# Land-use change contributing almost half of future diversity change of global terrestrial vertebrates under climate change

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**Abstract**

Global biodiversity is lost at an unprecedented ratio driven by climate change and land-use change. However, little is known about the combined effects of climate and land-use change on future biodiversity on a global scale. Here, we first build the indices of land-use naturalness and the land-use intensity to depict the land-use change on a global scale. By using random forest models, we establish the empirical relationship to quantify this combined effect and further predict future changes of terrestrial vertebrates can be predicated under the Shared Socio-economic Pathways (SSPs). The relative contributions of climate change and land-use change to terrestrial vertebrates are finally separated through quantitative analysis. We find that future land-use change contributes to 48.52% of richness changes, slightly lower than that of climate change. Nearly 45.82% of the Earth's land will suffer richness losses of terrestrial vertebrates by 2050 even under the middle-high scenario of SSP3, mainly located at low latitudes, such as Southeast Asia, Latin America and sub-Saharan Africa. Moreover, the analysis at the country-specific level reveals that nearly half of the world's countries would experience species richness loss in the nearby future. These findings make clear that both climate change and land-use change pose comparably significant threats to global biodiversity. More immediate attention and effective actions are urgently needed from local governments for vulnerable regions.

**Keywords**: biodiversity loss; richness changes; climate change; land-use change; terrestrial vertebrates; Shared Socio-economic Pathways (SSPs)

## Plain Language Summary

With the increasing rate of climate change and human pressure on land, mitigating the loss of global biodiversity is a major challenge for the world's organizations and nations. In this study, we assess the combined effect of climate change and land-use change on diversity changes of global terrestrial vertebrates under the shared socioeconomic pathways (SSPs) and evaluate the relative contributions of climate change and land-use change to these changes. We find that approximately 45.82% of the Earth's land will suffer the richness loss of terrestrial vertebrates by 2050 even under the middle-high scenario of SSP3. All the projections of these five SSPs scenarios show that species richness changes of terrestrial vertebrates have unique geographical variations. Low latitudes (20°S – 25°N) will experience a sharp decline in species richness, while high latitudes (> 60°N) will experience a slight increase. Moreover, nearly half of the world's countries would experience diversity loss in the nearby future. These changes are predicted to contribute more climate change (accounting for 51.48%) than land-use change (nearly 48.52%) at a global scale under SSPs, which indicates that global land-use change plays a comparable role, compared with climate change, in future biodiversity.

# 1. Introduction

Global biodiversity plays an important role in ecosystem functions, as well as in the development of human well-being (Xu et al., 2021). Biodiversity is strongly associated with the productivity and resilience of terrestrial ecosystems through changing the rate of decomposition (Balvanera et al., 2006), carbon cycle (Midgley, 2012) and interspecies relationships (Wardle, Bardgett, Callaway, & Van der Putten, 2011). Moreover, it is also closely related to products, such as food supply and pharmaceutical products, that are essential in human life by mediating pollination and other processes (Booth et al., 2021). Nevertheless, global biodiversity has experienced an increasing loss since the Anthropocene (Johnson et al., 2017). The "Global Risk Report 2020" published by the World Economic Forum (WEF) also ranked "biodiversity loss" as the second most impactful and third most likely risk for the next decade. Factors driving biodiversity loss are widely varied, ranging from natural processes to anthropogenic activities (Maxwell, Fuller, Brooks, & Watson, 2016). Many studies attribute the biodiversity loss to climate change (Di Marco et al., 2019; Hickling, Roy, Hill, Fox, & Thomas, 2006; Mantyka-pringle, Martin, & Rhodes, 2012). Land-use change also poses a serious threat to global biodiversity. However, we, at present, cannot fully understand the combined effect of climate and land-use change on biodiversity loss at a global scale.

Climate change is considered as a primary factor driving biodiversity loss.

Continuous rising of temperature can directly change the natural environment of habitats, which eventually leads to a widespread species extinction. Recent studies have shown that species exhibit several responses to climate change. For instance, Parmesan (2006) found that evolutionary adaptations to warmer conditions were important for species against climate change. Poleward shifts of species' ranges (Hickling et al., 2006) and species invasion (Dornelas et al., 2014) are also common responses to climate change. However, not all species can shelter themselves from the negative effects of climate change by adaptation or migration. Some studies indicated that range-restricted species, like species ranged in polar or mountaintop, are more likely to undergo extinct (Dullinger et al., 2012).

Land-use change can increase the risk of species extinction combined with climate change by exacerbating the removal and fragmentation of native habitat in some regions. Peters et al. (2019) suggested that land-use change in climate-sensitive areas is likely to amplify the negative effect caused by climate change. For example, the land-use change in arid and semi-arid lands which is sensitive to climate conditions can increase the risk of species richness loss (Davies et al., 2012). Similarly, the agricultural expansion and urban sprawl aggravate the richness loss of soil organic carbon caused by climate change in wetland areas (Rojas, Munizaga, Rojas, Martínez, & Pino, 2019). On the other hand, the negative effects of climate change on biodiversity can also be ameliorated by land-use change. More recently, studies noticed that building protected areas could effectively resist the negative effects of climate change (Maiorano, Falcucci, Garton, & BOITANI, 2007; Shi et al., 2020). Besides, land-use conversions with less attention paid on, such as from agricultural land to forests, can also offset part of the negative effects from climate change (Manaye, Negash, & Alebachew, 2019). In addition, the magnitude of land-use intensity varies markedly at a global scale may cause varied consequences to different biodiversity changes (Pekin & Pijanowski, 2012).

To comprehensively reveal the combined effect on biodiversity changes, a solid understanding of the potential effects of future change on biodiversity as well existing status is necessary. Scenario-based biodiversity projection is essential for predicting the potential biodiversity loss. Scenario-based biodiversity projection should be essential for predicting the potential biodiversity loss and measuring the effectiveness of protection measures. Future scenarios, in general, should incorporate social-economic factors, such as human population density, economic development and greenhouse gases emissions. This requirement can be addressed by the recently generated scenario, the Shared Socio-economic Pathways (SSPs) (Riahi et al., 2017). However, limited studies have been carried out to quantify the combined effect of climate and land-use change on biodiversity change. It is unclear about which factors may dominate the biodiversity change on the global scale and what is the spatial heterogenicity of their influences.

Here we attempt to quantify the combined effect of climate and land-use change on diversity changes of terrestrial vertebrates under SSPs, and explore the relative contributions of climate change and land-use change to these changes. To be specific, we aim to answer: (a) How the combined effect of climate and land-use change on diversity changes of terrestrial vertebrates at the global scale? (b) Compared with climate change, how much does future land-use change contribute to diversity changes of terrestrial vertebrates?

# 2. Materials and methods

This section provides a summary of dataset collection and some methods used in this paper. First, the land-use naturalness and land-use intensity proxies on a global scale were generated for global land-use change with land-use data, net primary productivity (NPP) and population density. Second, we built the species distribution models with climatic and land-use variables by using empirical data. Two methods, generalized additive models (GAM) and random forest (RF) methods, were then evaluated to choose the best with a higher value of $R^2$ for the prediction. Third, the combined effect of climate and land-use change on terrestrial vertebrates was assessed by projecting the species richness changes under SSPs. Finally, we evaluated the relative contributions of climate and land-use change for future biodiversity change which may depend critically on the land-use change on the global scale.

## 2.1 Diversity measures

Species richness, which measures the number of different species in an ecological sample, is a biodiversity index that formed the basis for various biodiversity studies (Jenkins, Pimm, & Joppa, 2013). The species richness was also adopted as a proxy of global diversity of terrestrial vertebrates in this paper. For amphibians and mammals, we employed the geographical distribution database from the International Union for the Conservation of Nature (IUCN) Red List (https://www.iucnredlist.org/). As for birds, we used the species distribution data from the Birdlife International (http://www.birdlife.org/).

To generate richness maps on a global scale, we first removed the species range polygons which were classified as “extinct”, “extinct in the wild”, “not evaluated” and “data deficient” categories, and unionized polygons with the same taxonomic name. We then created a fishnet with a spatial grain of 1km×1km by using ArcGIS, and counted the overlap between species range polygons in each grid cell. The final generated world’s richness maps of terrestrial vertebrates involved 4,708 mammal species, 5,208 amphibian species, and 17,228 bird species.

### 2.2 Climate and land-use variables

To incorporate climatic variables and elevation into our analysis, we considered the following climate variables: mean annual temperature (Fadrique et al., 2018), mean annual precipitation (Garcia, Cabeza, Rahbek, & Araújo, 2014), mean annual wind speed (Porter, Budaraju, Stewart, & Ramankutty, 2015) and mean elevation (Elsen & Tingley, 2015). The mean elevation was chosen to reflect the effect of altitude on species richness when building species distribution models. Climate variables were derived from the Global Surface Summary of the Day (https://data.noaa.gov/dataset/global-surface-summary-of-the-day-gsod) and the Coupled Model Intercomparison Project Phase 6 (CMIP 6, https://esgf-node.llnl.gov/). The dataset of the global Surface Summary of the Day and the CMIP6 were used for building RF models and predicting the future geographic distribution of terrestrial vertebrates, respectively. Here, we chose the climate variables from the CMIP6 with the combination of SSP1-RCP1.9, SSP2-RCP4.5, SSP3-RCP7.0, SSP4-RCP6.0 and SSP5-RCP8.5 for 2050. We resampled these four climate variables and the mean elevation into 30-arc resolution (http://www.fao.org/), and excluded the Antarctic area and the grid cells with missing climate information.

As the species richness of terrestrial vertebrates is also sensitive to land-use change (Newbold et al., 2016). We defined land-use naturalness (LUN) and the land-use intensity (LUI) as two proxies to detect the land-use change on a global scale. As shown in equation (1)，the LUN was described as the product of the average naturalness (*Anat*) and net primary productivity (NPP, from http://files.ntsg.umt.edu/). The LUI was related to *Anat* and population density of human being (POP, from https://landscan.ornl.gov/landscan-datasets).

$$\mathrm{LUN} = Anat \times \mathrm{NPP} \tag{1}$$

$$\mathrm{LUI} = (1 - Anat) \times \mathrm{POP} \tag{2}$$

where, *Anat* was associated with the land-use categories and values of naturalness.

To calculate the LUN and LUI, the Intergovernmental Panel on Climate Change land categories and the European Space Agency Climate Change Initiative Land Cover (CCI-LC) land dataset (http://maps.elie.ucl.ac.be/CCI/viewer/index.php), with 300-meter spatial resolution in 2017 and its corresponding land categories were adopted. According to the correspondence of the two categories (Table 1), the CCI-LC land-use classes were grouped into the six IPCC land categories, for instance, agriculture, forest, grassland, wetland, settlement and other land. The value of naturalness in each land-use class was referred from Montesino et al.(2014). We further calculated the values *Anat* for five land use classes according to Equation (3).

$$Anat = \frac{\sum_{i=0}^{k} nat_i \times ncell_i}{\sum_{i=0}^{k} ncell_i} \tag{3}$$

In which, $nat_i$ and $ncell_i$ are the value of naturalness and the number of grid cells in the *i*th land cover class, respectively. *k* is the number of land cover classes.

For calculating the two land-use proxies under SSPs, we also employed the projected land use data, NPP and world population density from the Integrated Model to assess the Global Environment (IMAGE, https://dataplatform.knmi.nl/?q=PBL) (Popp et al., 2017). As the projected land-use data were cover percentages of different land-use classes in each grid cell, the detailed calculation of land-use naturalness and land-use intensity was according to Equation (4) and Equation (5).

$$\mathrm{LUN_{SSP}} = \left(\sum_{i=0}^{k} Anat_i\right) \times \mathrm{NPP_{SSP}} \tag{4}$$

$$\mathrm{LUI_{SSP}} = \left(\sum_{i=0}^{k} (1 - Anat_i)\right) \times \mathrm{POP_{SSP}} \tag{5}$$

In which, $\mathrm{LUN_{SSP}}$ and $\mathrm{LUI_{SSP}}$ were the LUN and LUI under SSPs. $\mathrm{NPP_{SSP}}$ and $\mathrm{POP_{SSP}}$ were the net primary productivity and population density under SSPs. *k* was the number of land cover classes.

$$cell_j = \frac{Vcell_j - raster_{min}}{raster_{max} - raster_{min}} (j = 1,2, \dots, n) \tag{6}$$

All climate and land-use variables in our analysis were normalized according to Equation (6). In which, $Vcell_j$ was the original value in the *j*th grid cell, $raster_{min}$ and $raster_{max}$ were the minimum and maximum values in raster data, respectively. *n* indicated the number of grid cells in raster data.

**Table 1** The correspondence between the land categories and values of naturalness in each land classes

| Land categories (IPCC) | Average naturalness | Land categories (CCI-LC) | Naturalness |
|---|---|---|---|
| **Agriculture** | 0.22 | Rained cropland | 0.20 |
| | | Irrigated cropland | 0.25 |
| | | Mosaic cropland (>50%) / natural vegetation (tree, shrub, herbaceous cover) (<50%) | 0.30 |
| | | Mosaic natural vegetation (tree, shrub, herbaceous cover) (>50%) / cropland (< 50%) | 0.90 |
| **Forest** | 0.87 | Tree cover, broadleaved, evergreen, closed to open (>15%) | 0.95 |
| | | Tree cover, broadleaved, deciduous, closed to open (> 15%) | 0.90 |
| | | Tree cover, needleleaved, evergreen, closed to open (> 15%)） | 0.90 |
| | | Tree cover, needleleaved, deciduous, closed to open (> 15%) | 0.85 |
| | | Tree cover, mixed leaf type (broadleaved and needleleaved) | 0.70 |
| | | Mosaic tree and shrub (>50%) / herbaceous cover (< 50%) | 0.60 |
| | | Tree cover, flooded, fresh or brakish water | 0.50 |
| | | Tree cover, flooded, saline water | 0.45 |
| **Grassland** | 0.77 | Mosaic herbaceous cover (>50%) / tree and shrub (<50%) | 0.40 |
| | | Grassland | 0.80 |
| **Wetland** | 0.85 | Shrub or herbaceous cover, flooded, fresh-saline or brakish water | 0.85 |
| **Settlement** | 0.00 | Urban | 0.00 |
| **Other** | 0.17 | Shrubland | 0.30 |
| | | Lichens and mosses | 0.15 |
| | | Sparse vegetation (tree, shrub, herbaceous cover) | 0.20 |
| | | Bare areas | 0.10 |

### 2.3 Statistical analysis

The species distribution model (SDM) is commonly used for predicting the geographical distribution of species and providing some evidence for species endangerment assessment. The SDM assumes that the niche for each specie depends on the environmental factors in its habitat. According to recent studies (Barbet-Massin, Thuiller, & Jiguet, 2012; Thuiller, Lafourcade, Engler, & Araújo, 2009), generalized additive models (GAM) and machine learning algorithms are more widely used for solving the geographic distribution of species. For example, Montesino et al.(2014) adopted GAM to assess the effect of future land-use change on biodiversity in global protected areas. Marmion et al.(2009) compared eight modelling techniques for predicting plant geographical distribution in North-eastern Finland and found that RF method performed the best. However, it remains unclear which one performs better on a global level.

Therefore, we compared GAM with RF for accessing the potential effects of climate and land-use change on species richness of terrestrial vertebrates, as well as that of different taxa. We parameterized GAM by default settings with the pyGAM package in Python 3.6. For random forest methods, the number of trees and the maximum number of features were set to be 100 and 6, respectively. To evaluate model performance, we split the dataset into training and testing sets through 10-fold cross-validation and calculated the adjusted $R^2$. The Terrestrial Ecoregions of the

World (TEOW) data was also introduced to improve the accuracy of the species distribution model. The TEOW data was derived from the World Wildlife Fund and defined 867 terrestrial ecoregions that classified into 14 biomes across the globe (Olson et al., 2001). For each biome, we carried out species distribution models and selected the model with a higher adjusted $R^2$ from GAM and RF.

### 2.4 Contributions of climate and land-use factors to richness changes

To quantify the contributions of climate change and land-use change to richness changes of terrestrial vertebrates, we predicted the spatially land-use-induced and climate-driven distribution of species richness under the SSPs with RF models respectively. Specially, the spatially land-use-induced species richness ($Bio_{land}$) was simulated by using the constant land-use dataset and future climate dataset. Similarly, the climate-driven species richness ($Bio_{climate}$) was projected with the constant climate dataset and future land-use dataset. Here, we considered the projected species richness with future climate and land-use dataset as the actual species richness under SSPs. Accordingly, we could calculate the difference between the actual species richness and the $Bio_{land}$, and the difference between the actual species richness and $Bio_{climate}$ using Equation (7) and Equation (8).

$$\Delta Bio_{\mathrm{land}} = Bio_{land} - Bio_{land\_climate} \tag{7}$$

$$\Delta Bio_{\mathrm{climate}} = Bio_{climate} - Bio_{land\_climate} \tag{8}$$

Following Wu et al.(2014) and Liu et al.(2019), we estimated the relative contributions of climate change and land-use change to richness changes of terrestrial vertebrates as Equation (9) and Equation (10). Here, we considered the sum of contributions of climate change and land-use change to be 100%. The final contributions of climate change and land-use change to the loss under different SSPs were processed according to the terrestrial biomes using the zonal statistics of ArcGIS.

$$\mathrm{Contr}_{\mathrm{land}} = \frac{|\Delta Bio_{land}|}{|\Delta Bio_{land}|+|\Delta Bio_{climate}|} \times 100\% \tag{9}$$

$$\mathrm{Contr}_{\mathrm{climate}} = \frac{|\Delta Bio_{climate}|}{|\Delta Bio_{land}|+|\Delta Bio_{climate}|} \times 100\% \tag{10}$$

# 3. Results

### 3.1 Performance of species distribution models

After determining the correlation between species richness and climate and land-use variables with Pearson correlation analysis (SI. Figure 1), we used random forest (RF) models to build species distribution models for global terrestrial vertebrates, and compared the results with those from a generalised additive model (GAM). The results show that models including climate and land-use variables have higher explanatory power for species distribution than models that only use climate variables (SI. Table 1). Additionally, the RF methods show generally higher performance than GAM for terrestrial vertebrates, as well as for amphibians, mammals and birds (Figure 1). Specifically, the RF methods have higher explanatory power for the species richness of terrestrial vertebrates in Tropical and Subtropical

Coniferous Forests (TSC, abbreviations of all terrestrial biomes can be referred to SI. Table 2) than GAM ($R^2$ = 0.79 for RF and $R^2$ = 0.55 for GAM). Similarly, the species richness of amphibians, mammals and birds are also can strongly explained by using random forest methods, but moderately explained by GAM, especially in TSC and MWS (with $R^2$ = 0.70, 0.81 and 0.72 for RF and with $R^2$ = 0.49, 0.53 and 0.59 for GAM). Even under the poorest situation, the RF method still behaves fairly with the GAM. For example, the species richness of mammals in BRF explains by RF method with $R^2$ = 0.62 and by the GAM with $R^2$ = 0.63, which is slightly higher than random forest method (but less than 0.01). Therefore, we choose the RF methods to predict the species richness of terrestrial vertebrates under SSPs.

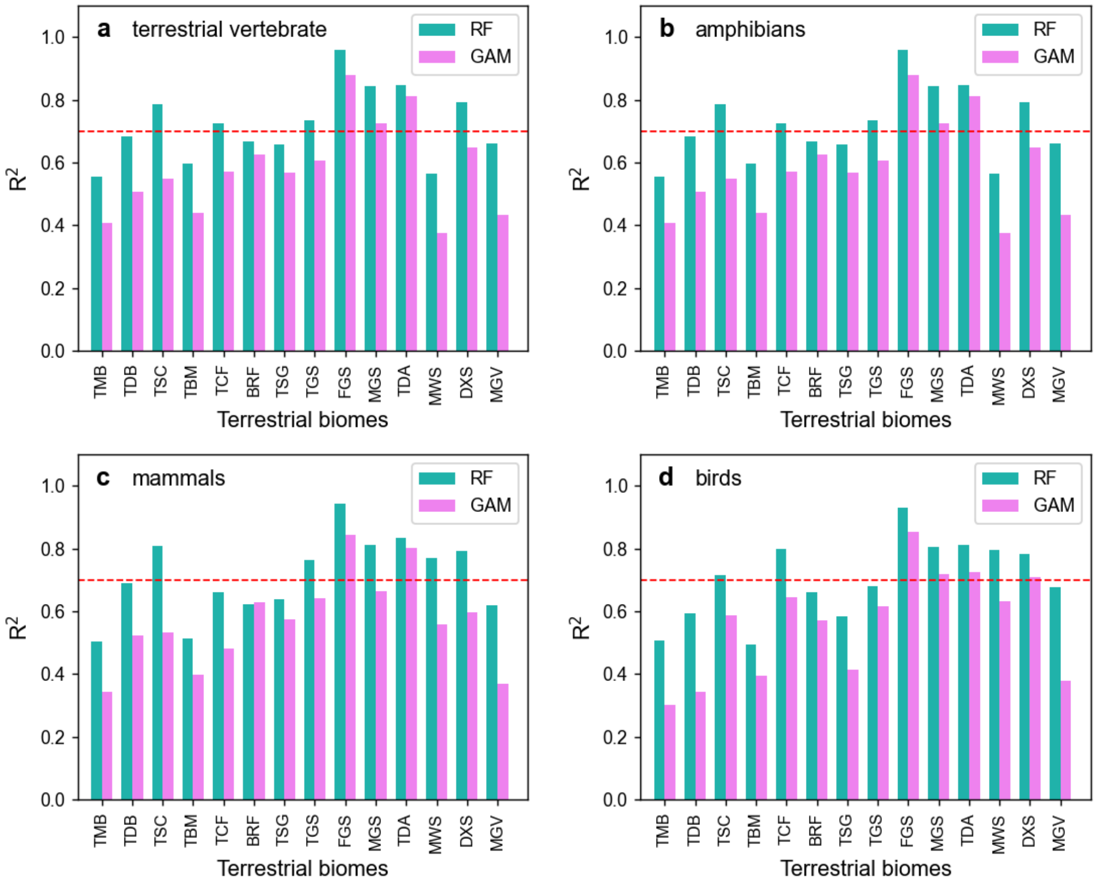


**Figure 1** $R^2$ of generalized additive models (GAM) and random forest (RF) methods. Response variables in a-d are the species richness of terrestrial vertebrates, amphibians, mammals and birds, respectively. The red dash line represents the value of $R^2$ equals 0.7. TMB, TDB, and TSC denote the biomes of Tropical and Subtropical Moist Broadleaf Forests, Tropical and Subtropical Dry Broadleaf Forests, and Tropical and Subtropical Coniferous Forests. TBM, TCF and BRF represent the biomes of Temperate Broadleaf and Mixed Forests, Temperate Coniferous Forests, and Boreal Forests/Taiga. TSG, TGS, and FGS are the biomes of Tropical and Subtropical Grasslands, Savannas, and Shrublands, Temperate Grasslands, Savannas, and Shrublands, and Flooded Grasslands and Savannas. MGS, TDA, and MWS are the biomes of Montane Grasslands and Shrublands, Tundra, and Mediterranean Forests, Woodlands, and Scrub. DXS and MGV are the biomes of Deserts and Xeric Shrublands and Mangroves, respectively. The abbreviation of 14 terrestrial biomes also can be referred to SI. Table 2.

### 3.2 Projected richness changes under SSPs

We predicted the changes of species richness for terrestrial vertebrates across the globe under SSPs with the combined effects of climate and land-use change. The estimation shows that about 45.99% of the world’s land would suffer a loss of species richness between 2017 and 2050 under climate and land-use change. The magnitude and geographic distribution of the changes vary under the five different SSPs (SI. Figure 3 – 6). In general, the heaviest richness loss is projected under SSP5 (with 46.29% of terrestrial land suffering richness loss), but the lowest species richness under SSP3, with about 45.82% of global land experiencing richness loss (Table 2). To be specific, the differences between the five SSPs are mainly distributed in Latin America and Southeast Asia. For instance, the magnitude of richness loss in the Guiana Highlands is largest under SSP5, followed by that under SSP2. In contrast, the loss of species richness under SSP3 is estimated the least compared with the other four SSPs, no matter in magnitudes or geographical ranges. As shown in Figure 2, Southeast Asia will suffer the most significant richness loss of terrestrial vertebrates, with a maximum loss of 305 species (nearly 83.33% of the present species richness) in the Malay Archipelago by 2050 under SSP3. These richness losses are close to the results of Chaudhary and Mooers (Chaudhary & Mooers, 2018), who predicted a loss of nearly 281 species under land-use change from 2050 to 2100. Interestingly, the richness loss in Latin America is concentrated in the east of the Brazilian plateau and the North Cordillera Mountains but scattered around the Amazon Basin. In terms of quantity, the richness loss in Latin America is slightly lower than that in Southeast Asia, with a maximum richness loss of 187 species.

**Table 2** The percentages of terrestrial land with richness loss under SSPs (%)

| SSPs | Terrestrial vertebrates | Amphibians | Mammals | Birds |
|---|---|---|---|---|
| SSP1 | 45.98 | 40.90 | 42.94 | 38.92 |
| SSP2 | 46.00 | 40.52 | 42.62 | 38.94 |
| SSP3 | 45.82 | 40.75 | 42.82 | 38.61 |
| SSP4 | 45.85 | 40.21 | 42.37 | 38.75 |
| SSP5 | 46.29 | 41.13 | 43.07 | 39.16 |

For different taxa, we find that mammals have the largest geographical range size with richness loss by 2050 (about 42.76% of the world's land), followed by amphibians (about 40.70% of the world's land). Although mammals show the largest geographical range size with richness loss, the quantity of richness loss is far less than that of other taxa. To be specific, the heaviest richness loss of amphibians is estimated to be 84 species, while that of mammals is 65 species. Furthermore, the richness changes for different taxa shows geographical variation. The richness loss of amphibians is mainly distributed in the Amazon Basin and the Brazilian Plateau in Latin America, south Congo Basin and the Atlantic Coastal Plain, whereas the richness increase of amphibians is distributed in the north Amazon, the Congo Basin, the Yunnan-Guizhou Plateau, and Papua Islands. For birds, the richness increase under SSP3 is mainly located in the Congo Basin, Papua Islands and the Yunnan-Guizhou Plateau.

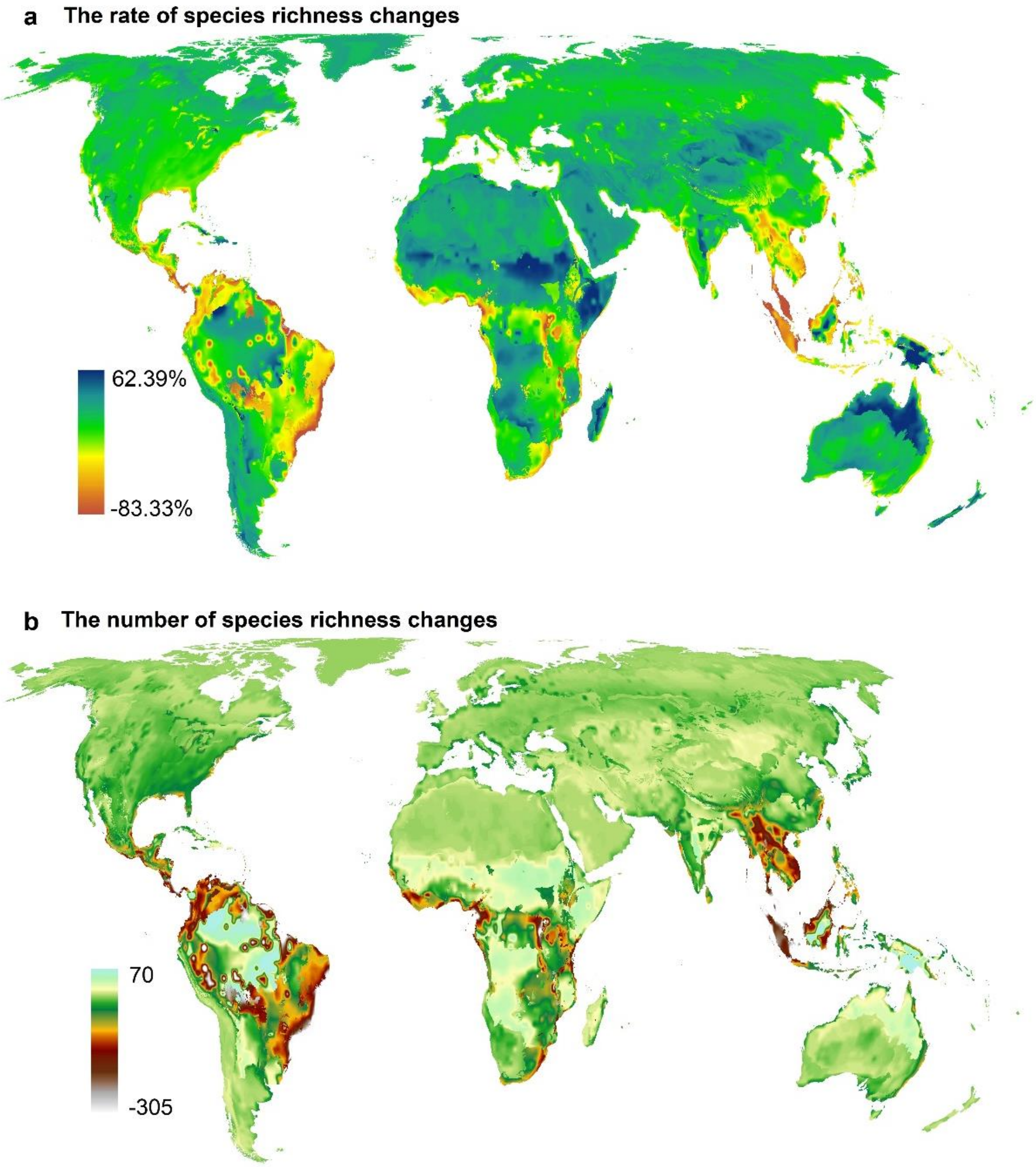


**Figure 2** Richness changes of terrestrial vertebrates between 2017 and 2050 under SSP3. **a**. the rate of richness changes (%), **b**. the number of richness changes.

In addition, richness changes at low latitudes (20°S – 25°N) and low elevation (< 1500 meter) are projected to decline sharply. As shown in Figure 3, the richness losses of terrestrial vertebrates, as well as amphibians, mammals, and birds, are mainly distributed at latitudes between 20°S and 25°N under the SSPs and are projected to experience a large fluctuation in magnitude. For instance, the species richness of terrestrial vertebrates will decline by nine species per year but increase by two species per year from the present to 2050. In contrast, the magnitude of richness changes around the 60° magnetic latitude and higher is relatively small, showing a slightly increasing trend. These results show a whole range shift from low latitude to high latitude as a result of climate and land-use change, coincident with those of previous studies (Chen, Hill, Ohlemüller, Roy, & Thomas, 2011; Hill, Griffiths, & Thomas, 2011; Pauli et al., 2012). The comparison between different taxa emphasizes that mammals are more likely to suffer richness loss in the middle of the 21th Century, no matter at low latitudes (Figure 3b, c, d). Furthermore, our projections find the loss of species richness is concentrated at low altitudes (< 1500m). Taking SSP3 for example (SI. Figure 2), the largest loss of species richness below 1500m reached five species per year, with birds experiencing the largest loss, followed by mammals.

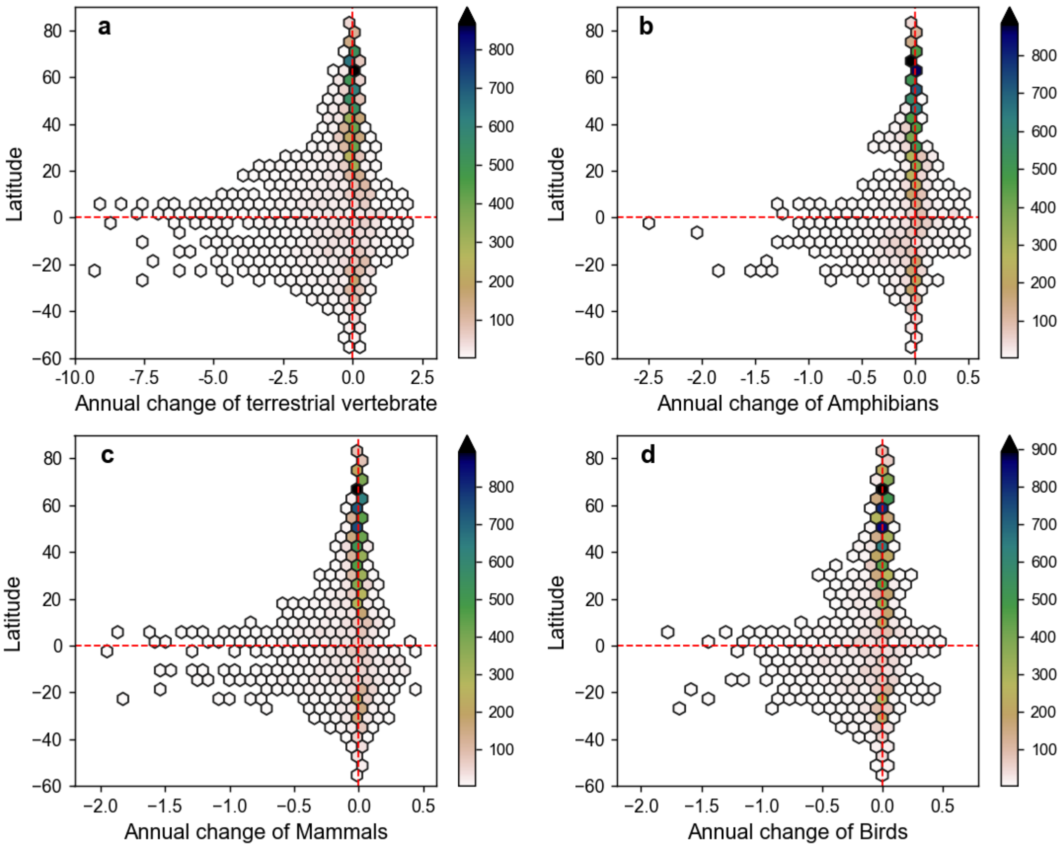


**Figure 3** Annual changes of species richness along with magnetic latitudes between 2017 and 2050 under SSP3 for **a.** terrestrial vertebrates, **b.** amphibians, **c.** mammals and **d.** birds. Colour bar shows the number of grid cells that located in annual change of richness species and latitude.

The projection also indicates that nearly half of the world's countries would experience a richness loss by 2050. In general, approximately 19.62% of world's countries have an average rate of species-richness loss over 30.00%, and 17.72% of countries have an average rate of increase over 30.00%. By introducing the Human Development Index (HDI), the numbers of high-income countries with richness loss and increase are almost equal, but the rate of increase is larger than the rate of loss (Figure 4b). Similarly, for low-income countries, the number of countries with richness loss is also equivalent to that with richness increase. However, compared with countries at the high-income level, the magnitudes of species-richness changes are much slighter. It is worth mentioning that the largest rate of species-richness loss (74.17%) is estimated at middle-income countries.

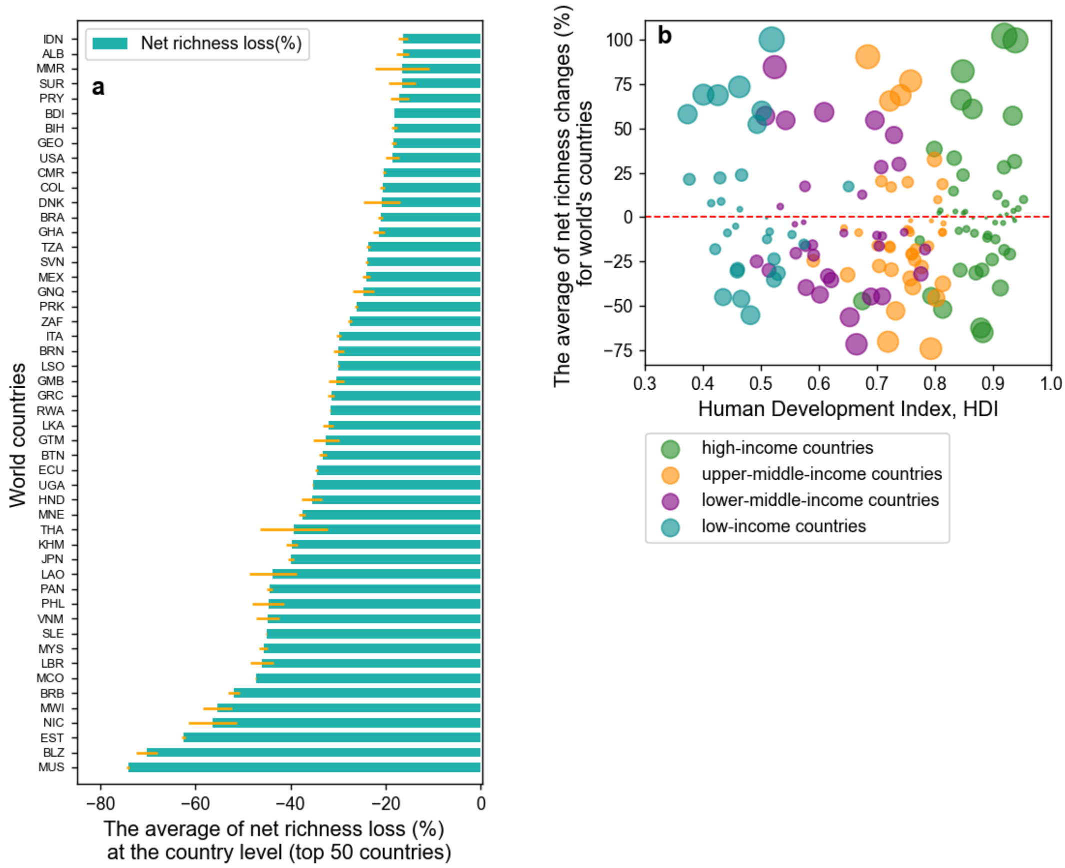


**Figure 4** The average of net richness changes (%) for terrestrial vertebrates at the country level. **a**. the average richness loss of terrestrial vertebrates for the top 50 of the world's countries between 2017 and 2050 under SSPs. Orange solid lines indicate the 95% confidence interval of country-specific richness loss. Labels in vertical axis are the country code (ISO3) of the top 50 world countries. **b**. Country-level richness changes between 2017 and 2025 in relation to countries' human development index (HDI). Colours represent the countries in different income levels and the point diameter indicates the value of species-richness loss.

### 3.3 Contributions of climate change and land-use change

We estimated the relative contributions of future climate change and land-use change to species richness changes. The analysis reveals that the contribution of land-use change to biodiversity changes can reach 48.52% on average, which is even slightly lower than that of climate change (51.48%) on the global scale. However, the relative contributions of climate change and land-use change are varied among the five scenarios of SSPs. For instance, the climate-related contribution is the largest under SSP5 (accounting for 51.29%) but lowest under SSP3 (estimated at 50.45%).

Contributions of climate change and land-use change show obvious variations in terrestrial biomes. Taking SSP5 as an example, climate change shows the greatest effect on richness changes in FGS (68.78%), followed by that in TSC (66.05%), whereas land-use change has the strongest influence in BRF (68.72%). As table 3 shows, the biomes of TSC, TGS and FGS are highly explained by climate change under the five SSPs (with climate-related contribution beyond 60%), which indicates that terrestrial vertebrates in these biomes are more vulnerable to climate change than land-use change. Instead, the biomes of BRF and TDA are prone to be influenced by land-use change under all the SSPs, with land-use-related contributions at 69.43% and 60.88% in SSP3, respectively.

**Table 3** Contributions of climate and land-use change on future richness changes of terrestrial vertebrates (%)

| Biomes | SSP1 | | SSP 2 | | SSP 3 | | SSP 4 | | SSP 5 | |
|---|---|---|---|---|---|---|---|---|---|---|
| | climate change | land-use change | climate change | land-use change | climate change | land-use change | climate change | land-use change | climate change | land-use change |
| **TMB** | 45.32 | 54.68 | 46.50 | 53.50 | 46.46 | 53.54 | 45.91 | 54.09 | 46.33 | 53.67 |
| **TDB** | 46.86 | 53.14 | 47.44 | 52.56 | 49.35 | 50.65 | 47.14 | 52.86 | 51.10 | 48.90 |
| **TSC** | 60.42 | 39.58 | 64.01 | 35.99 | 63.78 | 36.22 | 61.15 | 38.85 | 66.05 | 33.95 |
| **TBM** | 48.40 | 51.60 | 47.31 | 52.69 | 48.10 | 51.90 | 45.59 | 54.41 | 47.95 | 52.05 |
| **TCF** | 54.25 | 45.75 | 51.60 | 48.40 | 53.30 | 46.70 | 52.88 | 47.12 | 52.19 | 47.81 |
| **BRF** | 31.44 | 68.56 | 30.37 | 69.63 | 30.57 | 69.43 | 30.65 | 69.35 | 31.28 | 68.72 |
| **TSG** | 45.84 | 54.16 | 47.04 | 52.96 | 47.64 | 52.36 | 46.36 | 53.64 | 47.36 | 52.64 |
| **TGS** | 65.98 | 34.02 | 63.99 | 36.01 | 65.72 | 34.28 | 65.45 | 34.55 | 64.77 | 35.23 |
| **FGS** | 62.94 | 37.06 | 66.03 | 33.97 | 62.62 | 37.38 | 65.80 | 34.20 | 68.78 | 31.22 |
| **MGS** | 59.84 | 40.16 | 58.13 | 41.87 | 59.65 | 40.35 | 58.53 | 41.47 | 60.88 | 39.12 |
| **TDA** | 40.28 | 59.72 | 39.78 | 60.22 | 39.12 | 60.88 | 38.42 | 61.58 | 36.38 | 63.62 |
| **MWS** | 61.50 | 38.50 | 63.82 | 36.18 | 62.25 | 37.75 | 60.71 | 39.29 | 58.38 | 41.62 |
| **DXS** | 40.72 | 59.28 | 42.65 | 57.35 | 42.82 | 57.18 | 42.87 | 57.13 | 41.27 | 58.73 |
| **MGS** | 53.53 | 46.47 | 53.02 | 46.98 | 52.87 | 47.13 | 51.45 | 48.55 | 54.84 | 45.16 |

*Note*: TMB, TDB, and TSC denote the biomes of Tropical and Subtropical Moist Broadleaf Forests, Tropical and Subtropical Dry Broadleaf Forests, and Tropical and Subtropical Coniferous Forests. TBM, TCF and BRF represent the biomes of Temperate Broadleaf and Mixed Forests, Temperate Coniferous Forests, and Boreal Forests/Taiga. TSG, TGS, and FGS are the biomes of Tropical and Subtropical Grasslands, Savannas, and Shrublands, Temperate Grasslands, Savannas, and Shrublands, and Flooded Grasslands and Savannas. MGS, TDA, and MWS are the biomes of Montane Grasslands and Shrublands, Tundra, and Mediterranean Forests, Woodlands, and Scrub. DXS and MGV are the biomes of Deserts and Xeric Shrublands and Mangroves, respectively. The abbreviation of terrestrial biomes also can be referred to SI. Table 2.

# 4. Discussion

Land-use change is a critical driver of historical change of biodiversity under the global climate change (Jung, Rowhani, & Scharlemann, 2019). In this study, we assess the combined effects of future climate and land-use change on terrestrial vertebrates and separate the relative contributions of climate change and land-use change at a global scale under SSPs. The results reveal various spatial distribution responses of terrestrial vertebrates across the globe, enabling us to understand the combined effects of climate and land-use change, and identifying the priority for biodiversity conservation.

## 4.1 Relative contributions of climate change and land-use change

Climate change has been demonstrated to be a contributor to reshaping the richness and geographical ranges of terrestrial vertebrates, with a relative contribution of 51.48%. The importance of RF models further reveal that mean annual temperature and mean annual precipitation are the dominant climate factors influencing the richness changes of terrestrial vertebrates (SI. Table 3), which is consistent with previous studies that measured the effects of climate change from different perspectives (Garcia et al., 2014; Urban, 2015). The climate-related effects on terrestrial vertebrates are different among terrestrial biomes. For all tropical biomes, the diversity of terrestrial vertebrates is largely influenced by mean annual temperature, followed by mean annual precipitation. This phenomenon may originate from that the tropical species are systematically more sensitive to climate variations than species at other locations (Deutsch et al., 2008; Freeman & Class Freeman, 2014). Higher spatial heterogeneity of climate change usually means wider environmental tolerance (Bonebrake & Mastrandrea, 2010). Since tropical biomes are characterized by low spatial heterogeneity in temperature, species in the tropics, compared with temperate species, have to move farther along latitude to offset the adverse effect of rising temperature (Colwell, Brehm, Cardelús, Gilman, & Longino, 2008). Although complex topography can alleviate the negative effect caused by the warming climate, the niche of the indigenous montane species would be under threat (Elsen & Tingley, 2015). Meanwhile, the increase in the length of the dry season caused by the precipitation variation in tropical areas will directly affect the phenology and duration of bird reproductive activities and the availability of food resources, resulting in nearly one-third of tropical birds suffering population decline (Brawn, Benson, Stager, Sly, & Tarwater, 2017).

Land-use change is also identified the other important determinant for terrestrial vertebrates across the globe under all five SSPs, averagely resulting in 48.52% of global richness changes, which is in line with many existed studies (Jantz et al., 2015; Jetz, Wilcove, & Dobson, 2007; Mantyka-Pringle et al., 2015). This suggests that land-use change also plays a significant role in shifting species ranges and changing richness diversity of terrestrial vertebrates. However, the effect of land-use change on terrestrial vertebrates often shows a superposition or mitigation effect on the effect of climate change. For instance, Jung et al. (2019) claimed that abrupt land-use change could lower local species and abundance by 4.2% and 2.0%, but this loss could completely recover after ten years with a constant climate condition. Moreover, our analysis shows that the land-use naturalness, in some terrestrial biomes (e.g. BRF), contributes more to richness changes by comparison with climate variables, such as the mean annual temperature and the mean annual precipitation. This high land-use-related contribution may largely be associated with agricultural expansion (Dobrovolski, Diniz-Filho, Loyola, & De Marco Júnior, 2011). According to the high level of projected population growth (Gerland et al., 2014) and the dietary transitions to more calories and animal-based foods (Willett et al., 2019), more natural land needs to be converted into agricultural land for satisfying basic food systems, thereby making natural habitats more fragmented and leading to species extinctions (Williams et al., 2020).

### 4.2 Regional differences of species richness changes

The combined effects of climate and land-use change on terrestrial vertebrates show substantial latitudinal differences with a large decline at low latitudes, this result is consistent with those of previous studies which suggest a sharp biodiversity loss at low latitudes (Chaudhary & Mooers, 2018; Schipper et al., 2019). However, unlike numerous studies focusing on a poleward shift of terrestrial vertebrates in the future (Chen et al., 2011; Hickling et al., 2006; Hill et al., 2011), we warn that the richness changes at low latitudes should be paid much more attention to. The main reason is that low-latitude regions have a considerably number of species and the most abundant biological resources on the planet (Gaston, 2000; Jenkins et al., 2013). For instance, the Amazon Basin is home to nearly one-quarter of terrestrial species. Besides that, the low latitudes are subject to some of the locations that most disturbed by anthropogenic activities (Barlow et al., 2018), including land-use change and degradation (Keenan et al., 2015), pollution (Lewis, Silburn, Kookana, & Shaw, 2016) and overexploitation (Ingram et al., 2018). Multiple anthropogenic stressors have caused tropical ecosystems more vulnerable (Buisson et al., 2019; Cole, Bhagwat, & Willis, 2014) and transform from species-rich systems to species-poor systems (Veldman & Putz, 2011).

Furthermore, our result at the country-specific level indicates that the richness loss is mainly concentrated in the countries at the middle-income level which is highly consistent with that of the study by Waldron et al.(2017). Their study finds that biodiversity declines as the gross domestic product (GDP) grows, but the effect of GDP growth is not significant in the poorest countries and can be partly offset by improvements in the quality of national governance. Obviously, countries at different income levels have different abilities to cope with the effects of climate change, as well as varied social consciousness and paid willingness for biodiversity conservation (Jacobsen & Hanley, 2009; Turpie, 2003), leading to different magnitudes of species-richness changes. Meanwhile, the phenomenon is also closely related to economic activities. Some other studies have shown that high-income countries can shift their pressure on species to low- and middle-income countries through importing of products and services (Holland et al., 2019; Lenzen et al., 2012). These telecoupled activities make the country-specific richness changes more complex.

### 4.3 Implications for biodiversity conservation

Global biodiversity will be affected by both climate change and land-use change, and climate change is considered the dominant cause of species extinction. How society responds to climate change will seriously affect biodiversity changes, because effective climate change mitigation policies will significantly alleviate the direct effect of climate change on biodiversity (Mantyka-Pringle et al., 2015; Schipper et al., 2019). Our analysis shows that under the scenario of the highest greenhouse gas emissions, that is, the SSP5 scenario, the diversity of terrestrial vertebrates will decline the most in the middle of 21st century, and the relative contribution of climate change is also the highest (51.97%), comparing with the climate-related contribution under SSP4 scenario by 50.92%. This demonstrates that our society must immediately implement sustainable development strategies through transforming energy production and consumption, improving renewable energy technologies, reducing greenhouse gas emissions, and slowing down the rate of climate change.

What’s more, reasonable land-use planning is equally important for biodiversity conservation, especially at a country-specific level. First, reducing deforestation and agricultural expansion are the most direct ways to conserve species through protecting habitats. A market-based protective payment mechanism, such as REDD+ (Agrawal, Nepstad, & Chhatre, 2011; McDermott, Coad, Helfgott, & Schroeder, 2012), can be employed to higher the cost of deforestation for private-sector actors (Lambin et al., 2018). Improved agricultural production efficiency (Grassini & Cassman, 2012) and proactive food system changes (Booth et al., 2021; Williams et al., 2020) are also essential approaches to reducing biodiversity threats. Second, the establishment of protected areas and protected area networks for extinct species is an effective tool to relieve pressure caused by land-use change (like infrastructure development). The effectiveness of global protected areas is not optimistic as before it designed because of ignoring the importance of management (Jones et al., 2018). By introducing the protected area networks, merely protected areas in Europe have reached the expected effectiveness and have the potential to resist future climate change (Araújo, Alagador, Cabeza, Nogués-Bravo, & Thuiller, 2011). Third, establishing laws for local species is proven to be beneficial to strictly prohibit overexploitation and illegal trade of endangered species (Mothes et al., 2021). Other channels, including newly-established economic regulations like payment for ecosystem services (Grima, Singh, Smetschka, & Ringhofer, 2016; Redford & Adams, 2009), are substantial tools as financial supports for biodiversity conservation. In addition, strengthening the cooperation between science and policy at all levels is fundamental to integrate scientific, indigenous and local knowledge to support land-use decision-making at the country-specific level.

## 5. Conclusions

Climate and land-use change are considered major factors causing biodiversity loss. However, previous studies rarely take the combined effect of climate and land-use change on global biodiversity. By using empirical data, we assess the combined effect of climate and land-use change on species richness of terrestrial vertebrates and evaluate the relative contributions for climate change and land-use change. Land-use change is evaluated to account for nearly half of future richness changes of global terrestrial vertebrates, but slightly lower than the contribution of climate change. With the combined effect of climate and land-use change, approximately 45.99% of Earth's land would experience richness losses of terrestrial vertebrates, especially in Southeast Asia, sub-Saharan Africa and Latin America. The analysis on the country-specific level also shows that nearly half of the countries in the world would confront biodiversity loss, of which 19.62% had average species richness loss rates of over 15%. These findings demonstrate that land-use change, like climate change, plays a comparably significant role in the richness changes of terrestrial vertebrates. More importantly, such insight into attribution analysis of biodiversity loss is required for future biodiversity conservation, such as the Aichi biodiversity targets and the post-2020 global biodiversity framework.

There are several limitations in our analysis. First, the interspecies relationships and energy requirements are not considered in our species distribution models. Second, the contribution of land-use intensity in our analysis may be underestimated as the land-use intensity is calculated by using population density and the naturalness of each land-use class. Although the population density can represent the number of people dwelling in each grid cell, this population aggregation is unable to comprehensively be illustrated by the land-use intensity. Although some limitations to our projections, this paper goes much beyond previous analysis in three main ways: (1) we generate the proxies of land-use naturalness and land-use intensity to quantify the effects of land-use change. (2) we build the relationship between the combined effects of climate and land-use change and diversity changes using machine learning techniques at a global scale. (3) The relative contributions of climate change and land-use change to terrestrial vertebrates are firstly assessed, which is critical to mitigation policies and conservation strategies, such as the new post-2020 global biodiversity framework.

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dataset, including temperature, precipitation and wind speed, are from the Global Surface Summary of the Day (https://data.noaa.gov/dataset/global-surface-summary-of-the-day-gsod). The elevation grid that support the findings of this study is available at FAO (http://www.fao.org/). The future climate dataset (temperature, precipitation and wind speed in 2050) adopted in this study are derived from the CMIP6 (https://esgf-node.llnl.gov/). The historical and future land-use map are from the European Space Agency Climate Change Initiative Land Cover (CCI-LC, http://maps.elie.ucl.ac.be/CCI/viewer/index.php) and the Integrated Model to assess the Global Environment (IMAGE, https://dataplatform.knmi.nl/?q=PBL), respectively. The historical population density and NPP dataset are from https://landscan.ornl.gov/landscan-datasets and http://files.ntsg.umt.edu/. The future population density and NPP dataset used for projection are available at https://dataplatform.knmi.nl/?q=PBL.

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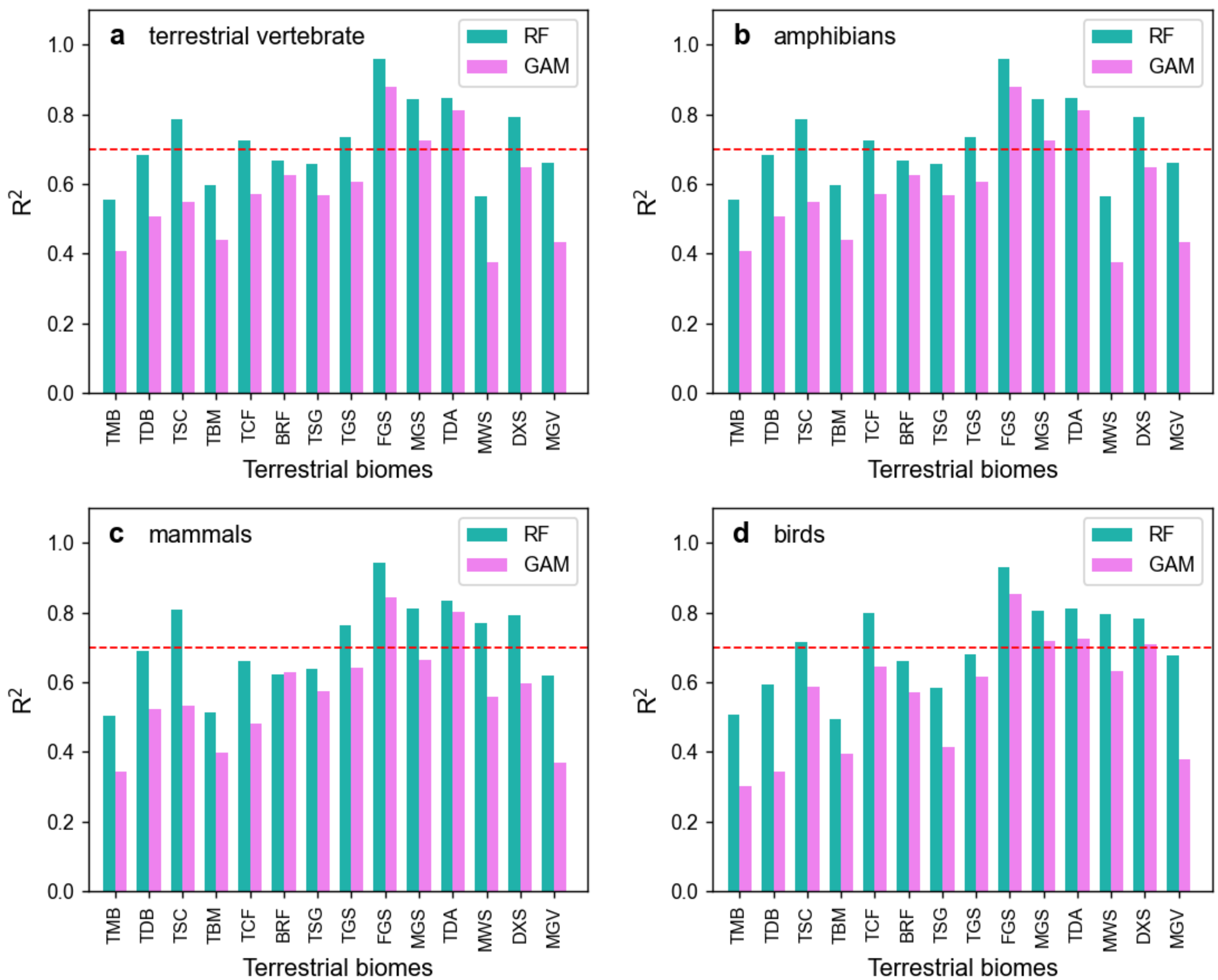
**Figure 1.**



a terrestrial vertebrate
b amphibians
c mammals
d birds
RF
GAM
R2
1.0
0.8
0.6
0.4
0.2
0.0
TMB
TDB
TSC
TBM
TCF
BRF
TSG
TGS
FGS
MGS
TDA
MWS
DXS
MGV
Terrestrial biomes

**Figure 2.**

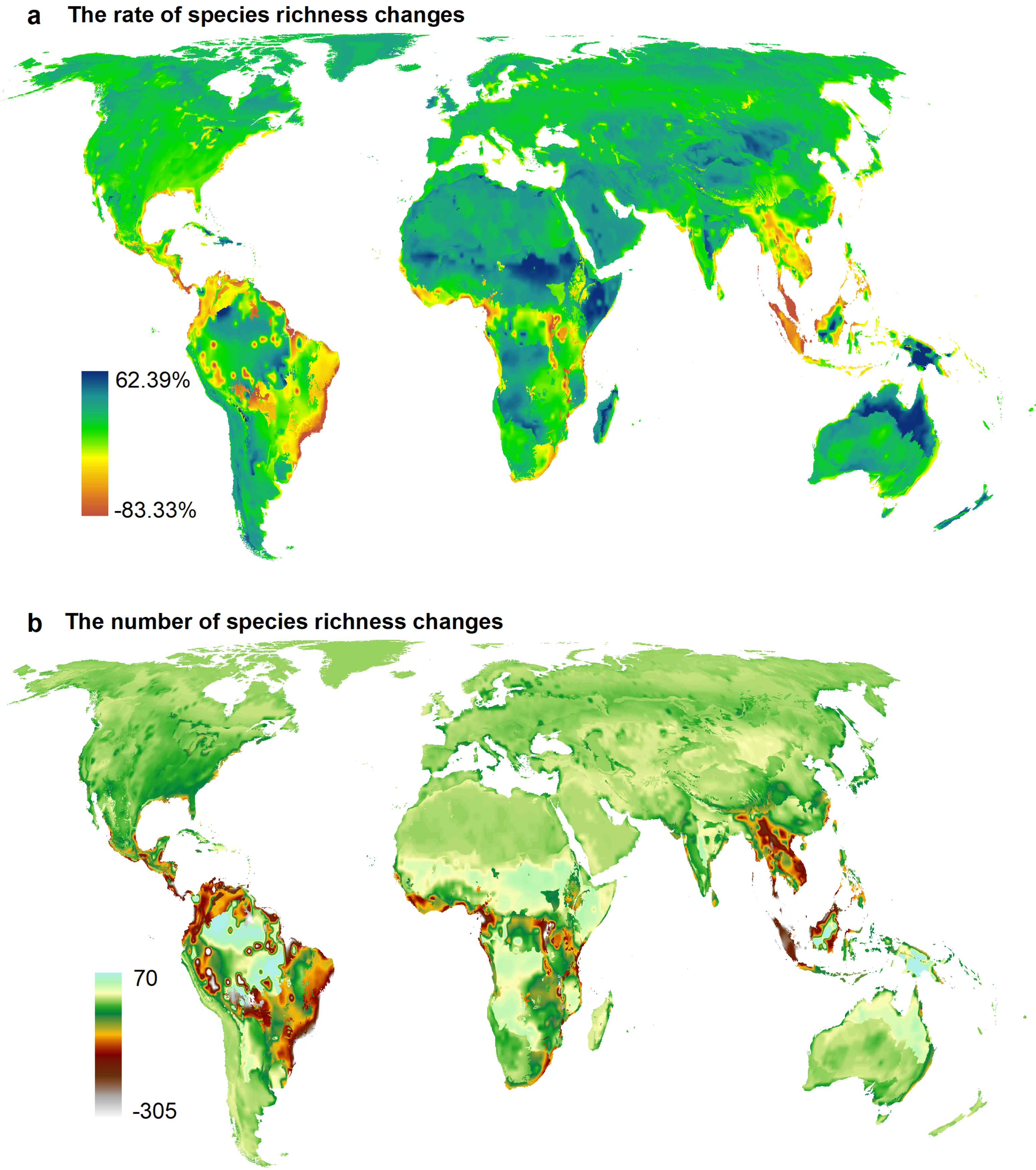

a The rate of species richness changes
62.39%
-83.33%
b The number of species richness changes
70
-305

**Figure 3.**

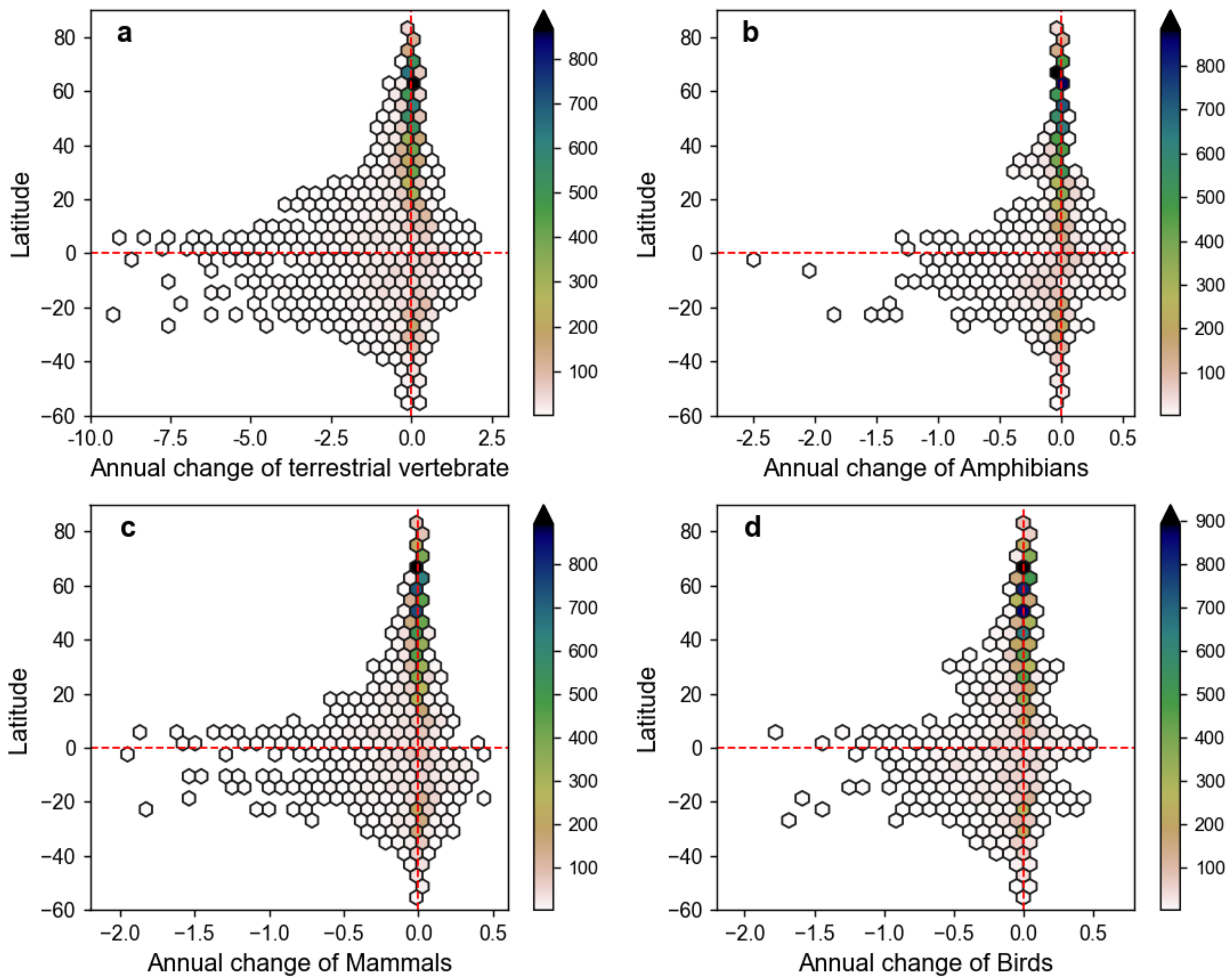
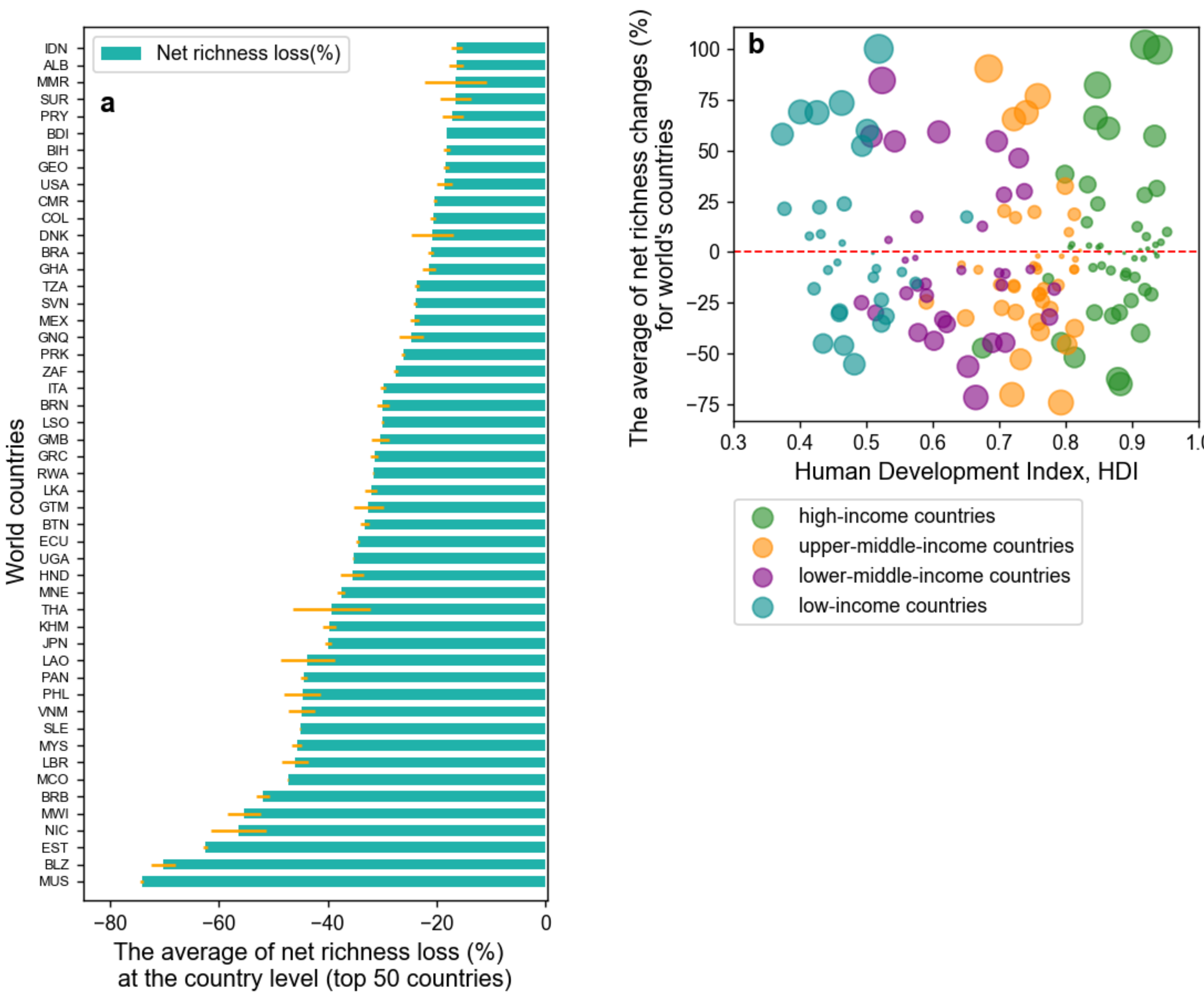

a
b
c
d
Latitude
Annual change of terrestrial vertebrate
Annual change of Amphibians
Annual change of Mammals
Annual change of Birds
80
60
40
20
0
−20
−40
−60
-10.0
-7.5
-5.0
-2.5
0.0
2.5
−2.5
−2.0
−1.5
−1.0
−0.5
0.0
0.5
100
200
300
400
500
600
700
800
900

**Figure 4.**



Net richness loss(%)
a
IDN
ALB
MMR
SUR
PRY
BDI
BIH
GEO
USA
CMR
COL
DNK
BRA
GHA
TZA
SVN
MEX
GNQ
PRK
ZAF
ITA
BRN
LSO
GMB
GRC
RWA
LKA
GTM
BTN
ECU
UGA
HND
MNE
THA
KHM
JPN
LAO
PAN
PHL
VNM
SLE
MYS
LBR
MCO
BRB
MWI
NIC
EST
BLZ
MUS
World countries
−80
−60
−40
−20
0
The average of net richness loss (%)
at the country level (top 50 countries)
b
100
75
50
25
0
−25
−50
−75
The average of net richness changes (%)
for world's countries
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
Human Development Index, HDI
high-income countries
upper-middle-income countries
lower-middle-income countries
low-income countries

**Table 1** The correspondence between the land categories and values of naturalness in each land classes

| Land categories (IPCC) | Average naturalness | Land categories (CCI-LC) | Naturalness |
|---|---|---|---|
| **Agriculture** | 0.22 | Rained cropland | 0.20 |
| | | Irrigated cropland | 0.25 |
| | | Mosaic cropland (>50%) / natural vegetation (tree, shrub, herbaceous cover) (<50%) | 0.30 |
| | | Mosaic natural vegetation (tree, shrub, herbaceous cover) (>50%) / cropland (< 50%) | 0.90 |
| **Forest** | 0.87 | Tree cover, broadleaved, evergreen, closed to open (>15%) | 0.95 |
| | | Tree cover, broadleaved, deciduous, closed to open (> 15%) | 0.90 |
| | | Tree cover, needleleaved, evergreen, closed to open (> 15%)） | 0.90 |
| | | Tree cover, needleleaved, deciduous, closed to open (> 15%) | 0.85 |
| | | Tree cover, mixed leaf type (broadleaved and needleleaved) | 0.70 |
| | | Mosaic tree and shrub (>50%) / herbaceous cover (< 50%) | 0.60 |
| | | Tree cover, flooded, fresh or brakish water | 0.50 |
| | | Tree cover, flooded, saline water | 0.45 |
| **Grassland** | 0.77 | Mosaic herbaceous cover (>50%) / tree and shrub (<50%) | 0.40 |
| | | Grassland | 0.80 |
| **Wetland** | 0.85 | Shrub or herbaceous cover, flooded, fresh-saline or brakish water | 0.85 |
| **Settlement** | 0.00 | Urban | 0.00 |
| **Other** | 0.17 | Shrubland | 0.30 |
| | | Lichens and mosses | 0.15 |
| | | Sparse vegetation (tree, shrub, herbaceous cover) | 0.20 |
| | | Bare areas | 0.10 |

**Table 2** The percentages of terrestrial land with richness loss under SSPs (%)

| SSPs | Terrestrial vertebrates | Amphibians | Mammals | Birds |
|---|---|---|---|---|
| SSP1 | 45.98 | 40.90 | 42.94 | 38.92 |
| SSP2 | 46.00 | 40.52 | 42.62 | 38.94 |
| SSP3 | 45.82 | 40.75 | 42.82 | 38.61 |
| SSP4 | 45.85 | 40.21 | 42.37 | 38.75 |
| SSP5 | 46.29 | 41.13 | 43.07 | 39.16 |

**Table 3** Contributions of climate and land-use change on future richness changes of terrestrial vertebrates (%)

| Biomes | SSP1 | | SSP 2 | | SSP 3 | | SSP 4 | | SSP 5 | |
|---|---|---|---|---|---|---|---|---|---|---|
| | climate change | land-use change | climate change | land-use change | climate change | land-use change | climate change | land-use change | climate change | land-use change |
| **TMB** | 45.32 | 54.68 | 46.50 | 53.50 | 46.46 | 53.54 | 45.91 | 54.09 | 46.33 | 53.67 |
| **TDB** | 46.86 | 53.14 | 47.44 | 52.56 | 49.35 | 50.65 | 47.14 | 52.86 | 51.10 | 48.90 |
| **TSC** | 60.42 | 39.58 | 64.01 | 35.99 | 63.78 | 36.22 | 61.15 | 38.85 | 66.05 | 33.95 |
| **TBM** | 48.40 | 51.60 | 47.31 | 52.69 | 48.10 | 51.90 | 45.59 | 54.41 | 47.95 | 52.05 |
| **TCF** | 54.25 | 45.75 | 51.60 | 48.40 | 53.30 | 46.70 | 52.88 | 47.12 | 52.19 | 47.81 |
| **BRF** | 31.44 | 68.56 | 30.37 | 69.63 | 30.57 | 69.43 | 30.65 | 69.35 | 31.28 | 68.72 |
| **TSG** | 45.84 | 54.16 | 47.04 | 52.96 | 47.64 | 52.36 | 46.36 | 53.64 | 47.36 | 52.64 |
| **TGS** | 65.98 | 34.02 | 63.99 | 36.01 | 65.72 | 34.28 | 65.45 | 34.55 | 64.77 | 35.23 |
| **FGS** | 62.94 | 37.06 | 66.03 | 33.97 | 62.62 | 37.38 | 65.80 | 34.20 | 68.78 | 31.22 |
| **MGS** | 59.84 | 40.16 | 58.13 | 41.87 | 59.65 | 40.35 | 58.53 | 41.47 | 60.88 | 39.12 |
| **TDA** | 40.28 | 59.72 | 39.78 | 60.22 | 39.12 | 60.88 | 38.42 | 61.58 | 36.38 | 63.62 |
| **MWS** | 61.50 | 38.50 | 63.82 | 36.18 | 62.25 | 37.75 | 60.71 | 39.29 | 58.38 | 41.62 |
| **DXS** | 40.72 | 59.28 | 42.65 | 57.35 | 42.82 | 57.18 | 42.87 | 57.13 | 41.27 | 58.73 |
| **MGS** | 53.53 | 46.47 | 53.02 | 46.98 | 52.87 | 47.13 | 51.45 | 48.55 | 54.84 | 45.16 |

Note: TMB, TDB, and TSC denote the biomes of Tropical and Subtropical Moist Broadleaf Forests, Tropical and Subtropical Dry Broadleaf Forests, and Tropical and Subtropical Coniferous Forests. TBM, TCF and BRF represent the biomes of Temperate Broadleaf and Mixed Forests, Temperate Coniferous Forests, and Boreal Forests/Taiga. TSG, TGS, and FGS are the biomes of Tropical and Subtropical Grasslands, Savannas, and Shrublands, Temperate Grasslands, Savannas, and Shrublands, and Flooded Grasslands and Savannas. MGS, TDA, and MWS are the biomes of Montane Grasslands and Shrublands, Tundra, and Mediterranean Forests, Woodlands, and Scrub. DXS and MGV are the biomes of Deserts and Xeric Shrublands and Mangroves, respectively. The abbreviation of terrestrial biomes also can be referred to SI. Table 2.