions. For instance, funding schemes promoted by the United Nations Framework Convention on Climate Change (UNFCCC) such as REDD+ (reducing carbon emissions by decreasing deforestation and forest degradation) may need to be biased towards areas that are most negatively impacted by the interaction between climate change and habitat loss. In these types of problems, developing effective conservation strategies that are explicit about interactions among stressors will be critical for conserving and maintaining biodiversity.

ACKNOWLEDGEMENTS

We thank Mark Balman from BirdLife International and IUCN for access to data. This research was supported by a Queensland Government Smart Futures Scholarship, CSIRO Climate Adaptation Flagship, an Australian Government Postgraduate Award and the Australian Research Council's Centre of Excellence for Environmental Decisions.

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SUPPLEMENTARY MATERIAL

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix A. Supporting figures

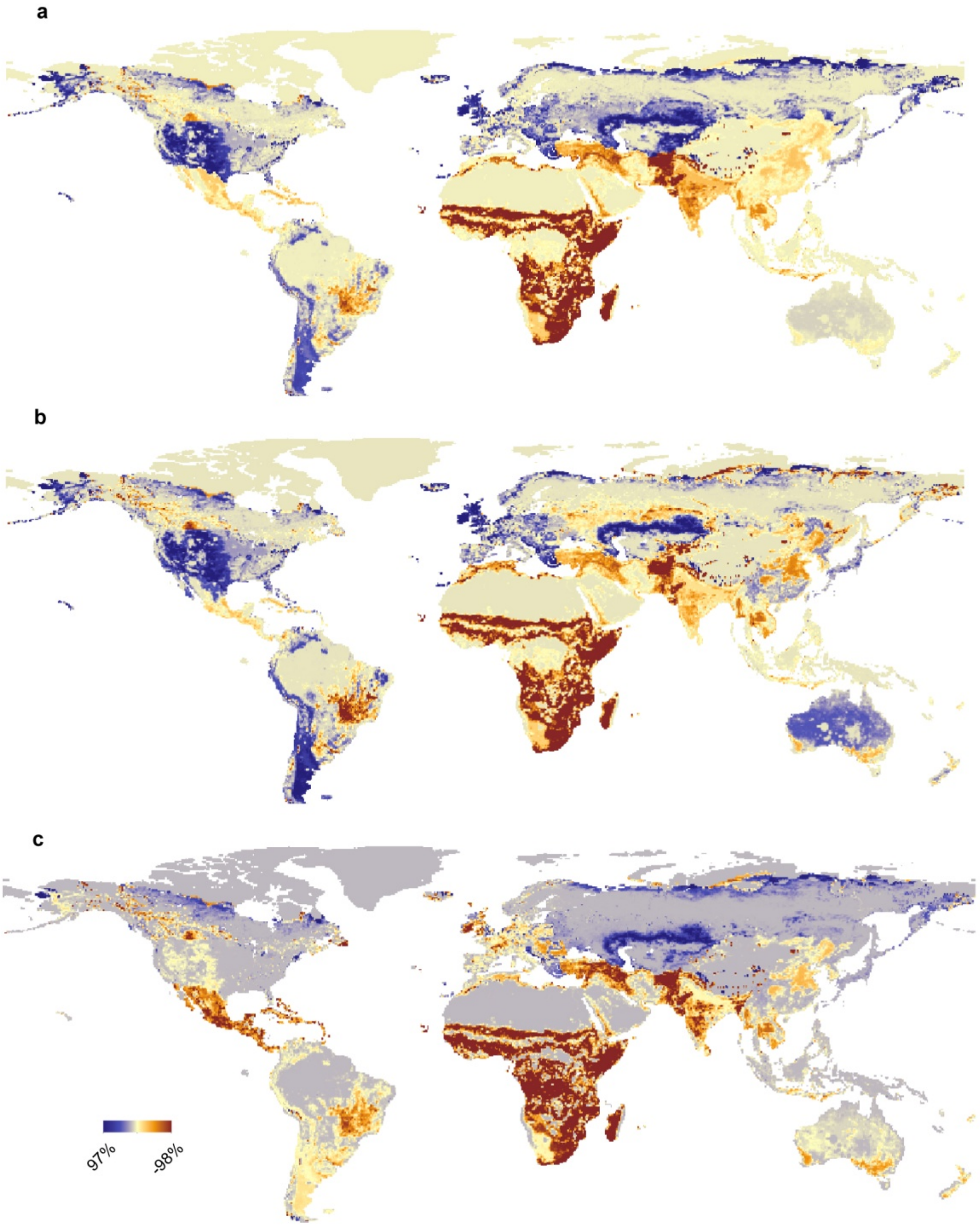

Figure A1. Percentage change in natural vegetation due to projected land-cover change by 2050. Patterns are given for the (a) "Global Orchestration" scenario, (b) "TechnoGarden" scenario, and (c) "Order from Strength" scenario from the Millennium Ecosystem Assessment (MEA, 2005). Light to dark orange indicates areas that show a decline in natural vegetation; light to dark purple indicates areas that show an increase in natural vegetation. See Table 1 in main paper for a description of all three scenarios.

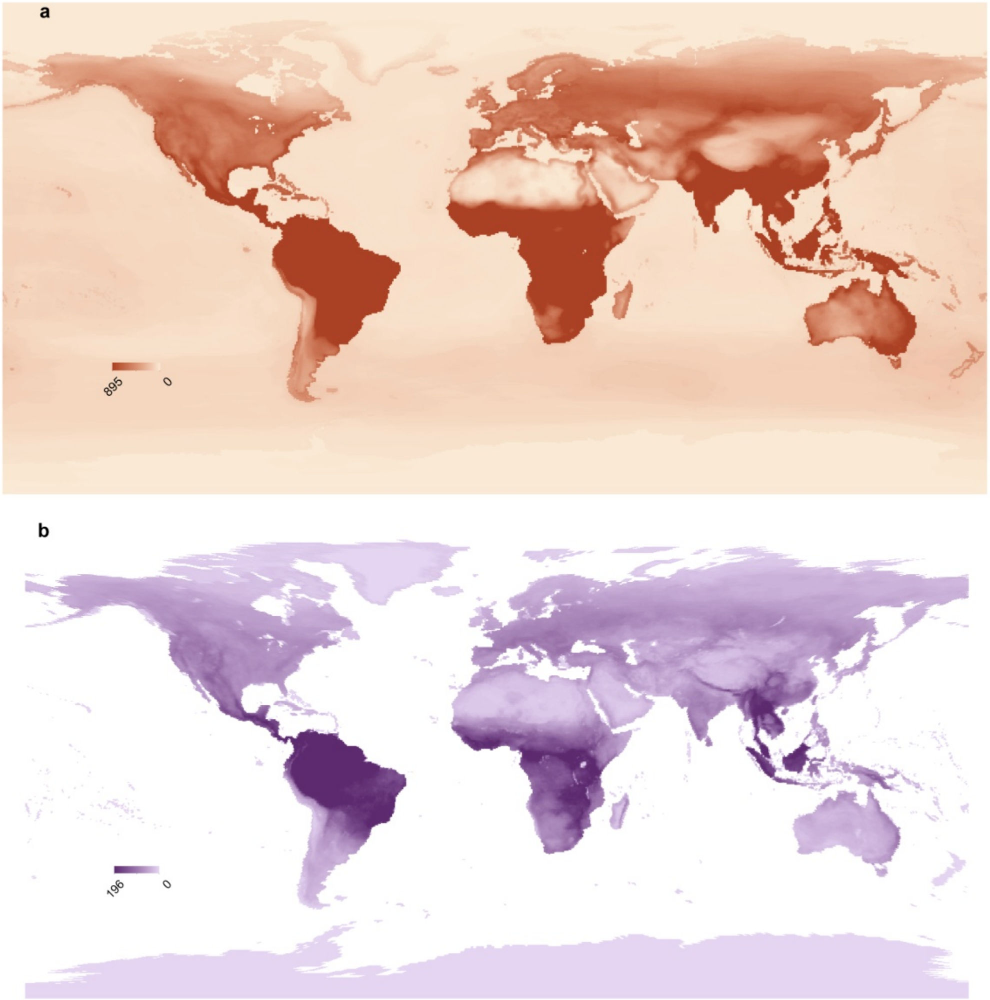

Figure. A2. Global richness maps for terrestrial (a) birds and (b) mammals. Colour gradients are linear with respect to species number. Richness of birds and terrestrial mammals were compiled by Birdlife International (http://www.birdlife.org/) and Rondinini et al. (2011).

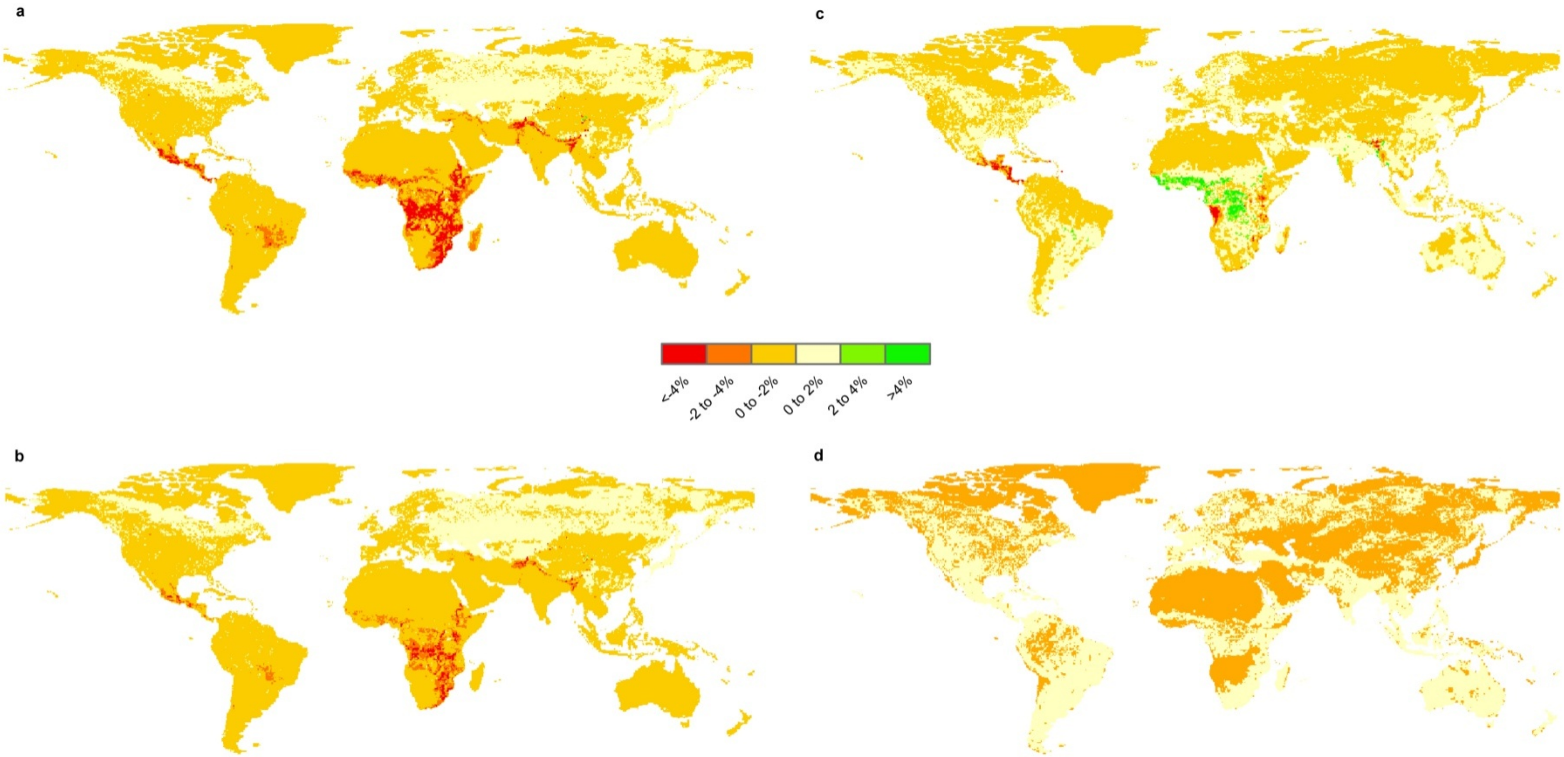

Figure A3a. The change in risk of birds being impacted once the climate and land-cover change interaction is accounted for. Values represent the proportional difference in risk of species being impacted for the “Order from Strength” land-cover scenario with and without accounting for future (SRES A2A) climate change as calculated in Eq. (3) due to: (a) mean temperature change, (b) maximum temperature of warmest month, (c) mean precipitation change, and (d) precipitation of driest month. Orange and dark red indicate areas where risk is predicted to increase; yellow and light to dark green indicate areas where risk is predicted to decline or remain unchanged.

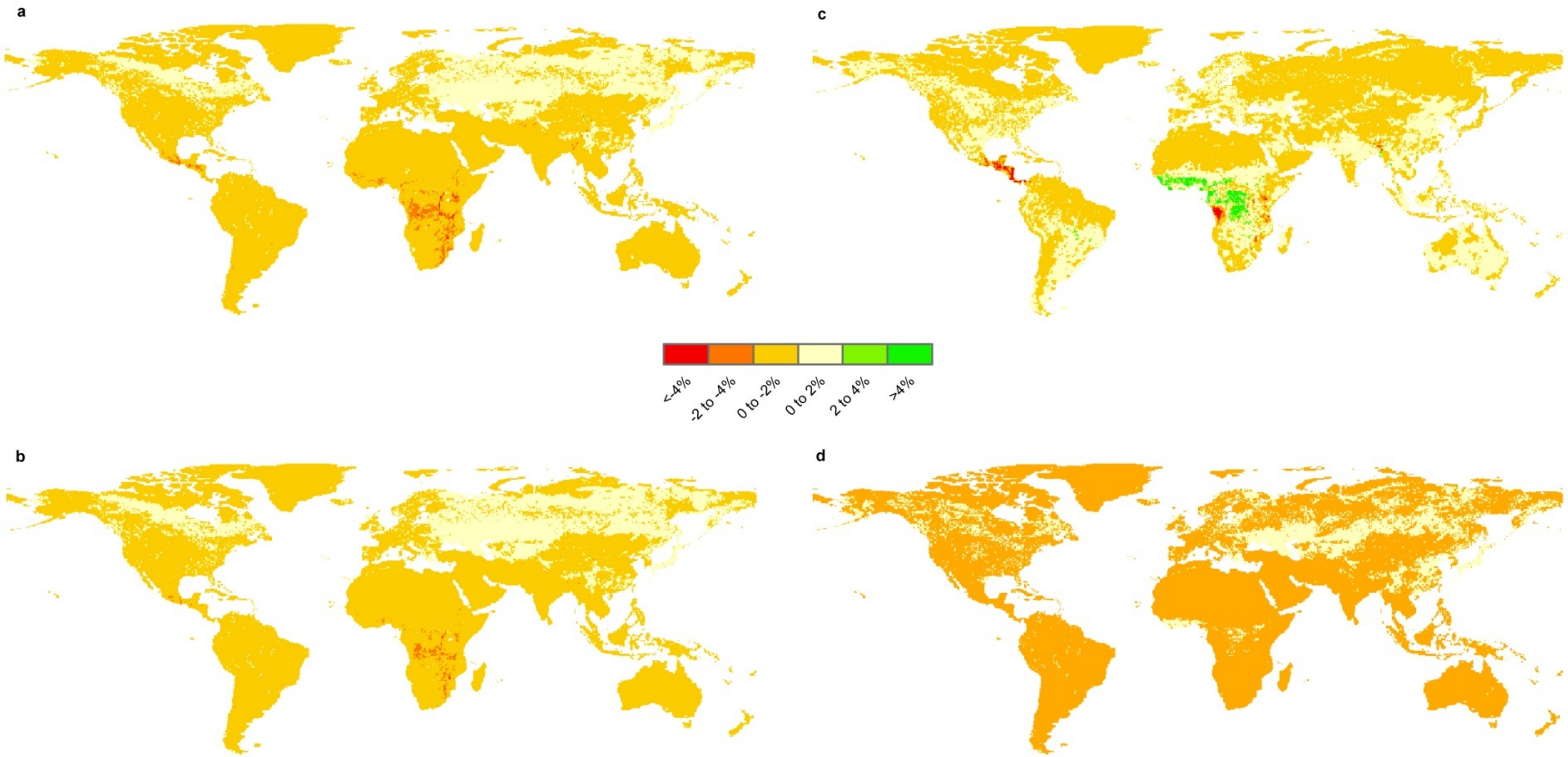

Figure A3b. The change in risk of terrestrial mammals being impacted once the climate and land-cover change interaction is accounted for. Values represent the proportional difference in risk of species being impacted for the “Order from Strength” land-cover scenario with and without accounting for future (SRES A2A) climate change as calculated in Eq. (3) due to: (a) mean temperature change, (b) maximum temperature of warmest month, (c) mean precipitation change, and (d) precipitation of driest month. Orange and dark red indicate areas where risk is predicted to increase; yellow and light to dark green indicate areas where risk is predicted to decline or remain unchanged.

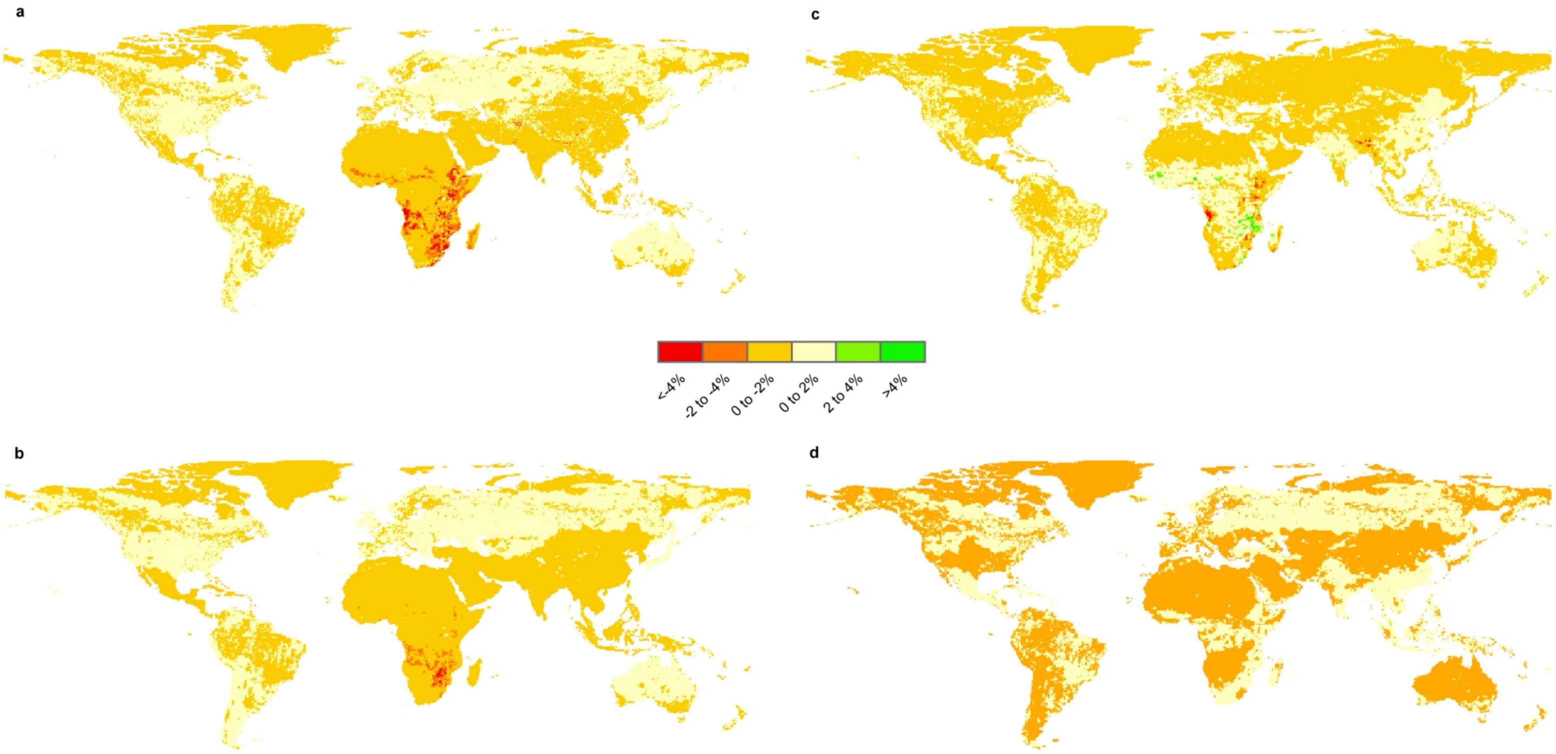

Figure A4a. The change in risk of birds being impacted once the climate and land-cover change interaction is accounted for. Values represent the proportional difference in risk of species being impacted for the "Global Orchestration" land-cover scenario with and without accounting for future (SRES A1B) climate change as calculated in Eq. (3) due to: (a) mean temperature change, (b) maximum temperature of warmest month, (c) mean precipitation change, and (d) precipitation of driest month. Orange and dark red indicate areas where risk is predicted to increase; yellow and light to dark green indicate areas where risk is predicted to decline or remain unchanged.

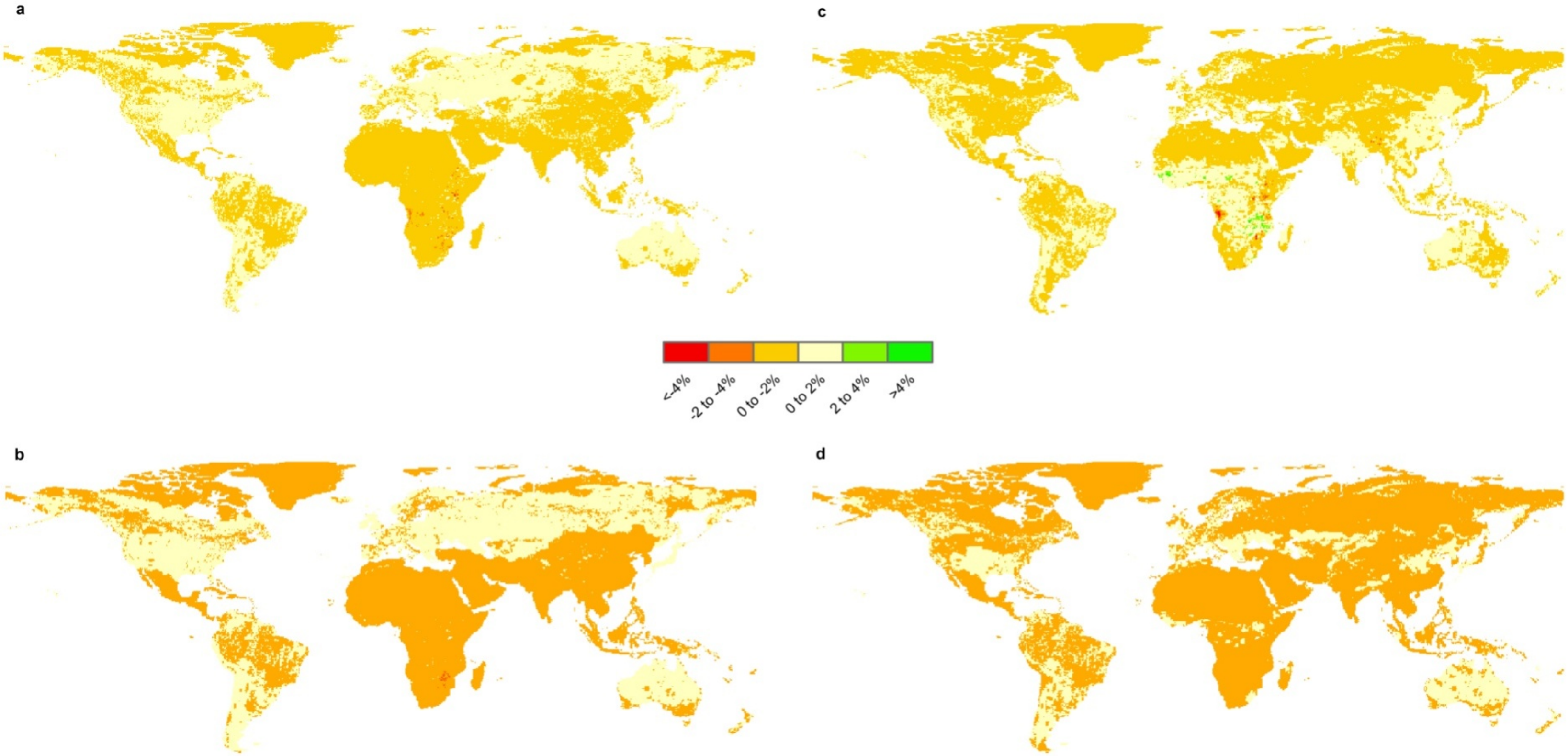

Figure A4b. The change in risk of terrestrial mammals being impacted once the climate and land-cover change interaction is accounted for. Values represent the proportional difference in risk of species being impacted for the "Global Orchestration" land-cover scenario with and without accounting for future (SRES A1B) climate change as calculated in Eq. (3) due to: (a) mean temperature change, (b) maximum temperature of warmest month, (c) mean precipitation change, and (d) precipitation of driest month. Orange and dark red indicate areas where risk is predicted to increase; yellow and light to dark green indicate areas where risk is predicted to decline or remain unchanged.

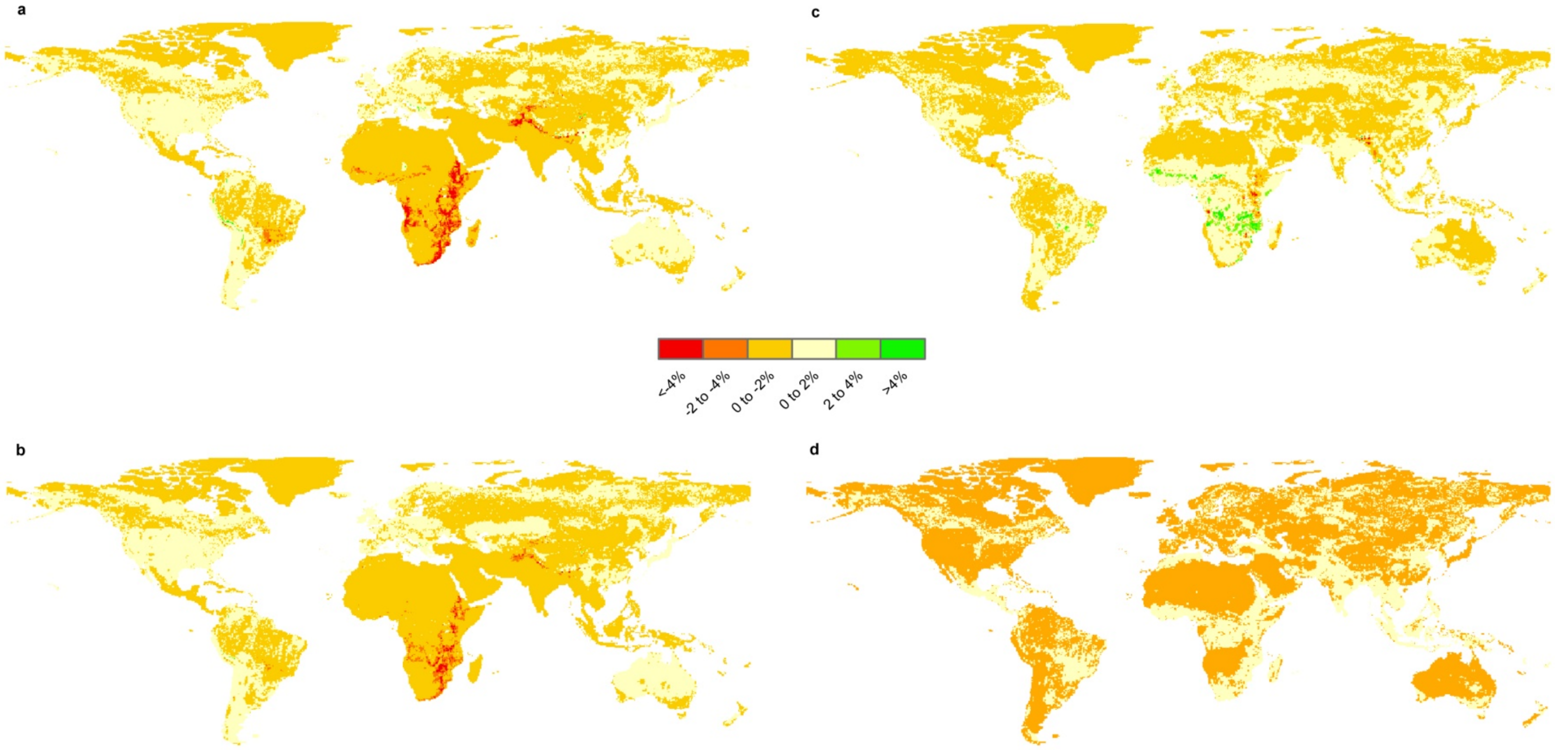

Figure A5a. The change in risk of birds being impacted once the climate and land-cover change interaction is accounted for. Values represent the proportional difference in risk of species being impacted for the "TechnoGarden" land-cover scenario with and without accounting for future (SRES B1) climate change as calculated in Eq. (3) due to: (a) mean temperature change, (b) maximum temperature of warmest month, (c) mean precipitation change, and (d) precipitation of driest month. Orange and dark red indicate areas where risk is predicted to increase; yellow and light to dark green indicate areas where risk is predicted to decline or remain unchanged.

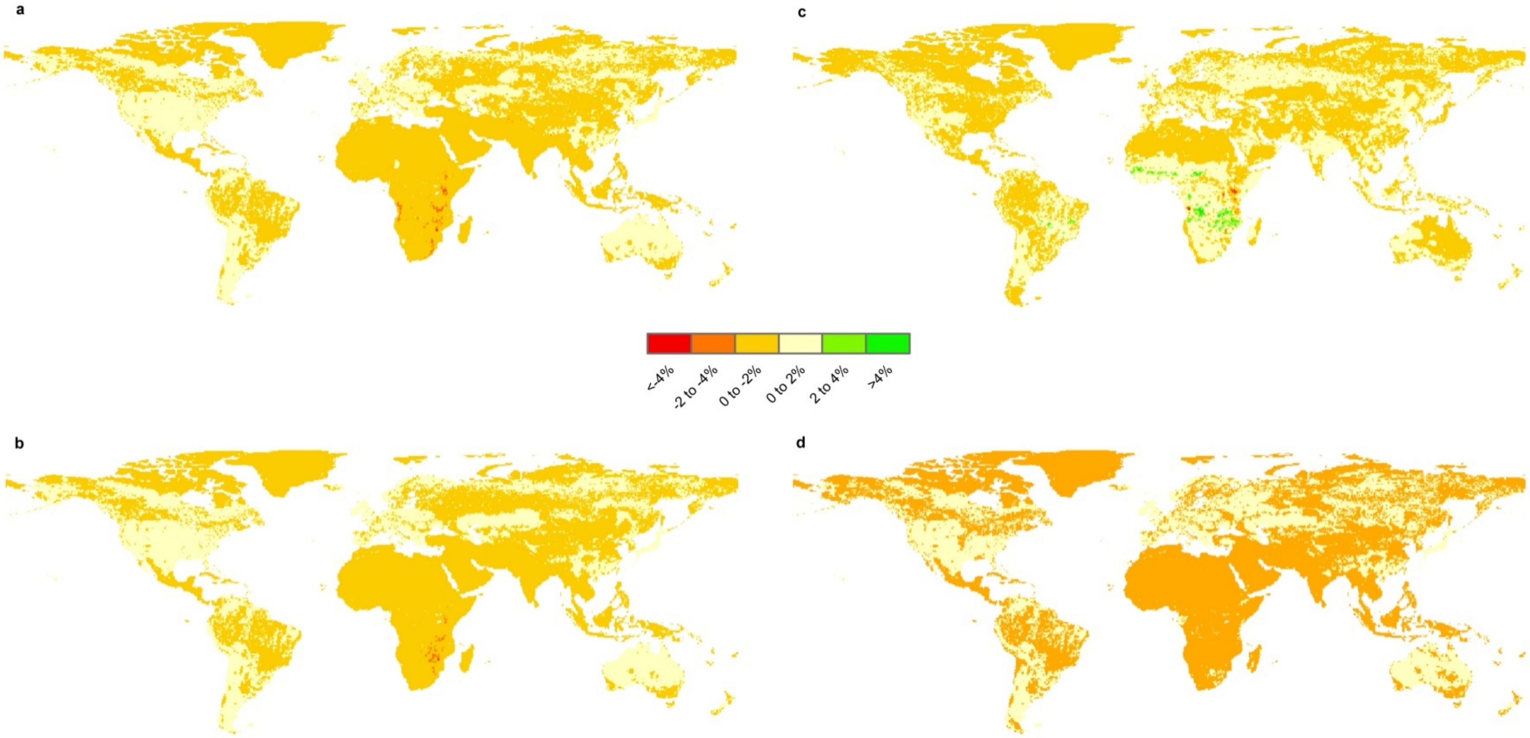

Figure A5b. The change in risk of terrestrial mammals being impacted once the climate and land-cover change interaction is accounted for. Values represent the proportional difference in risk of species being impacted for the "TechnoGarden" land-cover scenario with and without accounting for future (SRES B1) climate change as calculated in Eq. (3) due to: (a) mean temperature change, (b) maximum temperature of warmest month, (c) mean precipitation change, and (d) precipitation of driest month. Orange and dark red indicate areas where risk is predicted to increase; yellow and light to dark green indicate areas where risk is predicted to decline or remain unchanged.

Appendix B. Uncertainty analysis

We calculated prediction uncertainties using the standard errors of the vulnerability model parameter estimates based on the following five steps:

(1) Calculate the model averaged standard error for the linear predictor as

$$\mathrm{se}\left(\hat{\hat{\pi}}\right)=\sqrt{\begin{gathered}\left[\mathrm{se}\left(\hat{\hat{\theta}}_{\mathrm{intercept}}\right)\right]^2+\left[\mathrm{mtwm}\times\mathrm{se}\left(\hat{\hat{\theta}}_{\mathrm{mtwm}}\right)\right]^2+\left[\mathrm{podm}\times\mathrm{se}\left(\hat{\hat{\theta}}_{\mathrm{podm}}\right)\right]^2+\left[\mathrm{precdiff}\times\mathrm{se}\left(\hat{\hat{\theta}}_{\mathrm{precdiff}}\right)\right]^2\\+\left[\mathrm{tmxdiff}\times\mathrm{se}\left(\hat{\hat{\theta}}_{\mathrm{tmxdiff}}\right)\right]^2+\left[\mathrm{habper}\times\mathrm{se}\left(\hat{\hat{\theta}}_{\mathrm{habper}}\right)\right]^2\end{gathered}} \tag{1}$$

where $\hat{\hat{\theta}}_{\cdot\cdot}$ are the model averaged coefficient estimates for mammals or birds, $\mathrm{se}\left(\hat{\hat{\theta}}_{\cdot\cdot}\right)$ are the model averaged standard errors for the coefficients, $\hat{\hat{\pi}}$ is the model averaged prediction for the linear predictor, mtwm is the max temperature of warmest month, podm is the precipitation of driest month, precdiff is the mean precipitation change, tmxdiff is the mean temperature change, and habper is the percentage of habitat.

(2) An approximate 95% confidence interval for the linear predictor was calculated following Burnham and Anderson (2002) as

$$\hat{\hat{\pi}}\pm z_{1-\alpha/2}\mathrm{se}\left(\hat{\hat{\pi}}\right). \tag{2}$$

(3) We then back-transformed the linear predictor confidence interval to get the confidence interval on the [0,1] range for the probability of decline (vulnerability) using

$$\hat{\hat{V}}_{lower}=\frac{\exp\left(\hat{\hat{\pi}}-z_{1-\alpha/2}\mathrm{se}\left(\hat{\hat{\pi}}\right)\right)}{1+\exp\left(\hat{\hat{\pi}}-z_{1-\alpha/2}\mathrm{se}\left(\hat{\hat{\pi}}\right)\right)} \tag{3}$$

and

$$\hat{\hat{V}}_{upper}=\frac{\exp\left(\hat{\hat{\pi}}+z_{1-\alpha/2}\mathrm{se}\left(\hat{\hat{\pi}}\right)\right)}{1+\exp\left(\hat{\hat{\pi}}+z_{1-\alpha/2}\mathrm{se}\left(\hat{\hat{\pi}}\right)\right)}. \tag{4}$$

(4) We then calculated the confidence interval for the risk of terrestrial mammals and birds being impacted from future land-cover change (*R*) based on the upper and lower intervals for *Vulnerability* as

$$R_{lower} = E \times \hat{\bar{V}}_{lower} \times H \tag{5}$$

and

$$R_{upper} = E \times \hat{\bar{V}}_{upper} \times H \tag{6}$$

where R_{lower} and R_{upper} are the lower and upper confidence bounds for risk (i.e., an index of the expected number of species impacted by habitat loss), E is exposure (i.e., number of species), $\hat{\bar{V}}_{lower}$ and $\hat{\bar{V}}_{upper}$ are the lower and upper confidence bounds for vulnerability (i.e., probability of a negative effect of habitat loss), and H is hazard (i.e., percent loss of habitat).

(5) Finally, as a measure of uncertainty we calculated the range between the upper and lower confidence bounds for risk standardised by the number of species as

$$Uncertainty = \frac{abs(R_{upper}) - abs(R_{lower})}{E}. \tag{7}$$

References

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, USA.

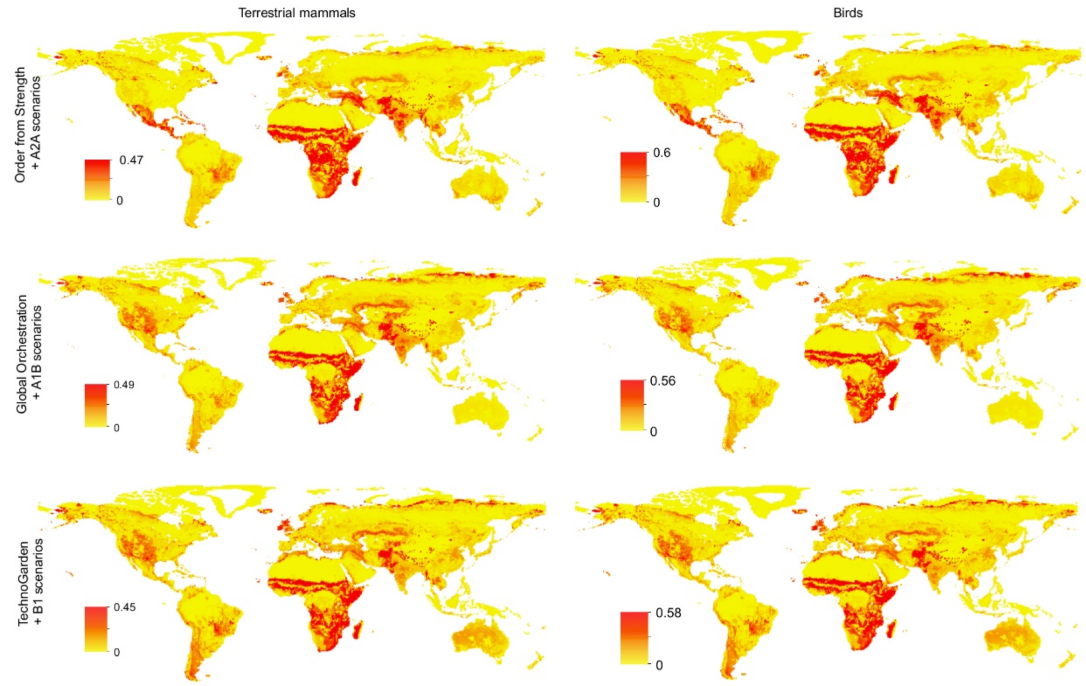

Figure A6. The coefficient of variation for risk of terrestrial mammals and birds impacted from future land-cover change (R_a). Values are calculated as the difference between the upper and lower confidence intervals standardised by the number of species as shown above. Land-cover and climate change scenarios are described in Table 1 of main paper (MEA 2005, IPCC 2007). Global richness of birds and terrestrial mammals were compiled by Birdlife International (http://www.birdlife.org/) and Rondinini et al. (2011). Dark red indicate areas where the confidence interval size is high, whereas yellow indicate areas where the confidence interval size is low.