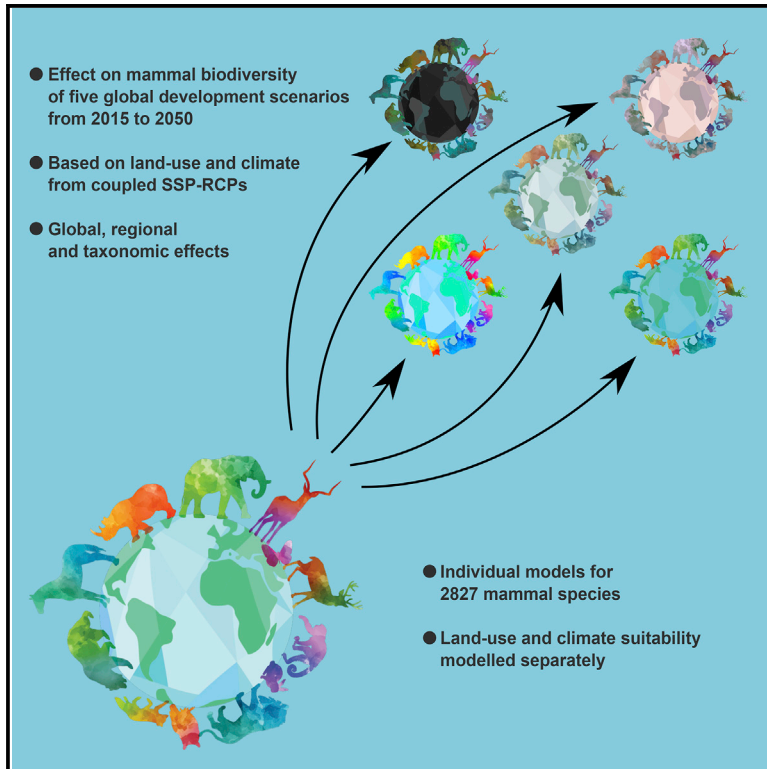


# Projected Global Loss of Mammal Habitat Due to Land-Use and Climate Change

## Graphical Abstract



## Highlights

- By 2050, mammal habitat is expected to decline globally by 5%–16% of the 2015 level
- Africa and South America are expected to be the most affected regions
- Tackling this loss would require a mix of actions across scales

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## In Brief

We used the InSiGHTS framework to model impacts of land-use and climate change on future habitat for 2,827 terrestrial mammals under five contrasting global scenarios based on combinations of representative concentration pathways and shared socio-economic pathways, between 2015 and 2050. Mammal habitat declined globally by 5%–16% depending on the scenario and regionally up to 25%. Tackling this loss would require a mix of actions across scales, including a global shift toward sustainability, addressing land-use change, and helping endemic species track climate change.



## Article

# Projected Global Loss of Mammal Habitat Due to Land-Use and Climate Change

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**SCIENCE FOR SOCIETY** Human pressure is the main driver of modern biodiversity loss. Biodiversity and ecosystem services are universally agreed to be a precious resource for human societies and essential for human survival. Global scenarios of societal development can help us understand the implications of international policies on nations' abilities to secure access to food, energy, and resources, but they commonly ignore impacts on biodiversity. It is therefore essential that we be able to understand and anticipate the possible effects of these decisions on biodiversity. We find that a single strategy might have widely different impacts on biodiversity in different world regions. Also, seemingly valid strategies (from a societal perspective) could have serious negative repercussions on mammals, with expected losses of between 5% and 16%. A great deal of cooperation and more ambitious strategies than the ones currently being studied will be needed if we are to avoid the greatest impacts on the world's species.

## SUMMARY

Human pressure on the environment is driving a global decline of biodiversity. Anticipating whether this trend can be reverted under future scenarios is key to supporting policy decisions. We used the InSiGHTS framework to model the impacts of land-use and climate change on future habitat availability for 2,827 terrestrial mammals at 15 arcmin resolution under five contrasting global scenarios based on combinations of representative concentration pathways and shared socio-economic pathways between 2015 and 2050. Mammal habitat declined globally by 5%–16% depending on the scenario. Africa (with declines up to 25%) and South America were the most affected regions. African insectivores, primates, Australian carnivorous marsupials and marsupial moles, and South American opossums declined the most. Tackling this loss would require a mix of actions across scales, including a global shift toward sustainability, addressing land-use change in sub-Saharan Africa, and helping endemic species track climate change in South America.

## INTRODUCTION

Anthropogenic pressures on the environment are driving a global decline of biodiversity.<sup>1</sup> Globally, vertebrate population abundances have been declining for decades with an estimated reduction of 60% since 1970<sup>2</sup> and a consequent increase in extinction risk.<sup>3</sup> The main direct drivers of current decline have been identified and include habitat loss (the threat with the highest relative frequency among vertebrates), overexploitation, invasive species, and pollution.<sup>4</sup> Climate change is projected to match these drivers in intensity and possibly outpace them

in the next 50 years.<sup>5</sup> One-quarter of the 5,692 species of mammals are threatened with extinction,<sup>4</sup> and recent increases in human pressure have pushed them closer to extinction.<sup>6</sup> If the trend continues, the rate of defaunation and species extinctions would be equivalent to that of the five mass-extinction events.<sup>7</sup>

Halting biodiversity loss has been on the international agenda for more than 25 years,<sup>8</sup> and goals and targets for biodiversity conservation have been set and updated over time.<sup>9,10</sup> Addressing the direct drivers of biodiversity decline has a positive impact, and the trajectory of decline would have been steeper in the absence of conservation action, but it is insufficient.<sup>3</sup> It has



thus been proposed that halting or reverting the trend of decline would require transformational socio-economic changes to reduce anthropogenic pressures on the environment.<sup>11–14</sup> Demographic trends, economic and technological development, and governance are in fact the indirect drivers that represent the root causes of all important direct drivers of biodiversity loss.<sup>15</sup>

Representative concentration pathways (RCPs) are a set of pathways of climate forcings (greenhouse gas concentrations and land use) developed for the climate-modeling community as a basis for scenario modeling.<sup>16</sup> RCPs have been translated by climate modelers into climate projections with the use of global circulation models (GCMs). Shared socio-economic pathways (SSPs) have been produced by the climate-change research community to describe alternative scenarios of socio-economic development.<sup>17</sup> The five SSP narratives encompass a wide range of uncertainty in indirect drivers of change. SSPs can be coupled in a scenario matrix architecture with climate scenarios based on RCPs.<sup>17</sup> Given that species' habitat can be described in terms of climate and land use, coupled SSP-RCP scenarios can be used for projecting the response of species to changes in indirect drivers.<sup>18</sup> Biodiversity models applied to global change scenarios of indirect drivers provide the tools to support international policy decisions on broad pathways of socio-economic development.<sup>19</sup> Exploratory scenarios based on plausible futures have already proved invaluable for agenda setting and policy formulation in biodiversity, energy, climate, and agricultural research.<sup>20–24</sup>

The effects of global change on biodiversity are mostly projected to be negative.<sup>25,26</sup> A review of published studies found that climate change alone is projected to drive extinction up to 16% of the world's species under high (4.3°C) temperature increase.<sup>27</sup> Decreases in abundance and local extinctions are projected worldwide under a business-as-usual scenario for land-use change,<sup>5,28</sup> where losses are concentrated in biodiversity-rich but economically poor countries. Scenarios based on InSiGHTS (Integrated Scenarios of Global Habitat for Terrestrial Species), a modeling framework that combines the impacts of climate change and land-cover change on future habitat availability, showed that business as usual will result in accelerating range and abundance declines in terrestrial mammalian carnivores and ungulates and that radical changes in production and consumption are required to reverse this loss by 2030.<sup>14,29</sup>

Here, we extended previous work by applying InSiGHTS to the majority of terrestrial mammals with the new SSP and RCP scenarios. We obtained land-use and climate layers representing SSP and RCP scenarios for the years 2015 and 2050 from the Land Use Harmonization project version 2 (LUH2)<sup>30,31</sup> and WorldClim 1.4,<sup>32</sup> respectively. Land-use scenarios under SSP-RCP couplings are primarily driven by SSPs but were projected in order to align with the associated RCP;<sup>18</sup> we therefore interpreted the species' responses to RCP scenarios as direct responses to climate change and their responses to SSP scenarios as direct responses to land-use change (which includes indirect feedbacks from climate change). We used these as inputs for the InSiGHTS modeling framework in order to measure species-specific area of habitat (AOH) at a resolution of 15 arcmin for 2,827 terrestrial mammals. These represent all mammals for which we could model both climate and habitat suitability. We

developed and calculated the InSiGHTS index (*ii*), a metric of change in habitat availability, and applied it across five SSP-RCP scenarios. Results were aggregated globally and at the level of IPBES (Intergovernmental science-policy Platform on Biodiversity and Ecosystem Services) regions and subregions.<sup>33</sup> We identified the regions and taxonomic orders projected to undergo the most significant changes in habitat availability for terrestrial mammals.

## RESULTS

### Mammal Habitat Declined in All Scenarios

Global habitat availability for mammals declined in all five scenario combinations from 2015 to 2050. SSP1-RCP2.6 (sustainability) had the least impact, driving a median *ii* decrease of 5%, whereas SSP2-RCP4.5 (middle of the road), SSP3-RCP6.0 (regional rivalry), SSP4-RCP6.0 (inequality), and SSP5-RCP8.5 (fossil-fueled development) resulted in median *ii* decreases of 10%, 12%, 11%, and 16%, respectively (Figure 1).

When the direct effects of land-use change and climate change on habitat availability were quantified separately, the direct effect of climate change appeared as the main driver of loss. Climate change resulted in median *ii* declines of between 5% and 11%, whereas land-use change resulted in median *ii* declines of between 0% and 5% across the five scenarios (Figure S1). Land-use change increased the amount of habitat available to 43%, 15%, 18%, 22%, and 19% mammal species under SSPs 1, 2, 3, 4, and 5, respectively.

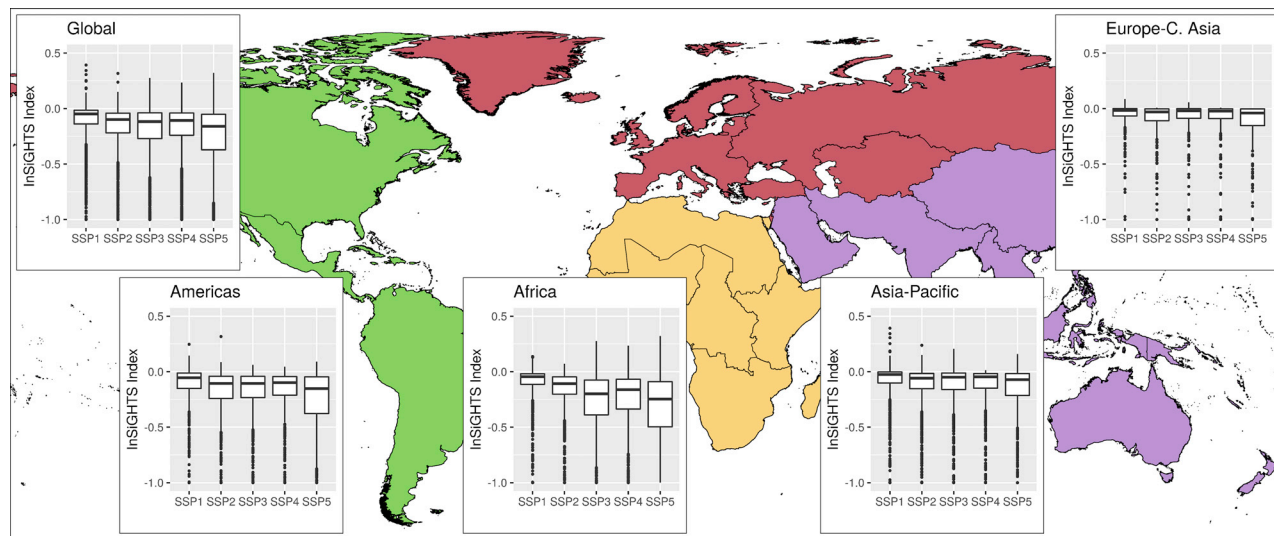
### Projected Declines Are Highest in Africa and South America

With median *ii* declines between 5% and 25% under the five scenarios, Africa was the IPBES region suffering the greatest impact (Figure 1). Africa was the only region where the SSP3-RCP6.0 scenario had a higher impact than SSP4-RCP6.0 (Figure 1), and this impact was driven by land-use change (Figures S2 and S3). In general, land-use change had the largest impact in Africa among all IPBES regions (Figure S3). The SSP2-RCP4.5 scenario had the highest impact in North Africa, the SSP3-RCP6.0 scenario had the highest impact in Southern Africa, and the SSP5-RCP8.5 scenario had the highest impact in Central, East, and West Africa (Figure 2).

With median losses between 5% and 15% across the five scenarios, the Americas were the second most affected region (Figure 1). Losses in this region were predominantly driven from South America (median losses between 8% and 22% and the highest losses under SSP2-RCP4.5 and SSP5-RCP8.5) given that for all other American subregions, median losses under the five scenarios were contained between 0% and 4% (Figure 2). Notably, SSP4-RCP6.0 had a higher impact than SSP5-RCP8.5 for North America.

The Asia-Pacific region had median *ii* declines of between 3% and 7% (Figure 1). Continental subregions (North-East Asia, South Asia, and West Asia) showed more limited losses (medians across SSPs 1–5 between 0.2% and 3%; Figure 1), whereas Oceania suffered the greatest losses in the region (medians between 8% and 14%).

With median *ii* declines between 2% and 4%, Europe and Central Asia were the least affected IPBES regions (Figure 1).



**Figure 1. InSiGHTS Index of Habitat Availability for Terrestrial Mammals for the Five Combined SSP-RCP Scenarios**

The InSiGHTS index was calculated for years between 2015 and 2050 globally and across IPBES regions. The median, interquartile range, and outliers (more than 1.5 times the interquartile range from the interquartile range limits) are represented in boxplots. SSP1, SSP2, SSP3, SSP4, and SSP5 stand for the following scenario combinations, respectively: SSP1-RCP2.6, SSP2-RCP4.5, SSP3-RCP6.0, SSP4-RCP6.0, and SSP5-RCP8.5. See also [Figures S1–S3](#).

Impacts within the three subregions (Central and Western Europe, Central Asia, and Eastern Europe) were similar ([Figure 2](#)).

### Mammalian Taxa that Suffered the Highest Impact

We observed marked variations in the response across taxonomic orders ([Figure 3](#)). Afrosoricida and Notoryctemorphia suffered particularly steep declines with a median *ii* reduction of more than 50% under all scenarios. Dasyuromorphia, Didelphimorphia, and Primates also showed substantive declines under all scenarios.

### DISCUSSION

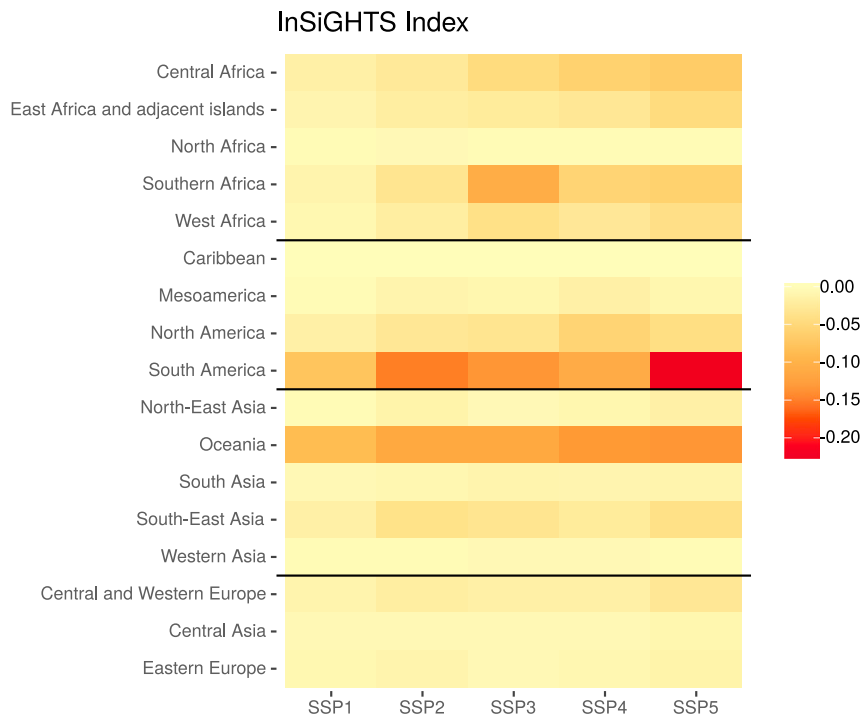
Under all the combinations of climate and land-use change scenarios that we explored, the habitat available to mammals declined globally between 2015 and 2050, but there were significant differences among scenarios. Under SSP1-RCP2.6, the sustainability scenario, we projected the smallest impact on habitat availability for mammals globally. This is consistent with the fact that this combination of scenarios corresponds to the lowest greenhouse gas emissions and lowest climate change<sup>16</sup> and to an expansion of forest and other natural land at the expense of cropland and pasture.<sup>17</sup> The potential effectiveness of sustainable pathways in reducing the pace of biodiversity loss has been demonstrated before.<sup>5,28</sup> This article expands on previous work by including the majority of large and small terrestrial mammals (2,827 mammal species here versus ca. 400 species of large mammals)<sup>28</sup> and by modeling the impacts of land-use and climate change individually on each species rather than modeling the general impact on vertebrate species richness.<sup>5</sup> At the other extreme of the range of scenarios, the SSP5-RCP8.5 scenario combination (fossil-fueled development) projects the highest emissions of greenhouse gases and a mean global temperature increase of 4.8°C by 2100<sup>22</sup> in association

with the highest increase in human population, as well as in agricultural land and pasture at the expense of forest and other natural land.<sup>17</sup>

The impacts of the combined climate and land-use change scenarios varied regionally. In Africa, SSP3-RCP6.0 had a higher impact on habitat available to mammals than everywhere else, and this impact was driven mostly by land-use change in Southern Africa. This result is in accordance with previous scenario analysis that projected high losses of mammalian habitat in sub-Saharan Africa as a result of conversion of savannas to cultivated land.<sup>28</sup> Under regional competition scenario archetypes (which include the SSP3-RCP6.0 scenario), Africa's population is projected to double by 2050 to approximately 2.5 billion people,<sup>34</sup> and the increased food demand would have to be met by local and regional markets.

Oceania and South America suffered high losses of mammalian habitat across all scenarios. Most of the mammalian species living in Oceania are endemic, and many of them have restricted geographic distributions confined to relatively small islands.<sup>35</sup> Average temperatures in this region have increased, particularly since 1950,<sup>36</sup> with a consequent increase in drought severity and negative effects on fire regimes and flooding.<sup>37</sup> In the face of increasing climate change, island species are unlikely to be able to track their climate and move into new suitable areas. Therefore, the high rates of temperature change that these species are likely to experience in the coming decades will have deleterious consequences for their survival.<sup>28</sup> South America was particularly susceptible to SSP5-RCP8.5 such that half of its species locally lost more than 20% of their total habitat and one-quarter lost more than 50%. This could be the effect of high climate velocity in the lowland portion of the Amazon basin,<sup>38</sup> leading to rapid loss of climatically suitable habitat for mammals.

Habitat loss was not distributed uniformly across taxa. Afrosoricida (Southern African golden moles and Madagascan



**Figure 2. Median InSiGHTS Index of Habitat Availability for Mammals across IPBES Subregions for Five Combined SSP-RCP Scenarios**

The InSiGHTS index was calculated for years between 2015 and 2050. SSP1, SSP2, SSP3, SSP4, and SSP5 stand for the following scenario combinations, respectively: SSP1-RCP2.6, SSP2-RCP4.5, SSP3-RCP6.0, SSP4-RCP6.0, and SSP5-RCP8.5.

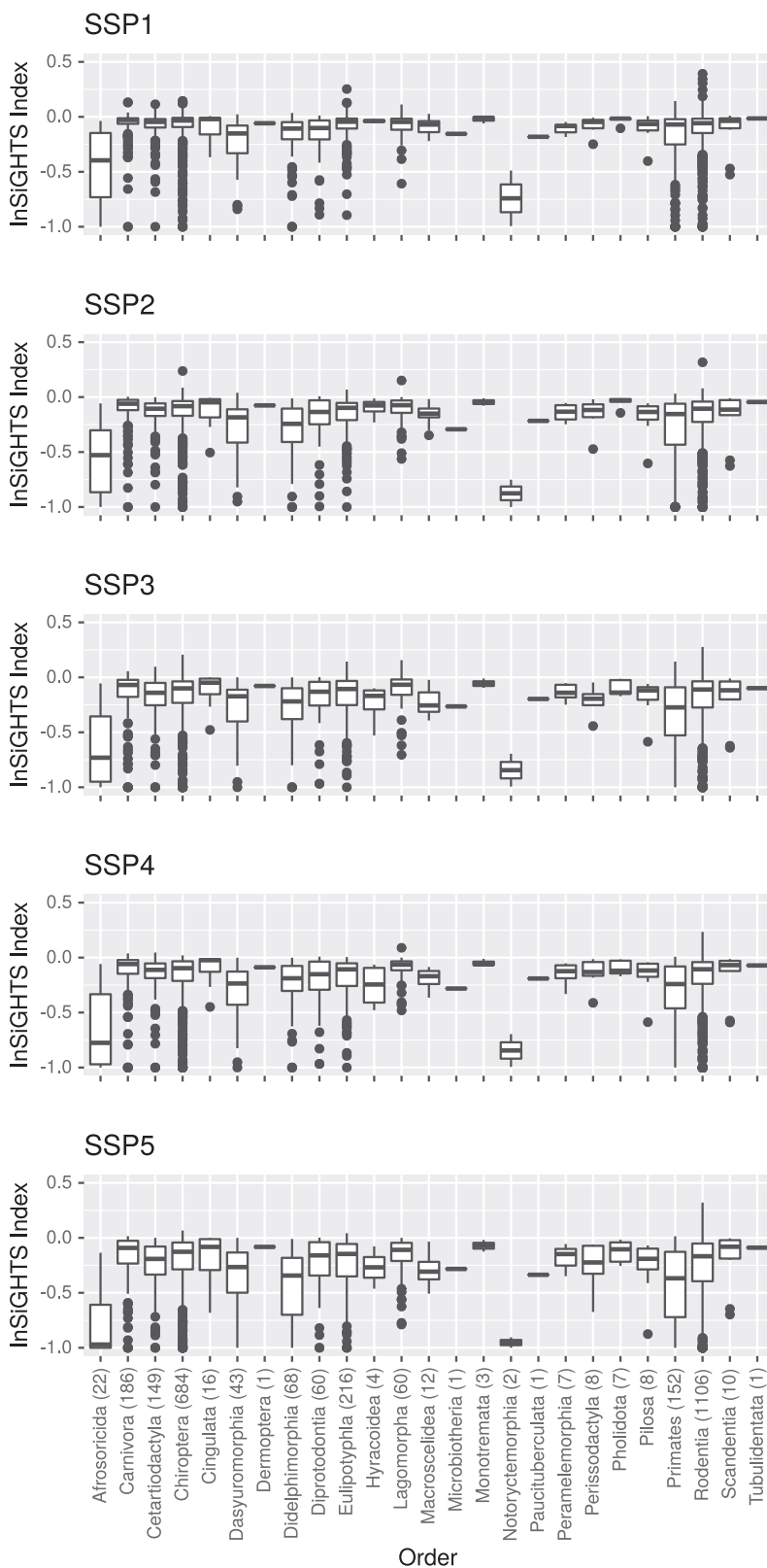
of one climatically suitable pixel produced an effect equal to the loss of four suitable land-use pixels. However, this result is consistent with previous research<sup>5</sup> predicting that the effects of climate change will match or exceed those of land-use change in the next decades.

The InSiGHTS framework combines a number of models and modeled inputs, and all introduce potential errors and uncertainties in the output. Some of them are shared across most biodiversity models that project into the future. For example, climate-envelope models assume,

among others, that the species' observed climatic niche is representative of the fundamental niche and that species respond to climate independently from other species.<sup>41</sup> Projections of land use and climate are highly uncertain.<sup>42,43</sup> LUH2 currently provides harmonized land-use models from differing integrated assessment models (IAMs); although the comparison of unaligned IAMs on land-use outputs suggested that inter-model effects can exceed the effect of the scenario variation,<sup>42</sup> it is still unclear how much of this variation still remains after LUH2's harmonization process. Our assumption of no colonization of new habitat outside the geographic range limited the potential expansion of species to the colonization of new habitat inside the range. If the aforementioned climate-envelope model assumptions hold true, this means that our analysis is able to measure climatically driven habitat loss but not climate-driven gains that could only occur through range expansion. Although colonization of new areas outside the current range is possible, its effect would be marginal in 35 years given that the median dispersal distance of mammals is on the order of less than 1 km per generation,<sup>44</sup> which would result in an expansion of one 15 arcmin cell beyond the current range if that cell becomes climatically suitable. In addition, dispersal is limited by biophysical and ecological barriers, including impermeable habitats, human disturbance, and other threats that could impede colonization of new habitats within the projected bioclimatic envelopes. In accordance with our results, a large model inter-comparison exercise showed that most biodiversity models applied to RCP-SSP scenarios project losses across all scenarios irrespectively of the assumptions made and the indicators projected.<sup>23</sup> Finally, in previous applications, the use of three different colonization assumptions in the InSiGHTS model changed only the offset and not the ranks of habitat loss across scenarios.<sup>14,29</sup> Our results on taxonomic orders should also be robust with

tenrecs) were among the taxa that lost more habitat under all scenarios, including SSP1-RCP2.6. Approximately one-third of these species in this taxonomic order is threatened with extinction, a higher proportion than the average 25% estimated across mammals.<sup>4</sup> All their major threats are related to habitat conversion (main drivers include shifting agriculture and urbanization), which was projected fastest in the Southern Africa subregion. Primates also consistently lost habitat across all scenarios, with the exception of limited losses under the SSP1-RCP2.6 scenario. Primates are one of the mammalian orders at highest risk of extinction in that approximately half of the species is threatened, a fraction that has constantly increased in the last decades.<sup>39</sup> Other susceptible taxa include Dasyuromorphia (Australian carnivorous marsupials), Notoryctemorphia (Austrian marsupial moles), Didelphimorphia (South American opossums), and Microbiotheria (represented by just one extant South American species, the monito del monte). This result is in accordance with the finding that Oceania and South America were the subregions suffering the highest losses of habitat for mammals and also highlights the high degree of phylogenetic uniqueness<sup>40</sup> of the biodiversity at risk in these subregions. For some species, mostly among rodents and lagomorphs, habitat availability was projected to increase slightly. This expansion is likely due to the expansion of agricultural areas, which are suitable to generalist species that live in open areas.

Globally, in our analysis climate change directly affected habitat availability to mammals more than land-use change. Because our study was not designed to compare the direct effects of the two drivers, we interpret this result cautiously. The most likely reason for this result is that RCP climate scenarios project far more change than SSP land-use scenarios,<sup>23</sup> and this is reflected in the results. Furthermore, the resolution of climatic models was coarser than that of habitat models, so the loss



**Figure 3. InSiGHTS Index of Habitat Availability for Mammals for Taxonomic Orders**

Impacts for the mammalian taxa (number of species in parentheses) are shown for the five combined SSP-RCP scenarios between 2015 and 2050. The median, interquartile range, and outliers (more than 1.5 times the interquartile range from the interquartile range limits) are represented in boxplots. SSP1, SSP2, SSP3, SSP4, and SSP5 stand for the following scenario combinations, respectively: SSP1-RCP2.6, SSP2-RCP4.5, SSP3-RCP6.0, SSP4-RCP6.0, and SSP5-RCP8.5.

regard to the assumption of no colonization given that the orders that lost more habitat are well known to be poor dispersers.

The InSiGHTS index we used to summarize species-specific results across regions presents a number of advantages over simpler indexes. First, compared with simple measures of proportional change (e.g., change in regional AOH divided by the region's original AOH), it can be calculated even for sites where the species is not originally present. This metric can therefore be used in modeled scenarios where site colonization is a possible outcome. Second, the score is normalized to a reference status, allowing for local-to-global direct comparisons of impact across species with widely differing ranges or across regions with differing surfaces. Third, for any one species, the score within a larger region can be obtained by simple addition of all sub-regional scores. Fourth, the sum of all local scores for any one species converges to a global proportion of change. Fifth, the index is adimensional, and any measure of abundance can be used in place of AOH.

## Conclusion

Pathways of sustainable development more aggressive than SSP1-RCP2.6 might be needed to bend the curve of biodiversity loss.<sup>45</sup> For mammals in particular, a mix of actions at different scales, in addition to a global shift of socio-economic development pathways toward sustainability and climate-change mitigation, would be needed. At the regional level, addressing land-use changes projected in sub-Saharan Africa will be especially important. Locally, conservation action to help endemic mammals in tracking climate change in Oceania and South America should receive special consideration.

## EXPERIMENTAL PROCEDURES

### Resource Availability

#### Lead Contact

Further information and requests for resources and reagents should be directed to and will be fulfilled by the Lead Contact, Daniele Baisero ([daniele.baisero@gmail.com](mailto:daniele.baisero@gmail.com)).

#### Materials Availability

This study did not generate new unique materials.

#### Data and Code Availability

The datasets and code supporting the current study have not been deposited in a public repository but are available from the Lead Contact on request.

### Climate Data

Bioclimatic layers from average climatic conditions in the years 1986–2005 presented in a previous paper<sup>14</sup> were used as present conditions. Climate forecasts for the year 2050 for RCP scenarios 2.6, 4.5, 6.0, and 8.5 were obtained in the form of bioclimatic variables at a resolution of 30 arcmin from WorldClim 1.4.<sup>32</sup> For each RCP scenario, the median value of climate layers from the 13 GCMs that provided all four RCP scenarios was taken per cell. The rationale for this was to mitigate the large uncertainties that can be found between different GCMs in climate-change projections.<sup>46</sup>

### Land-Use Data

Forecasts of land-use change were obtained from LUH2 (<http://luh.umd.edu>). LUH2 estimates the fractional land-use patterns and the underlying land-use transitions annually for the time period 850–2100 at 15 arcmin resolution, resulting in 12 land-use classes. The five SSPs represent contrasting narratives of plausible futures and have been developed by different IAMs: IMAGE for SSP1 (sustainability), MESSAGE-GLOBIOM for SSP2 (middle of the road), AIM for SSP3 (regional rivalry), GCAM for SSP4 (inequality), and REMIND-MAGPIE for SSP5 (fossil-fueled development).<sup>17</sup> We used snapshots for the

years 2015 (present) and 2050. We associated each SSP scenario to one RCP scenario as follows:<sup>18</sup> SSP1-RCP2.6, SSP2-RCP4.5, SSP3-RCP6.0, SSP4-RCP6.0, and SSP5-RCP8.5.

### InSiGHTS Modeling Framework

The InSiGHTS framework<sup>14,29</sup> combines (1) a climate-envelope model, used for projecting the boundaries of a species geographic range on the basis of climate suitability and assumptions on a species' capability to move into suitable climatic space with (2) a habitat suitability model, used for projecting the AOH that can be potentially used by a species inside its projected geographic range. Therefore, for each species, a cell inside the range is considered suitable only if it contains suitable climate and suitable land use.

We obtained presence data by regularly sampling a 30 arcmin grid within their native geographic range, downloaded from the IUCN Red List website.<sup>4</sup> We excluded from the analysis all mammals with fewer than 30 presence points and those whose range almost entirely covered a land mass and thus didn't allow us to sample sufficient pseudo-absence points to fit the model. We obtained pseudo-absences by randomly sampling 80% of available points (up to a maximum of 1,000) along a 30 arcmin grid outside the species range but within the biogeographical realm(s) and land masses intersected by the range. The pseudo-absence draw was performed five times. For each pseudo-absences draw, we performed a bootstrapping procedure by keeping 80% of the data to calibrate the model and using the remaining 20% for validation; this process was repeated three times for each pseudo-absence draw.

We fitted climate-envelope models by extracting the present climate from presences and pseudo-absences by using all bioclimatic layers that were not strongly collinear. We excluded isothermality (a ratio between mean diurnal temperature range and annual temperature range, collinear with both of these variables), maximum and minimum temperatures of the warmest and coldest months (collinear with mean temperatures of the warmest and coldest quarters, respectively), and precipitation of the wettest and driest months (collinear with precipitation of the wettest and driest quarters, respectively). The remaining variables are those usually considered most important for modeling species distributions at large scale<sup>47</sup> and include good proxies for extreme events such as droughts, fires, and flooding, which will most likely affect mammal species in the future.<sup>48</sup>

We obtained projected bioclimatic envelopes by extrapolating the fitted models to 2050 climate according to the four RCP scenarios. We fitted and extrapolated the generalized linear and additive models (GLM and GAM) from the R package *biomod2*.<sup>49</sup> We allowed the algorithm to fit up to a third-order polynomial of each variable in the GLM and to fit cubic splines at each knot in the GAM and then created an ensemble of the two models. In total, therefore, we had 30 models for each species, year, and climatic scenario from the combination of two statistical models, five pseudo-absences draws, and three input data resamples. We retained only models that obtained a true skill statistic (TSS)<sup>50</sup> score of 0.8 or higher, and the final climate suitability layer for each species was the cell-wise mode of the models retained.

For each species, we used the 2015 climate envelope from the ensemble model as 2015 distribution. We intersected the projected 2050 envelopes with the 2015 distribution, and only cells with suitable climate in both periods were retained as the projected distribution in 2050. We assumed that species were not able to colonize areas outside their 2015 distribution.

We obtained models of the AOH by translating the species-specific suitability scores<sup>51</sup> to GlobCover version 2.1 to the legend of the LUH2 dataset. For every 15 arcmin cell, we calculated the proportion of suitable land use for each species in the years 2015 and 2050. We intersected habitat suitability in 2015 and 2050 with current and projected distribution, respectively, and then multiplied it by a layer of cell area (excluding water and permanent ice) and a layer of suitable elevation<sup>51</sup> in order to obtain cell-wise AOH.

### InSiGHTS Index (*ii*)

The index is a regionalized measure of proportional change in AOH. The study area (*A*, represented by the world in this analysis) was subdivided in local sub-areas (*a*, represented by an IPBES region or subregion in our analysis). We quantified a species' (*s*) *ii* as the change in local ( $a \in A$ ) AOH between  $t' = 2050$  and the reference year  $t = 2015$  divided by the species' total AOH for the reference year.

$$i_{s,a,t'} = \frac{\text{AOH}_{s,a,t'} - \text{AOH}_{s,a,t}}{\sum_{a \in A} \text{AOH}_{s,a,t}}$$

An  $i$  of  $-1$  indicates that the species has gone globally extinct and can be obtained only if area  $a$  contained the species' entire AOH in the reference year.

## SUPPLEMENTAL INFORMATION

Supplemental Information can be found online at <https://doi.org/10.1016/j.oneear.2020.05.015>.

## ACKNOWLEDGMENTS

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## AUTHOR CONTRIBUTIONS

Conceptualization, C.R.; Methodology, C.R., P.V., and D.B.; Software, D.B., P.V., and M.C.; Validation, D.B., C.R., and M.P.; Writing – Original Draft, D.B. and C.R.; Writing – Review & Editing, C.R., M.P., P.V., and D.B.; Supervision, C.R.

## DECLARATION OF INTERESTS

The authors declare no competing interests.

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