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Global habitat loss and extinction risk of terrestrial vertebrates under future land-use-change scenarios

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Habitat transformations caused by human land-use change are considered major drivers of ongoing biodiversity loss[1–3], and their impact on biodiversity is expected to increase further this century[4–6]. Here, we used global decadal land-use projections to year 2070 for a range of shared socioeconomic pathways, which are linked to particular representative concentration pathways, to evaluate potential losses in range-wide suitable habitat and extinction risks for approximately 19,400 species of amphibians, birds and mammals. Substantial declines in suitable habitat are identified for species worldwide, with approximately 1,700 species expected to become imperilled due to land-use change alone. National stewardship for species highlights certain South American, Southeast Asian and African countries that are in particular need of proactive conservation planning. These geographically explicit projections and model workflows embedded in the Map of Life infrastructure are provided to facilitate the scrutiny, improvements and future updates needed for an ongoing and readily updated assessment of changing biodiversity. These forward-looking assessments and informatics tools are intended to support national conservation action and policies for addressing climate change and land-use change impacts on biodiversity.

Human encroachment on habitats is a major cause of biodiversity change[1–3], and determining the specifics of these impacts is a key priority for biodiversity science and conservation. Recent work using climate and land-use change scenarios to project biodiversity trends has signalled steep declines, particularly under business-as-usual conditions[6,7]. For instance, under such a scenario, 440 mammalian carnivores and ungulate species were predicted to decline in abundance by 18–35% and increase in extinction risk by 8–23% by 2050[6], and 27 European large mammal species were predicted to lose 25% of their habitat by 2050[7]. Recent projections of worldwide deforestation suggest a potentially substantial increase in the extinction risk of forest-associated vertebrate species[8]. Identifying species and locations most exposed to changing habitats is key for prioritizing the reduction and management of biodiversity threats. However, they have usually remained taxonomically or geographically restricted, with a focus on large-bodied or temperate species. With declared international policy goals to prevent extinctions and global assessment processes of the Intergovernmental Platform for Biodiversity and Ecosystem Services (IPBES) underway, there is a need for a more comprehensive evaluation, ideally accompanied by infrastructure and workflows that enable ongoing updates as scenarios and data change.

Here we build on recent harmonized projections of anticipated changes in land-use to assess how the expected decrease of suitable habitat reduces geographic ranges and affects the extinction risk of terrestrial birds ($N=9{,}290$), mammals ($N=4{,}594$) and amphibians ($N=5{,}482$) worldwide. We first established a refined baseline estimate of geographical distributions and minimized the range size overestimates for the available expert-drawn range characterizations[9,10]. Building on earlier work[4], but with much extended data, we specifically related expert information on species habitat suitability and elevations to 1 km resolution remote sensing-based layers of fractional tree cover, minimum and maximum elevation[11], and also fractional land cover for 2015 at 0.25° resolution (derived from projected land-use states) to estimate the habitat-suitable range (HSR) in 2015. We then linked the same species habitat suitability information to future land-cover projections to estimate decadal changes in HSR from 2015 to 2070. We assumed that once pixels had transformed to being unsuitable they remained unsuitable in the future (no-regain assumption) or could secondarily be repopulated (regain assumption). The land-use projections informing land cover and suitable habitat are based on the newly released Land Use Harmonization dataset v2 (http://luh.umd.edu/)[12–14]. To determine how the implications for biodiversity may vary among different scenarios, we evaluated projections under four different shared socioeconomic pathways (SSPs)[14–16]. These connect to a specific representative concentration pathway (RCP), as provided by the associated integrated assessment models, specifically SSP1 (RCP2.6, IMAGE), SSP3 (RCP7.0, AIM), SSP5 (RCP8.5, MAGPIE) and SSP2 (RCP4.5, MESSAGE). Finally, we related the absolute levels and rates of change in HSR to the International Union for Conservation of Nature (IUCN) Red List Criteria[17] to characterize potential future trends in species threat status and to identify the regions of greatest, aggregate concern.

Figure 1 shows the approach and projected changes for four species (and the no-regain assumption) under SSP2, which represents a middle-of-the-road scenario of intermediate land-use change. Overall, we found large projected losses in HSR ranging from −6.2 to −10.7% per decade (Fig. 1; Supplementary Table 1). For example, the Lombok cross frog (*Oreophryne monticola*; https://mol.org/en/species/projection/landuse/Oreophryne_monticola), restricted to the islands of Bali and Lombok, is projected to lose over half its 2015 HSR by 2070, with only 190 km² of its estimated initial 403 km² HSR remaining. If standardized criteria that relate absolute amounts and rates of change in HSR to a putative Red List threat status (Supplementary Table 2) were applied, the species would be up-listed to Critically Endangered (CR) in 2070 – it currently has a Red List status of Endangered (EN) and is projected to lose more than 50%

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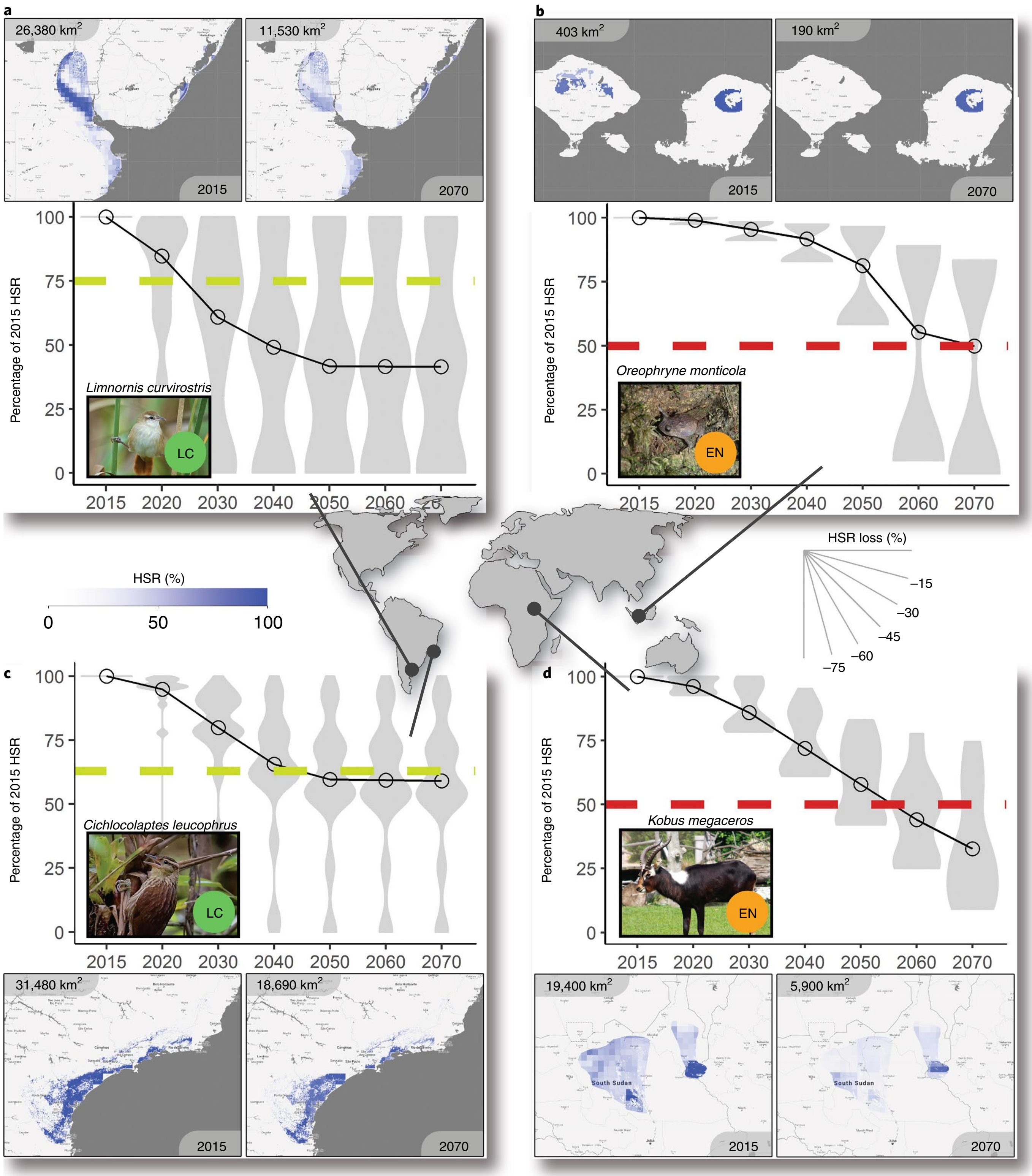

Fig. 1 | Projected land-use change effects on habitat-suitable range (HSR) of example species under projected harmonized land-use change. a–d, Map shows HSR per 1 km-refined 0.25° grid cell for the 2015 baseline and the projected 2070 time period under SSP2 (RCP4.5), assuming no-regain of habitats. Temporal plots show median (point) and variance (violins) of projected HSR as a percentage of 2015 HSR. Coloured dashed lines indicate area thresholds for potential up-listing under steep HSR loss, for example 20,000 km² and steep decline (10% of 2015 HSR) for up-listing from LC (green) to NT (red). IUCN Red List threat categories range from LC and NT to VU (Vulnerable), EN and CR. To view the projected HSR loss trends for analysed species, see, https://mol.org/en/species/projection/landuse Credits: Cláudio Dias Timm (*Limnornis curvirostris*, *Trepador-sobrancelha*), Sean Reilly (*Oreophryne monticola*), Karel Jakubec (*Kobus megaceros*), Google, ORION-ME (base maps).

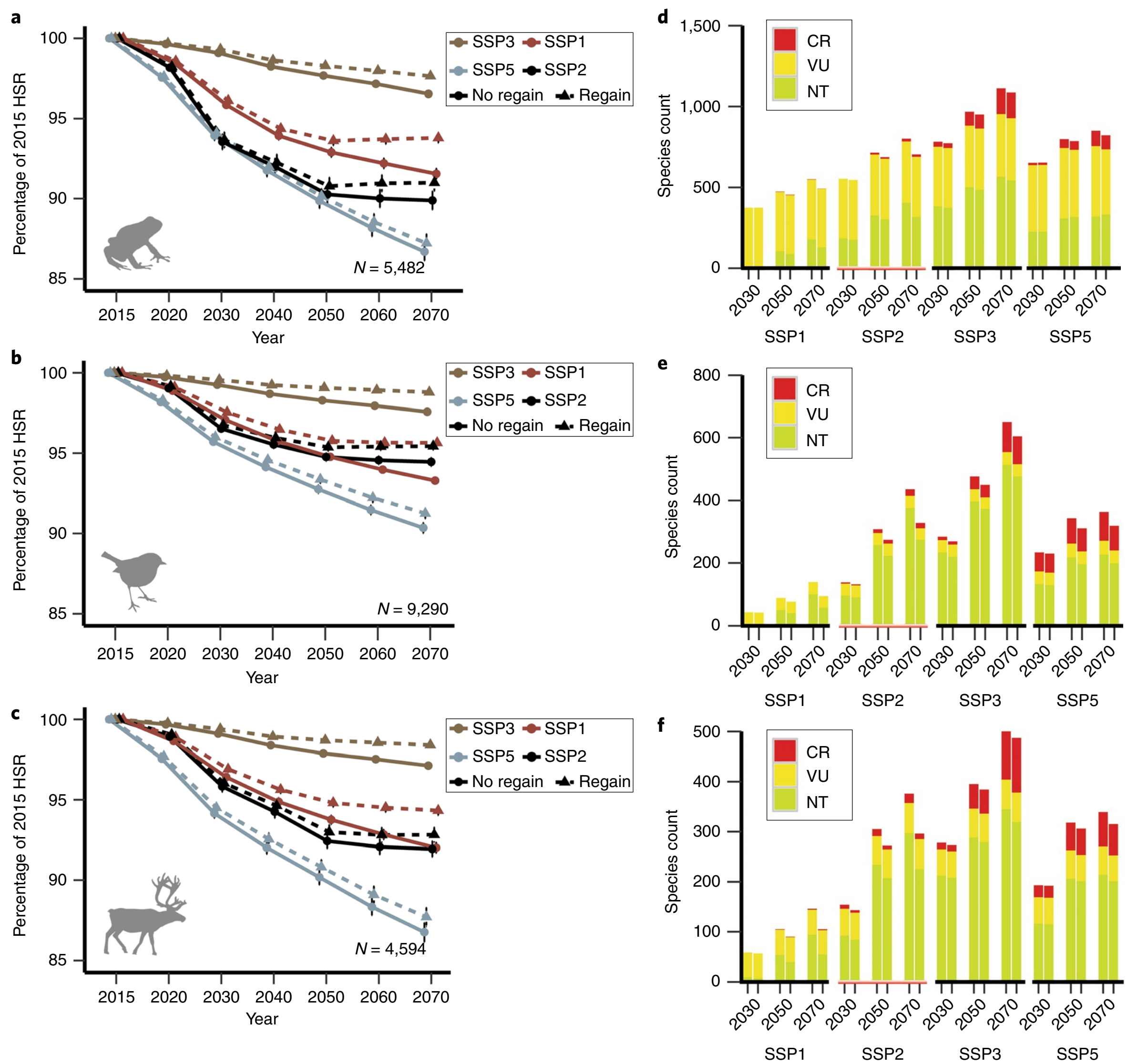

Fig. 2 | Projected trends in HSR and threat status up-listing based on harmonized land-use change projected under four different SSPs. a–c, The average (+/− 95% CI) projected HSR per SSP as a percentage of 2015. **d–f**, Counts of potentially up-listed species. The three paired bars in each SSP denote counts of elevated threat status for the 2015–2030, 2015–2050 and 2015–2070 epochs, respectively, and each pair addresses no regain (left bar) and regain assumption (right bar). We highlight SSP2, which is also used in Figs. 1, 3 and 4. In SSP2 we consider species currently designated as LC or DD with projected HSR of <20,000 km^2 and >10% loss of 2015 HSR as becoming NT, and species with projected HSR of <20 km^2 as VU. Species currently listed as VU or EN with projected >50% loss of 2015 HSR receive a future designation of CR. For other details, see Fig. 1.

of its original 2015 HSR by 2070 (Supplementary Table 1). The Nile lechwe (*Kobus megaceros*; URL) is expected to be up-listed to CR by 2060. The Pale-browed treehunter (*Cichlocolaptes leucophrus*; URL) and the Curve-billed reedhaunter (*Limnornis curvirostris*; URL) would be up-listed to Near Threatened (NT) by 2050 and 2030, respectively, under Red List Criterion B1 because they are projected to have a restricted range (HSR <20,000 km^2) and will undergo a range decline (>10% projected loss of 2015 HSR). Extending this evaluation to all 19,366 species, we observe frequent decreases in HSR, and many species are expected to have an elevated extinction risk (Fig. 2). For SSP2 and the no-regain assumption, expected HSR contraction/loss during the 2015–2070 period range from −8.4% for amphibians (95% confidence intervals (CI): −8.1% to −8.7%) to −6.7% for birds (95% CI: −6.5% to −6.9%) and −5.5% for mammals (95% CI: −5.2% to −5.8%). The number of species projected to be up-listed under SSP2 and the no-regain assumption is highest for amphibians (886 species), but also includes 436 birds and 376 mammals. Many of them are currently listed as Least Concern (LC) or Data Deficient (DD). These results confirm previous assertions about the particular threats faced by amphibians[18,19], with substantial habitat shrinkage projected to affect often already very small ranges (HSR <20 km^2). These habitat losses add to the reliance of amphibians on microhabitats, hydrological regimes and their limited dispersal abilities, which exacerbate their susceptibility to anticipated climate and land-use change[20].

Extending this evaluation to the three other SSPs illustrates the sensitivity of these outcomes to the specific future societal pathways and socioeconomic scenarios. Under SSP3 in particular, which foresees highly separate societies with substantial challenges to climate change mitigation and adaptation[14,15], dramatically higher losses in suitable habitat are projected and greater up-listing especially of already threatened species is expected. Despite being associated with a higher RCP, the fossil-fuelled but more collaboratively developed

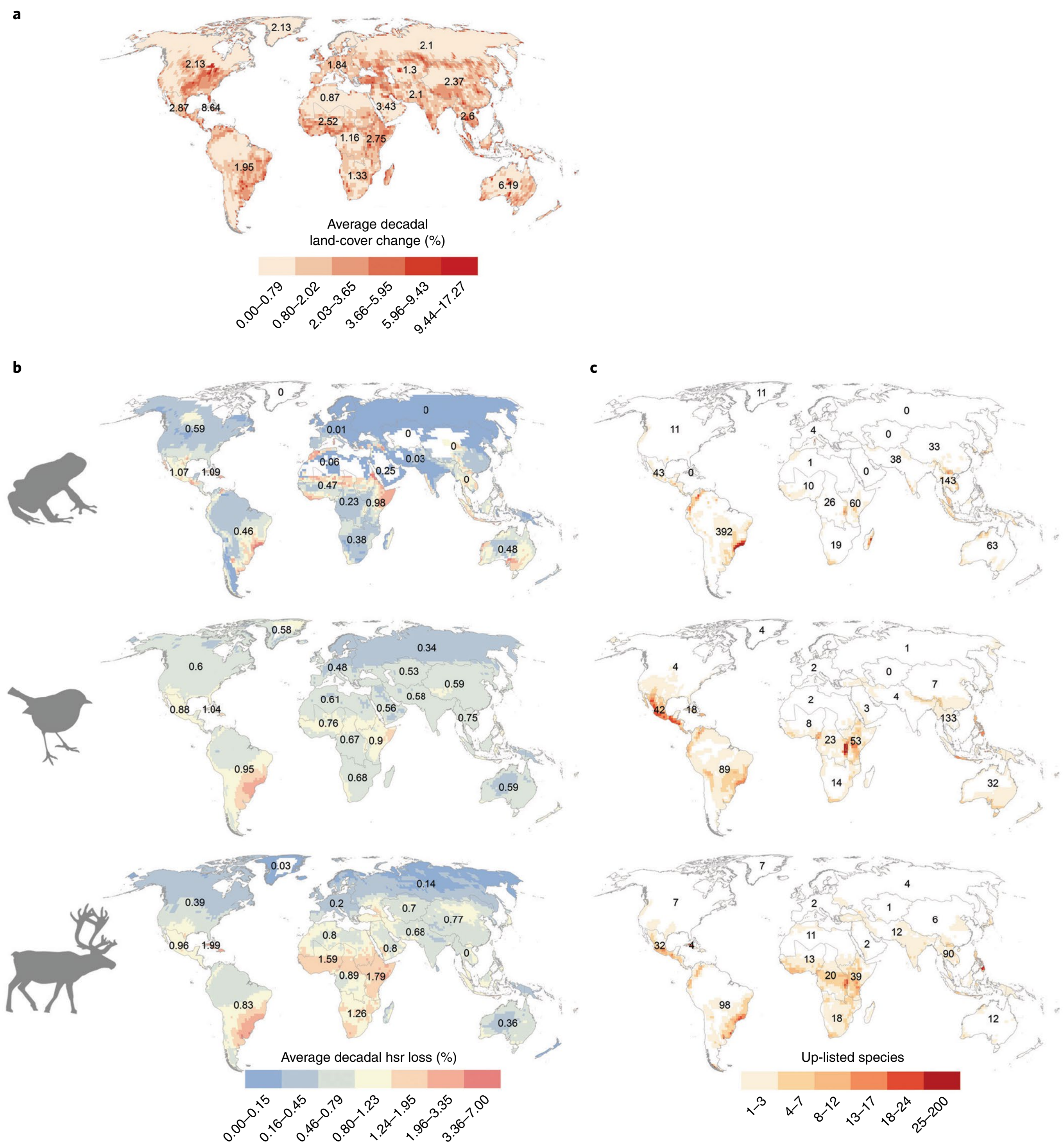

Fig. 3 | Spatial patterns for 2015–2070. a–c, Spatial patterns of projected land-use-driven land-cover changes 2015–2070 (**a**), projected losses in average HSR (**b**) and counts of potentially up-listed species (**c**). Maps are for the middle-of-the-road SSP2, assuming no habitat regain. Colours indicate values for grid cells of ~150 km size and the species they harbour. Numbers on map are IPBES subregion summaries.

world of SSP5 has slightly weaker losses in HSR, but again greater threats to already highly threatened species than the middle-of-the-road SSP2. As expected, SSP1, which represents a planet focused on sustainability, leads to the least but still noticeable HSR loss and also to an up-listing with the least impact on already threatened species. The overall differences among taxa are robust in specific SSP scenarios. Both HSR loss and the number of up-listed species are lower under the regain assumption, with an average increase of 1.25% for amphibians, 1.29% for birds and 2.15% for mammals (Fig. 2a,c,e), and between 2% and 32% fewer species seeing up-listing across SSPs (Fig. 2b,d,f; Supplementary Fig. 1).

The large variation in expected imperilment arises from geographically highly heterogeneous projected land-cover changes. Pressures on existing habitats are expected to be particularly severe

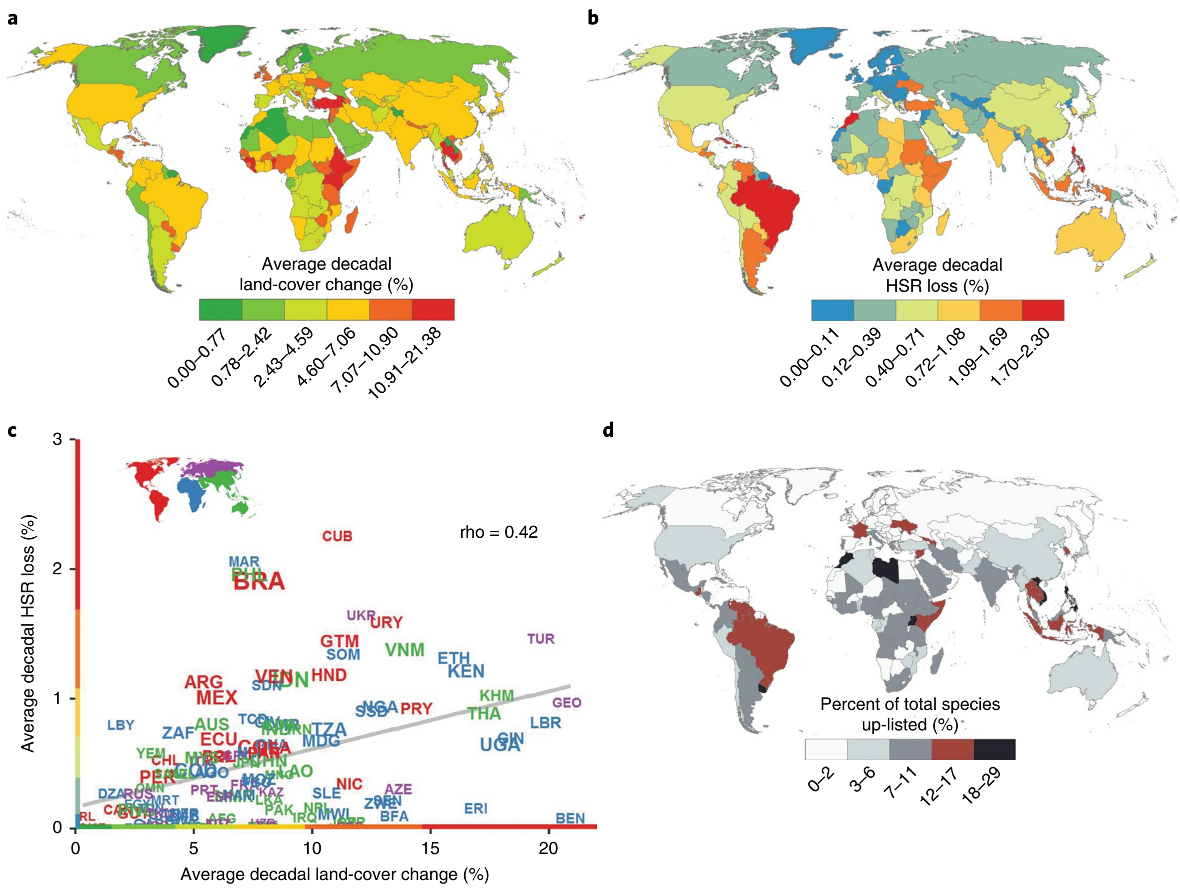

Fig. 4 | Country-level patterns for 2015–2070. a–d, Country-level patterns for 2015–2070 for projected land-use change (**a**), its estimated effect on stewardship-weighted species HSR loss (**b**,**c**) and the resulting up-listing (**d**). **b**, Country-level decadal HSR loss as a stewardship-weighted average. The weights are based on the portion of species' 2015 HSR in a given country, where species with a large stewardship drive the average HSR trend more strongly than species with a small HSR. This country-level metric represents a projection of the Map of Life Species Habitat Index (https://mol.org/indicators). **c**, Country-level average decadal HSR loss (as in **b**) in relation to country-level average decadal land-cover change (rho = 0.42, $P < 0.001$; text denotes country ISO codes, see Supplementary Table 6 for details). Axis colours relate to (**a**) and (**b**), font colour relates to inset map and font size is proportional to the count of species projected to be up-listed by 2070. **d**, Stewardship-weighted total of all contained up-listed species was divided by the stewardship-weighted average of all contained species. Patterns are shown for SSP2 and countries <50,000 km^2 in size are excluded.

in much of South America, Southeast Asia, Central and East Africa and Mesoamerica. This geography of land-cover change interacts with the current patterns of species threat, rarity and habitat specialization to result in distinct spatial patterns of projected threat. Under SSP2 with no-regain, species in East Africa, Southeast Asia and Mesoamerica are expected to experience particularly high average HSR loss and imperilment (Fig. 3a–c). Southeast Asia is a projected hotbed for range loss and up-listing, with an average HSR decadal loss of over 0.75% for birds and mammals; a total of 133 birds and 90 mammal species will probably deteriorate in threat status across the continent. For amphibians, the greatest number of up-listed species (392 in total) is expected for South America where the diversity of often already narrow-ranged species is projected to experience a small decadal HSR loss of 0.46%.

These projected increases in species threat status set up new challenges for nations to safeguard their biodiversity and meet broadly agreed policy targets. We assess this issue by quantifying the HSR loss and per-species increase in threat status across countries larger than 50,000 km^2, with contributions to these national averages weighted by countries' stewardship of a species, that is the portion of their global HSR inside national boundaries. Turkey, Georgia and Liberia are projected to have greatest land-cover change (Fig. 4a), and patterns of HSR loss and up-listing are accordingly expected to be among the highest. But stewardship-weighted HSR loss is as high for some Southeast Asian and African countries, such as Thailand, Cambodia, Ethiopia and Kenya. Across all countries and species the relationship between average decadal land-cover change and stewardship-weighted HSR loss is accordingly moderate, but not exceedingly so (rho = 0.42, $P < 0.001$; Fig. 4a,b,c). This highlights the importance of additional factors such as species geographic rarity and national stewardship when modifying the link between land-cover change and HSR. The association extends even further to country differences in the number of species expected to see up-listing, where a strong positive relationship exists between HSR loss and the number of up-listed species (rho = 0.73, $P < 0.001$). Globally, 847 species under the regain assumption (and 1,113 species under the no-regain assumption) are expected to become newly considered threatened by 2070 (and 560 become up-listed), with 578 from South America, 366 from Southeast Asia and 152 from East Africa.

We provide online infrastructure to examine projected HSR loss trends for all terrestrial vertebrates analysed (for example, https://mol.org/en/species/projection/landuse/Cichlocolaptes_leucophrus). This allows a direct examination of single species patterns and assumptions about current distribution and provides a transparent underpinning of the aggregate patterns shown in the study. This embedment in infrastructure also facilitates future extensions and re-assessment, including alternative or updated scenarios for future land-cover changes[21–23] or a projection of climate change-induced species range changes that may exacerbate or, through range expansion, buffer against losses of currently occupied range portions[13,24,25]. Future work should explore how land-use projections downscaled to finer spatial grains may modify species-specific findings, and also recognize that higher resolutions imply greater uncertainty in both occurrence and projection information, which requires an appropriate statistical framework. Although the new harmonized land-use information available for this work provides a much improved set of land-use states and transitions[12,13], future assessments will certainly benefit from more ecologically refined categories that better represent the range of species habitat types. Here, further insights may also be gained from alternative approaches that use different assumptions regarding habitat use and availability[26] or account for potentially latency effects and extinction debt[27]. One of the key benefits of the initial approach taken here is that it is simple, transparent and sidesteps many of the conceptual and methodological issues typically associated with more complex approaches[4]. However, like most global assessments, several important assumptions were inevitably made and other threats not accounted for. Specifically, we assumed that species' dispersal ability was limited and we did not investigate biotic interactions and adaptive potential. Threats that may further imperil species, such as exposure to hunting, invasive species and pollution, were not addressed[28–31]. Consequently, our results, although based on a range of SSPs, may potentially underestimate extinction risk, and all assumptions and contingencies underlying SSPs and harmonized land-use projections also apply to our results. Nonetheless, our results reveal important spatial and categorical insight into potential HSR loss and extinction risk trends. Evaluating different model parameters (that is, secondary habitat) for many species and taxonomic groups therefore provided otherwise unavailable insights and are key to understanding biodiversity reaction to global change.

Our findings have considerable implications for the spatial prioritization of future conservation efforts. The methodology described here demonstrates how readily available scenarios on projected land-use driven land-cover change can be used, with relatively straightforward models, to anticipate pressures on biodiversity. By highlighting species and regions most affected, our approach can assist in guiding the build-up of further knowledge and capacity to address the potential needs for global conservation. The proper treatment of land-use conversion impacts has become essential for the future prioritization of biodiversity conservation and resource management. To this end, geographically explicit, transparent, repeatable and updateable projections of affected areas and species are key, and have the potential to guide policy and improve the long-term effectiveness of conservation efforts.

Online content

Any methods, additional references, Nature Research reporting summaries, source data, statements of data availability and associated accession codes are available at https://doi.org/10.1038/s41558-019-0406-z.

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Author contributions

W.J. and R.P.P. conceived the study. R.P.P. performed the analysis. W.J. analysed the results. W.J. and R.P.P. wrote the manuscript.

Additional information

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Methods

Species and environmental data. Our analyses included 19,366 species of terrestrial birds ($N=9{,}290$), mammals ($N=5{,}482$) and amphibians ($N=4{,}594$). We used expert range information with further refinements (see later) as a base. Bird expert range maps were based on Jetz et al.[32], with non-breeding portions included, and are available at https://mol.org. Amphibian and mammal expert range maps were obtained from IUCN[33] and are available at http://www.iucnredlist.org. We excluded non-terrestrial portions of species ranges.

We used remotely sensed data to characterize elevation and current tree cover. Elevation data was derived from the CGIAR-CSI Shuttle Radar Topography Mission (SRTM) and ASTER GDEM v2 data products[34]. SRTM provides consistent elevation data across the landscape at a 90-m spatial resolution, with a 5-m vertical resolution[34]. The fusion of ASTER GDEM v2 with SRTM data allows for greater continuous global coverage of ~91%. Details of the processing and fusion methodology are outlined in Robinson et al.[35]. To derive tree cover, we used the 2010 coverage of Hansen et al.'s Global Forest Change (GFC) dataset[36], which documents global tree cover gains and losses using time series of cloud-free Landsat ETM+ data in 30-m resolution[36]. We acknowledge that this product addresses tree cover and is unable to separate natural forest from forest plantations in regions such as Southeast Asia[37].

Both the forest cover and elevation environmental layers were resampled (averaged) to a spatial resolution of 0.0083° or ~1 km.

Projected land-cover and land-use change data. Future impacts of land-use change on the land system were explored across different SSPs developed in the context of CMIP6[14–16]. These pathways represent a range of plausible futures based on different socioeconomic challenges for climate change mitigation (low in SSP1 and SSP 4; high in SSP5 and SSP3; intermediate in SSP2), for example through technological solutions and development, and also challenges for adaptation (low in SSP1 and SSP5; high in SSP3 and SSP 4; intermediate in SSP2), for example through international collaboration. Each SSP connects to a specific RCP and associated integrated assessment model, which includes different socioeconomic and land-use modules for the translation of narratives into consistent quantitative projections across scenarios. Although mostly determined by the SSP storylines, scenarios are consistent with their paired RCPs, including their associated levels of biofuel deployment to mitigate climate change. Our list of evaluated SSPs (and associated RCP and integrated assessment model, respectively) includes SSP1 (RCP2.6, IMAGE), SSP3 (RCP7.0, AIM), SSP5 (RCP8.5, MAGPIE) and SSP2 (RCP4.5, MESSAGE). Land-use projections from each of the integrated assessment models were harmonized for CMIP6 by Hurtt et al.[12] using an updated version of the land-use harmonization (LUH2) methodology[12,38], which was developed and widely used to support future projections[39]. LUH2 projections are available as gridded future projections at http://luh.umd.edu. Compared to the earlier version, the LUH version[39] provides fractional cover at higher spatial resolution (0.25° compared to 0.50°) and a larger range of land-use states and transitions. The LUH2 land-use state units are fractions of different land uses per grid cell, with up to 12 land states: two primary lands and two secondary lands subdivided into forest and non-forest, managed pasture, rangeland, urban land and five crop states. Here we used the fractional LUH2 data for 2015–2070 to assess land-use change for the four selected scenarios. Land-use state classes were then thematically aggregated (reclassified) into five general land-cover classes corresponding to the International Geosphere Biosphere Programme (IGBP) classes for defining the HSR (see Supplementary Tables 3 and 4).

Habitat-suitable range. Range maps typically overestimate the area of occupancy[10,40], and hence refining or omitting areas within range maps that are known to be unsuitable reduces potential biases in estimating range loss[4,41]. Following Jetz et al.[4], but with expanded and higher resolution information, we first developed an estimate of HSR as the baseline for change analysis. Specifically, we derived the HSR for each species by refining (masking out or omitting from) its current expert range map pixels when, as a result of current or projected land cover, the 2010 forest cover or elevation were unsuitable given a species known habitat preferences. In step 1, we related textual habitat preference information from the literature[42] and IUCN Red List threat assessments[33] to the corresponding land-use category, elevation and tree cover. We identified pixels for which the minimum or maximum elevation value (rounded to the nearest 100 m) was outside the known elevation limits of a species, based on the data in ref. [43] and available at https://mol.org/downloads. We then isolated and cut pixels falling outside the defined minimum and maximum forest cover values (rounded to the nearest 5%). For example, species labelled by expert sources as forest-dependent require a minimum of 75% GFC-based[36] tree cover per 1-km pixel. Finally, we linked habitat preference information first to the IGBP classification scheme (17 types; Supplementary Table 4) and then to the land-use states in the Land Use Harmonization dataset v2[12,13]. For an overview of frequencies for land cover, elevation and forest cover associations by taxonomic group, see Supplementary Table 5 (for species data, see individual species pages at https://mol.org). This yielded the current estimated suitable habitat (HSR) in km^2. In step 2, the refined species distributions were individually assessed for projected losses in HSR due to projected land-cover changes, using the same land-cover associations as in step 1, but linked to decadal future land-cover projections. The projected species HSR (in km^2) per decadal time point was calculated by adding the area of pixels to the suitable habitat (that is, the fractional area of suitable land-cover type within the 1-km pixel). In the case of a forest-dependent species, for example, only the forested fractional area of those pixels within the refined range contributed towards the calculated HSR at the assessed decadal increments. As such, in this example a pixel within the refined range that contains 80% forest land-cover type will add 0.8 km^2 to the HSR calculation. For the projected HSR calculations we explored two assumptions: regain and no-regain (see later). We acknowledge that our current and projected HSR estimates are limited by the spatial resolution of the currently available species distribution information and the relatively coarse spatial grain of land-use information. The transparency of species-level spatial patterns provided through the Map of Life web interfaces allows us to understand these challenges. Future biodiversity research on this theme will certainly benefit from higher resolution and uncertainty-assessed species occurrence predictions and land-use information. All underlying data (species range maps, environmental layers and habitat preferences) and map calculations were stored and executed using Google Earth Engine[44] and are integrated in a repeatable workflow in Map of Life[45].

Regain and no-regain assumption. There is lack of consensus about the suitability of secondary vegetation for sustaining biodiversity, and species responses are expected to be highly variable[46–49]. To address this variation, we separated two scenarios to reflect different assumptions about how well species would be able to recolonize land cover that was converted to potentially suitable during the projection period. Under the regain assumptions, pixels (as fractions of land cover) that transition from unsuitable to suitable land cover during the projection time frame would contribute to the HSR (but not beyond 2015 levels). Under the no-regain assumption any pixel land-cover fraction that changed to unsuitable was considered lost until at least 2050, and HSR could only decrease with time.

Projected effects on extinction risk. We estimated Red List category extinction risk trends for both the regain and no-regain assumption for three periods (2015–2030, 2015–2050 and 2015–2070) and also for each species by evaluating projected HSR against IUCN Red List Criteria B1 (small HSR size) and D2 (few locations and/or very small HSR size), and by other range contraction criteria (>50% loss of 2015 HSR). IUCN Red List Criterion B1 requires that at least one of two subcriteria be met: extreme fluctuations and/or continuing decline. We only considered the continuing decline subcriterion for B1 because of the lack of quantitative data for the extreme fluctuations. Under Criterion B1, species currently designated as LC or DD that are projected to have a restricted (HSR <20,000 km^2) and strongly declining range (>10% loss 2015 HSR) were up-listed to a NT Red List status. Under Criterion D2, species projected to become spatially rare (HSR <20 km^2) were assigned a VU status. For species currently designated as VU or EN and projected to experience large range declines (>50% loss 2015 HSR) were up-listed to a future CR status. (For a discussion of using IUCN Red List Criteria in this context, see ref. [50]).

Aggregate patterns. We summarized land-cover change and also HSR loss and threat status count by latitude–longitude grid cells of ~150 km near the Equator. For this we developed species lists for each grid cell based on the non-refined expert range maps and we calculated the average projected HSR loss and potential number of species with elevated threat status.

To characterize land-cover change effects on biodiversity across countries of sufficient size (>50,000 km^2), we calculated stewardship-weighted averages of our focal metrics, based on the proportion of species' non-refined range within each country. For HSR this was done according to equation (1):

$$\bar{x}_{\text{country}} = \frac{\sum_{i=1}^{n} w_i x_i}{\sum_{i=1}^{n} w_i} \quad (1)$$

where x represents a species mean decadal HSR loss and w is the proportion of the species' range that overlaps the country boundaries. This metric represents the Species Habitat Index developed in Map of Life (https://mol.org/indicators). Using a similar approach, we also calculated the potential total number and proportion of species with elevated threat status for each country. We did this by first calculating the weighted total of the up-listed species and all species, which is effectively the total of w. The proportion of up-listed species was calculated by dividing the up-listed species weighted total by the weighted total of all species. Full country results are provided in Supplementary Table 6.

Data availability

The data supporting the findings of this study are available in the Supplementary information and at the Map of Life website (https://mol.org).

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