Global range contractions of mammals, birds and amphibians from 10,000 BC to 2100 AD

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Abstract

The geographical range size of species strongly affects vulnerability to extinction [1,2], making habitat destruction from anthropogenic land use change (LUC) the main driver of global biodiversity loss [3,4]. How have the ranges of the world's species been impacted by the expansion of agricultural and urban areas through time? Here, we use reconstructions of global land use of the past 12,000 years, and four possible future scenarios until the year 2100, to estimate the range sizes of 16580 mammal, bird, and amphibian species from the beginning of agriculture to the end of this century. We find that LUC has caused an average 23% loss of species ranges thus far (2% by 1800, and 7% by 1900), and may account for up to 34% by 2100. Natural ecosystem variability over the past 12,000 years has had a negligible effect in comparison. The proportion of species that have lost more than half of their natural range has increased superexponentially over recent centuries, from 0.03% in 1800 and 0.4% in 1900, to currently 15%, and may reach up to 31% by 2100. There is substantial variability between species, with tropical, small-ranged, and endangered species being especially impacted. We find that range losses have been increasing disproportionately in relation to the size of converted land, driven by a long-term increase of LUC in tropical biodiversity hotspots. Our data suggests that reversing current trends is still possible, but requires concerted efforts to curtail land area required for food production [5], avoid future agricultural expansion into hotspot areas [6], and restore degraded habitat in centres of biological endemism [7,8].

Main text

The transformation of natural habitat across the planet to cropland, pastures and settlements, destroying and fragmenting habitats of species across all taxonomic groups, has become what is now considered the main driver of global terrestrial biodiversity loss [3,4]. In the last 500 years alone, at least 363 vertebrate species have gone extinct [9]; many of the remaining species have been decreasing in abundance [10,11] to the point where between 16 and 33% are now considered threatened [12]. The conversion of now almost half of the world's ice-free area to agricultural and urban areas [13] has reduced the ranges of 25 large herbivore species by an estimated 81% [14], and those of 173 declining mammal species by over 50% compared to the 19th century [15]. Future projections suggest that these trends are unlikely to change in the coming decades, with potentially devastating effects on ecosystem functions [16]. With global agricultural area forecast to increase drastically until 2100 [17], land use change is predicted to continue to impact terrestrial

biodiversity more than any other driver until the end of this century [4,18]. Estimates suggest that global mean species abundance will decrease by 9-17% by 2050 relative to 2000 [19], and up to 1341 birds and mammals may go extinct by 2100 [9].

Whilst the impact of habitat conversion on animal ranges is well documented for a large number of specific cases of species, location and time, a comprehensive global analysis through time and across taxonomic groups has been lacking. Such an assessment is crucial for quantifying long-term trends in extinction pressures on individual species and species communities [1,2], and represents an important addition to global time series of population sizes [20]. Here, we used empirical datasets on the global distribution of 3483 mammal, 8740 bird and 4357 amphibian species, and combined these with species-specific habitat preferences to determine local presences of species under natural vegetation, cropland, pasture and urban land cover (Methods) By overlaying these data with reconstructions of global biomes, and agricultural and urban areas for the last 12,000 years (Methods), we estimated species habitat ranges over time since the very beginning of agriculture. We then extended the analysis into the future using four projections of global land use until 2100, corresponding to Representative Concentration Pathway (RCP) scenarios 2.6, 4.5, 6.0 and 8.5 (Methods; Extended Data Fig. 1), in order to assess potential future pressures. Our approach does not allow for range losses as the result of human influence other than LUC, which we discuss later on. By only considering extant species, past global extinctions do not factor into our reconstructions of range losses; thus, our estimates represent lower boundaries for the true observable losses from combined pressures.

With only moderate impacts on species ranges up until the industrial revolution, the expansion of agricultural production and settlements alongside the rise in population growth since the 18th century has drastically reduced range sizes of mammals, birds and amphibians. We estimated that species had lost an average of 23% of their natural ranges by 2016 (2% by 1800, and 7% by 1900) (Fig. 1B). On average, mammals lost slightly more of their ranges (27%) than amphibians (23%) and birds (23%; consistent with an earlier estimate [21]). Predictions of average range losses by 2100 are strongly dependent on the RCP scenario assumed in the extrapolation of global land use, reaching 34% under a business-as-usual trajectory (RCP 8.5), and dropping to 14% in the best-case scenario (RCP 4.5) (Fig. 1C-F), assuming adequate restoration of abandoned areas. Consistent with previous arguments that small-range species disproportionately threatened by habitat loss [12,22], we found a significant, albeit weak, relationship between habitat loss and natural range size (Extended Data Fig. 2A). Species classified as vulnerable and endangered have lost slightly but significantly more habitat due to LUC than non-threatened species (Extended Data Fig. 2B). For most species, changes in global biome distribution due to past climatic change have had a negligible effect on range sizes compared to LUC: on average, ranges varied by less than 2% in the past 10,000 years due to vegetation dynamics (0% in the past 4,000 years) (Extended Data Fig. 3). 10% of species, capable of living in anthropogenic biomes but not in certain natural vegetation types that occur within their geographical ranges, have benefited from LUC (Fig. 1B).

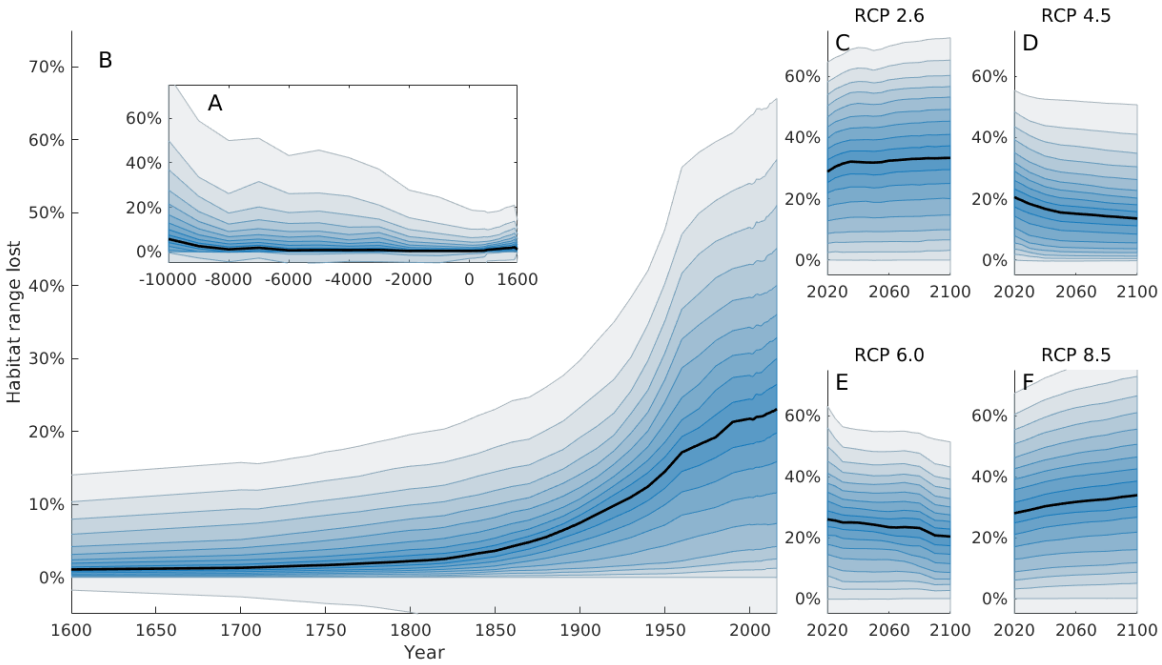

Fig. 1. Past and projected future habitat loss due to LUC across 16850 mammal, bird and amphibian species. Colour shades and the black line represent 5-95% percentiles and the median, respectively. Range changes are relative to present-day potential natural ranges.

A rapidly increasing number of species is critically impacted by land use. The proportion of species that lost more than half of their natural habitat to agricultural land and settlements has increased superexponentially over recent centuries from 0.03% in 1800, to 0.4% in 1900, 15% in 2016 (Fig. 2A-B), and may reach up to 31% by 2100 under a business-as-usual scenario (RCP 8.5) (Fig. 2C-F). While critical range loss affected grassland and temperate forest species most strongly until the mid-20th century, tropical species rapidly took over as the most impacted group in the decades to follow. Birds represent the taxonomic group most impacted by this shift (Extended Data Fig. 4). These trends are predicted to continue in all future scenarios with the exception of RCP 4.5 (Fig. 2D), in which LUC in tropical areas is lowest (Extended Data Fig. 1).

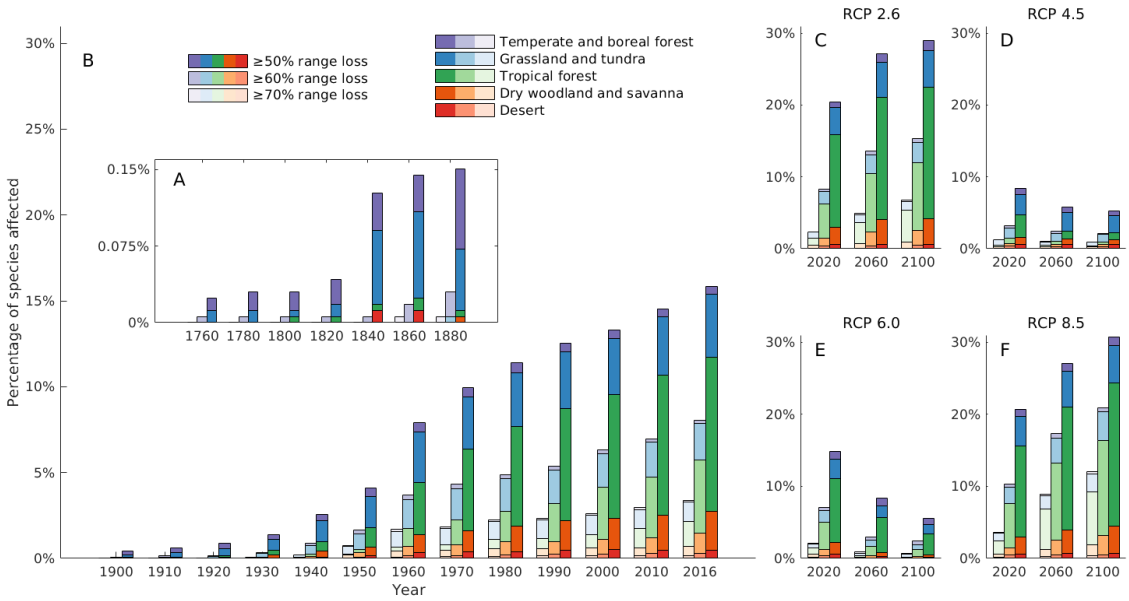

Fig. 2. Past and projected future critical range losses, broken down by species' primary mega-biome (Methods). Losses are relative to present-day potential natural ranges.

The magnitude of range contractions seen for the past 10,000 years is not merely the result of the increasing area of converted land. Over recent centuries and millennia, species habitat loss has increased approximately quadratically in relation to the total size of man-made land (Fig. 3A). Without accounting for biome changes, the first billion hectares of agricultural and urban areas (converted until c. 1720) caused an average 1% range loss, while the most recently converted half billion hectares (since c. 1950) are responsible for an average loss of 8% of natural range sizes. This trend is mirrored by a long-term increase in the marginal impact of newly converted areas on species ranges. The average loss of habitat caused by a unit of land converted in the 20th century was 125% higher than in the 19th century, and 234% higher than in the 18th century (Fig. 3B).

This increase is the marginal impact of land conversion on habitat loss is the result of a long-term trend in the location of LUC towards geographical regions with more species and smaller species ranges. We determined range rarity on newly converted areas through time, which is calculated as the sum of the inverses of natural ranges of local species; thus, it is a measure of the local concentration of small-range species. There is a strong correlation between the 90% percentile of range rarity across newly areas converted in a given time period and the effect that this conversion had on average global range sizes (Fig. 3B). Whilst a correlation between these two variables is intuitive, the strength of the relationship between a globally aggregated pattern (across-species average range loss) on the one hand, and a highly local value (peak biodiversity across converted areas) on the other hand, is not trivial. It also implies that a particularly effective strategy for reducing pressures on as many species as possible is given by steering future LUC away from areas with high range rarity. This reaffirms the need for conscious spatial planning in terms of both the conversion of new areas, and the abandonment and restoration of existing areas [6,23]. A range of policy mechanisms can help to implement these strategies [24].

The occurrence of LUC in areas of increasingly higher range rarity over time is consistent with maps of where new conversions have taken place. South East Asia and South America, after having been largely untouched for a much longer period than other parts of the world (Fig. 3C-F), have seen a rapid expansion of agriculture since the end of the 19th century (Fig. 3G-H). The conversion of natural land cover in these two regions, home to many small-range species, leaves a disproportionately large footprint on the global loss of species habitat, as it means not only the loss of habitat for a large number of species, but also that the lost habitat accounts for a high proportion of species' total ranges [25].

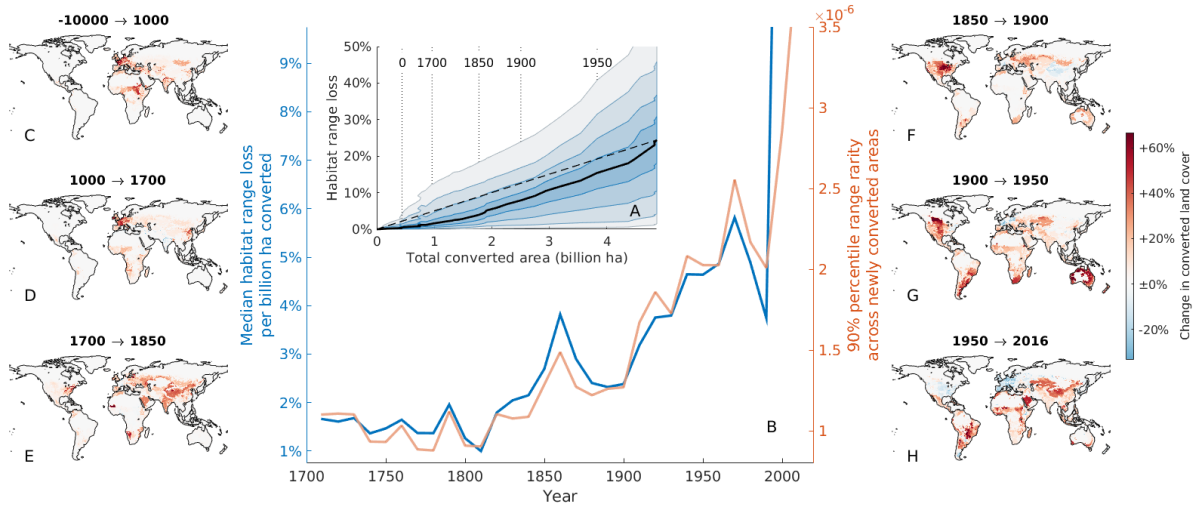

Fig. 3. Increase in the marginal impact of converted areas on species ranges over time. (A) Habitat range loss across species against cumulative global agricultural and urban area. Colour shades and the black line represent 5-95% percentiles and the median, respectively. The dashed black line illustrates the convexity of the median. (B) Across-species median of the marginal impact of LUC per unit of converted area (i.e. the derivative of the black line in (A) with respect to converted area; blue line), and peak range rarity across newly converted areas (orange line). (C)–(H) Global rates of land conversion through time.

Our estimate of the distribution of a species' habitat, under a given land use scenario, is an upper estimate for the actual distribution of the species. Habitats may be unsuitable as the result of human influence other than LUC, including pollution, suppression by introduced species, or hunting. Moreover, species can be absent even in potentially suitable areas: in the case of heavily fragmented habitats, genetic diversity within spatially isolated patches can be insufficient to maintain local population sizes. Species confined to small ranges are also disproportionally threatened by extinction from local stochastic events. In addition, the displacement of certain species due to LUC or other factors can trigger a local cascade extinction of others. Whilst we have not considered these effects in our analysis due to lack of suitable global data, they highlight that protecting and restoring habitat areas is equally important as it is to ensure that they are ecologically sustainable, in order to prevent runaway biodiversity loss.

Although the impacts of climate change on global biodiversity are projected to rank second to those of LUC until the end of this century [4], changes in temperature and precipitation patterns are likely to exacerbate range contractions [12] and trigger large-scale extinctions [26,27]. Our analysis does not account for climatic effects that do not manifest in biome changes. In principle, species distribution models can simulate the response of species ranges to changing climatic conditions; however, uncertainties can be substantial [28,29], and climate envelopes rarely fully capture the information presented in the empirical range data, which challenges the robustness of such an approach for the 16850 species considered here.

Our analysis demonstrates that future impacts of global LUC on species ranges are strongly dependent on the land use scenarios represented in the relevant RCP. Whilst the number of species affected by range contractions of more than 50% could more than double by the end of the century under a business-as-usual trajectory (RCP 8.5), the most optimistic scenario (RCP 4.5) suggests that current biodiversity impacts could in principle be reverted to pre-1950 conditions. In particular, our results confirm the effectiveness of preserving primary forest, closing agricultural yield gaps, encouraging dietary shifts, and stabilising population growth, assumed to different degrees in RCPs 4.5 and 6.0 [7,8]. Conversely, our analyses quantify the negative consequences for global biodiversity of further shifting agricultural production from developed to developing countries, large-scale increases in biofuel plantations, represented in RCPs 2.6 and 8.5. It is not yet too late to alleviate the pressures of global land use on terrestrial biodiversity. However, timely action to curtail the land area required for food production [5], steer production to agro-ecologically optimal areas when additional expansion is inevitable [6], and target land abandonment [23] and restoration in hotspots [7,8]. is crucial if we are to avert ever more contracting species ranges and increasing extinction risks in this century.

Methods

Land cover data

We used the Hyde 3.2 reconstructions of global cropland, pasture and urban areas for the past 12,000 years [13]. A total of 72 maps are available at 1000 year time steps between 10,000 BCE and 0 CE, at 100 year time steps between 0 CE and 1700 CE, at 10 year time steps between 1700 CE and 2000 CE and at 1 year time steps between 2000 CE and 2016 CE.

Projections of global land use between 2020 and 2100 for four Representative Concentration Pathway scenarios 2.6, 4.5, 6.0 and 8.5 – corresponding to the radiative forcing (in Wm^{-2}) reached by the year 2100 – are based on simulations of the IMAGE model, the MiniCAM model, the AIM model and the MESSAGE model, respectively [30,31]. Each of these four Integrated Assessment Models uses historical reconstructions of land cover up until 2005, and is based on a specific set of assumptions on land use, population, energy and climate (see ref. [30], Table 1 of ref. [32], and Extended Data Fig. 1 and Extended Data Fig. 5 in this paper).

We used a recent dataset of reconstructions of global biomes for the last 12,000 years at 1,000 year time steps [33] that were generated by using downscaled and bias-corrected climate data based on simulations of the HadCM3 and HadAM3H General Circulation Models [35] as inputs

for the Biome4 vegetation model [34]. We assumed that the global distribution of potential biomes would not change between now and 2100. While a continuation of current climatic trends will likely induce changes in the global distribution of biomes in the long-term (e.g. in the Amazon rainforest, the Boreal forest and the tundra [36]), it is unclear whether these changes will manifest until 2100, given that the local transition from one vegetation equilibrium to another can take up to centuries.

Species distribution data

We considered a bird, mammal or amphibian species to be present in a cell of a 5 arc-minute grid for potential natural land cover at a certain point in time if the species' spatial Extent of Occurrence [37,38] overlays the grid cell, and if its habitat preferences [37,38] include the local natural biome type present at the relevant time. This involves matching the available IUCN habitat categories with the vegetation types outputted by Biome4, which was done as shown in Extended Data Table 1. This approach is similar to the one in ref [21]. Analogously, a species was considered present in the portion of a grid cell that is cropland, pasture or urban area if the species' habitat preferences include the relevant one of these three categories. For any global distribution of cropland, pasture, urban areas and natural biomes at a given point in time, this approach allows us to estimate the portions of grid cells in which a certain species is present. By aggregating the areas of these portions, we determined each species' total range at the appropriate point in time. We defined the primary mega-biome of each species (used in Fig. 2) as the mega-biome (Extended Data Table 1) that accounts for the largest area of the species' present-day potential natural range.

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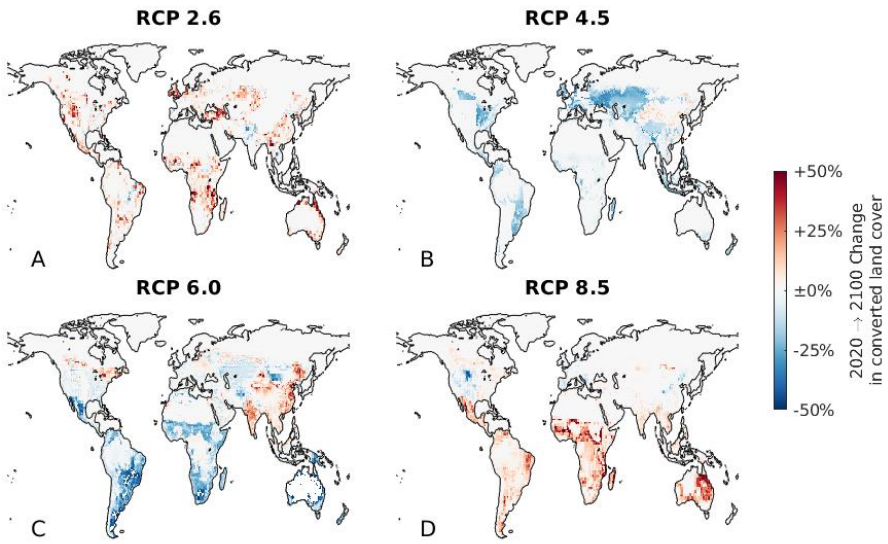
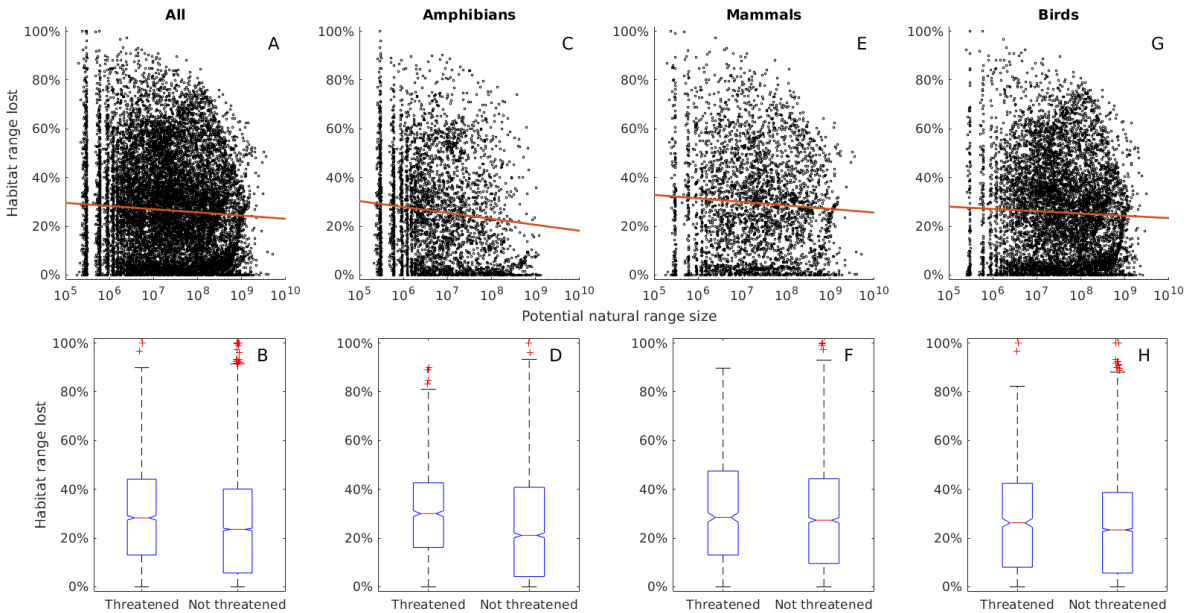
Data and materials availability: Data and code used in the analyses will be made available on the Open Science Framework repository upon acceptance of the manuscript.

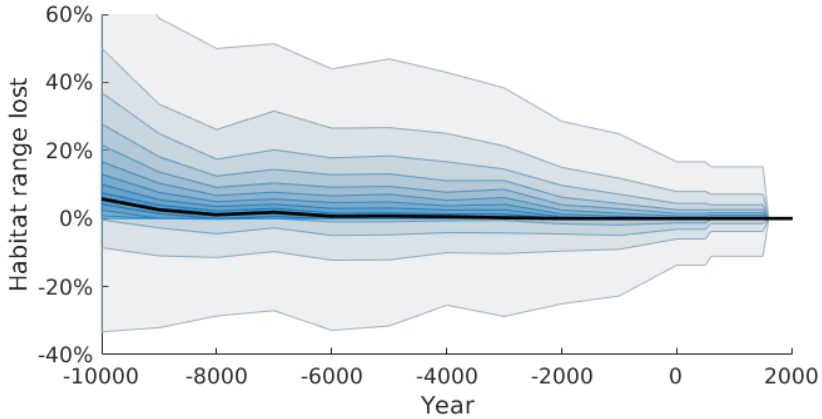
Extended Data



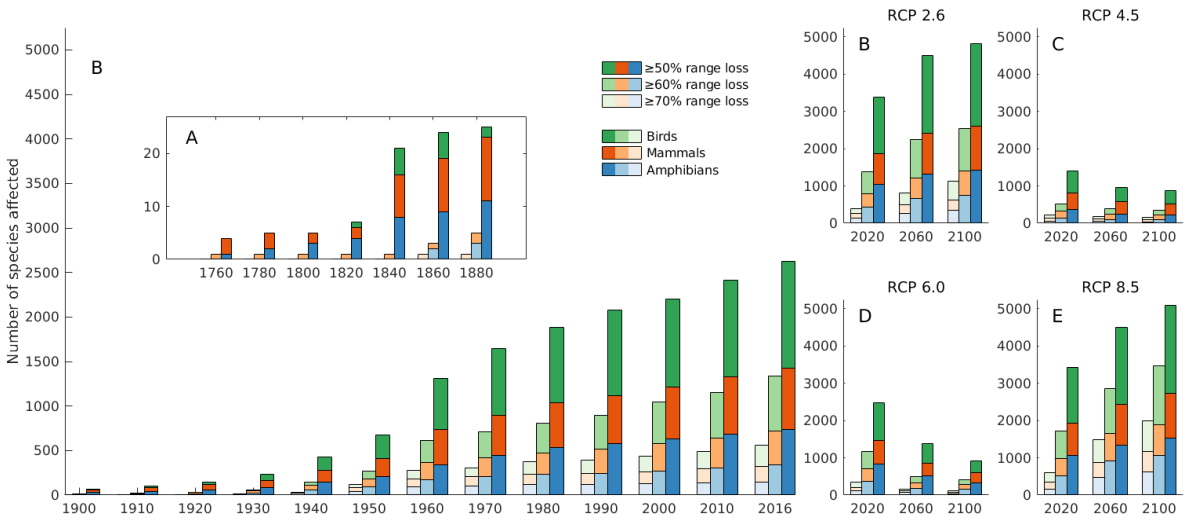
Extended Data Fig. 1. Rates of land conversion between 2020 – 2100 in the four RCP scenarios.



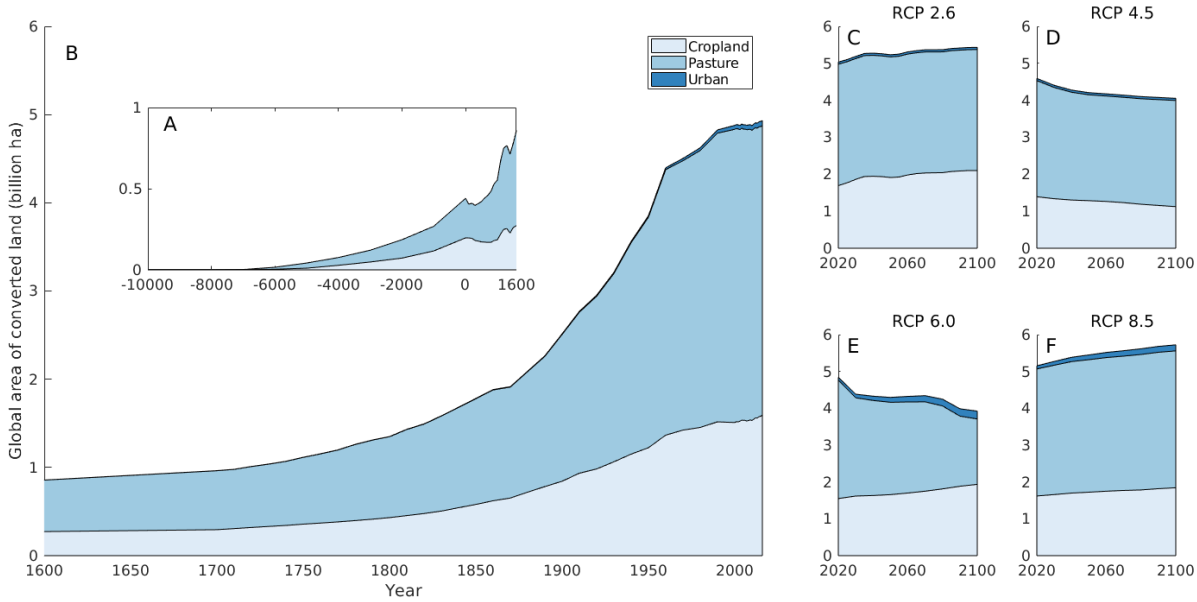
Extended Data Fig. 2. (A),(C),(E),(G) Range loss in 2016 against potential natural range size. The log-linear relationships (red lines) do not explain much variation of the data but they are significant ($R^2 < 0.1$ and $p < 0.01$ in all four panels). (B),(D),(F),(H) Habitat range loss for threatened and non-threatened species. Threatened species include those classified as vulnerable, endangered and critically endangered [37,38]. Mean range loss for threatened species was significantly higher ($p < 0.01$ in all four panels) than for non-threatened species.



Extended Data Fig. 3. Species range dynamics only based on biome changes through time (i.e. in the hypothetical absence of anthropogenic LUC). Colour shades and the black line represent 5-95% percentiles and the median, respectively. Changes are calculated with respect to present-day ranges.



Extended Data Fig. 4. Taxon-specific critical range losses.



Extended Data Fig. 5. Extent of global agricultural and urban area over time.

Biome4 categories	**Equivalent IUCN species habitat categories**	**Mega-biome**
Desert, Barren	Desert	Desert
Cold mixed forest Evergreen taiga Deciduous taiga	Boreal forest Subarctic forest Subantarctic forest	Boreal forest
Tropical evergreen forest Tropical semi-deciduous forest Tropical deciduous forest	Subtropical forest Tropical forest	Tropical forest
Temperate deciduous forest Temperate conifer forest Warm mixed forest Cool mixed forest Cool conifer forest	Temperate forest	Temperate forest
Boreal parkland Steppe tundra Dwarf shrub tundra Prostate shrub tundra Cushion forb lichen moss tundra	Subarctic grassland Subantarctic grassland Tundra	Tundra
Tropical grassland	Subtropical grassland Tropical grassland	Grassland and dry shrubland
Temperate grassland	Temperate grassland	Grassland and dry shrubland
Tropical savanna Temperate broadleaved savanna	Savanna	Dry woodland and savanna
Shrub tundra Drawf shrub tundra Prostate shrub tundra Cushion forb lichen moss tundra	Boreal shrubland Subarctic shrubland Subantarctic shrubland	Tundra
Temperate sclerophyll woodland Open conifer woodland	Mediterranean-type shrubby vegetation	Dry woodland and savanna

Tropical shrubland	Tropical shrubland	Grassland and dry shrubland
Temperate sclerophyll shrubland	Temperate shrubland	Grassland and dry shrubland
Land use maps categories		
Cropland	Arable Land	
Pasture	Pastureland	
Urban	Urban areas	

Extended Data Table 1. Matching between land cover types in the global land use and Biome4 data, and IUCN categories of species habitats. A species is considered present in the portion of a grid cell (contained in its geographical Extent of Occurrence) with the land cover specified in the first column, if its habitat preferences include any of the appropriate categories in the second column.

References

1. Gaston, K. J. & Fuller, R. A. The sizes of species' geographic ranges. *J. Appl. Ecol.* **46**, 1–9 (2009).
2. Staude, I. R., Navarro, L. M. & Pereira, H. M. Range size predicts the risk of local extinction from habitat loss. *Glob. Ecol. Biogeogr.* **0**,
3. Foley, J. A. *et al.* Global Consequences of Land Use. *Science* **309**, 570–574 (2005).
4. Sala, O. E. *et al.* Global Biodiversity Scenarios for the Year 2100. *Science* **287**, 1770–1774 (2000).
5. Springmann, M. *et al.* Options for keeping the food system within environmental limits. *Nature* **562**, 519 (2018).
6. Chaplin-Kramer, R. *et al.* Spatial patterns of agricultural expansion determine impacts on biodiversity and carbon storage. *Proc. Natl. Acad. Sci.* **112**, 7402–7407 (2015).
7. Chazdon, R. L. Beyond Deforestation: Restoring Forests and Ecosystem Services on Degraded Lands. *Science* **320**, 1458–1460 (2008).
8. Lamb, D., Erskine, P. D. & Parrotta, J. A. Restoration of Degraded Tropical Forest Landscapes. *Science* **310**, 1628–1632 (2005).

9. Johnson, C. N. *et al.* Biodiversity losses and conservation responses in the Anthropocene. *Science* **356**, 270–275 (2017).
10. Butchart, S. H. M. *et al.* Global Biodiversity: Indicators of Recent Declines. *Science* **328**, 1164–1168 (2010).
11. Dirzo, R. *et al.* Defaunation in the Anthropocene. *Science* **345**, 401–406 (2014).
12. Pimm, S. L. *et al.* The biodiversity of species and their rates of extinction, distribution, and protection. *Science* **344**, 1246752 (2014).
13. Klein Goldewijk, K., Beusen, A., Doelman, J. & Stehfest, E. Anthropogenic land use estimates for the Holocene – HYDE 3.2. *Earth Syst. Sci. Data* **9**, 927–953 (2017).
14. Ripple, W. J. *et al.* Collapse of the world's largest herbivores. *Sci. Adv.* **1**, e1400103 (2015).
15. Ceballos, G. & Ehrlich, P. R. Mammal Population Losses and the Extinction Crisis. *Science* **296**, 904–907 (2002).
16. Hooper, D. U. *et al.* A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature* **486**, 105–108 (2012).
17. Tilman, D. *et al.* Forecasting Agriculturally Driven Global Environmental Change. *Science* **292**, 281–284 (2001).
18. International Union for the Conservation of Nature. (2014).
19. Pereira, H. M. *et al.* Scenarios for Global Biodiversity in the 21st Century. *Science* **330**, 1496–1501 (2010).
20. Loh Jonathan *et al.* The Living Planet Index: using species population time series to track trends in biodiversity. *Philos. Trans. R. Soc. B Biol. Sci.* **360**, 289–295 (2005).
21. Jetz, W., Wilcove, D. S. & Dobson, A. P. Projected Impacts of Climate and Land-Use Change on the Global Diversity of Birds. *PLOS Biol.* **5**, e157 (2007).

22. Brooks, T. M. *et al.* Habitat Loss and Extinction in the Hotspots of Biodiversity. *Conserv. Biol.* **16**, 909–923 (2002).

23. Beyer, R. M., Manica, A. & Rademacher, T. T. Relocating agriculture could drastically reduce humanity's ecological footprint. *bioRxiv* 488841 (2019). doi:10.1101/488841

24. Phalan, B. *et al.* How can higher-yield farming help to spare nature? *Science* **351**, 450–451 (2016).

25. Myers, N., Mittermeier, R. A., Mittermeier, C. G., Fonseca, G. A. B. da & Kent, J. Biodiversity hotspots for conservation priorities. *Nature* **403**, 853 (2000).

26. Jantz, S. M. *et al.* Future habitat loss and extinctions driven by land-use change in biodiversity hotspots under four scenarios of climate-change mitigation. *Conserv. Biol.* **29**, 1122–1131 (2015).

27. Thomas, C. D. *et al.* Extinction risk from climate change. *Nature* **427**, 145 (2004).

28. Pearson, R. G. *et al.* Model-based uncertainty in species range prediction. *J. Biogeogr.* **33**, 1704–1711 (2006).

29. Heikkinen, R. K. *et al.* Methods and uncertainties in bioclimatic envelope modelling under climate change. *Prog. Phys. Geogr. Earth Environ.* **30**, 751–777 (2006).

30. Hurtt, G. C. *et al.* Harmonization of land-use scenarios for the period 1500–2100: 600 years of global gridded annual land-use transitions, wood harvest, and resulting secondary lands. *Clim. Change* **109**, 117 (2011).

31. Chini, L. P., Hurtt, G. C. & Frolking, S. Harmonized Global Land Use for Years 1500 – 2100, V1. Data set. Available on-line from Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, Tennessee, USA. (2014).

32. Newbold, T. *et al.* Global effects of land use on local terrestrial biodiversity. *Nature* **520**, 45–50 (2015).

33. Beyer, R., Krapp, M. & Manica, A. High-resolution terrestrial climate, bioclimate and vegetation for the last 120,000 years. *EarthArXiv* (2019). doi:10.31223/osf.io/qvpnx
34. Kaplan, J. O. *et al.* Climate change and Arctic ecosystems: 2. Modeling, paleodata-model comparisons, and future projections. *J. Geophys. Res. Atmospheres* **108**, 8171 (2003).
35. Valdes, P. J. *et al.* The BRIDGE HadCM3 family of climate models: HadCM3@Bristol v1.0. *Geosci. Model Dev.* **10**, 3715–3743 (2017).
36. Lenton, T. M. *et al.* Tipping elements in the Earth's climate system. *Proc. Natl. Acad. Sci. U. S. A.* **105**, 1786–1793 (2008).
37. BirdLife International. Bird species distribtution maps of the world. (2018).
38. NatureServe & International Union for the Conservation of Nature. The IUCN Red List of Threatened Species. (2016).