



Bioenergy cropland expansion may offset positive effects of climate change mitigation for global vertebrate diversity

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Climate and land-use change interactively affect biodiversity. Large-scale expansions of bioenergy have been suggested as an important component for climate change mitigation. Here we use harmonized climate and land-use projections to investigate their potential combined impacts on global vertebrate diversity under a low- and a high-level emission scenario. We combine climate-based species distribution models for the world's amphibians, birds, and mammals with land-use change simulations and identify areas threatened by both climate and land-use change in the future. The combined projected effects of climate and land-use change on vertebrate diversity are similar under the two scenarios, with land-use change effects being stronger under the low- and climate change effects under the high-emission scenario. Under the low-emission scenario, increases in bioenergy cropland may cause severe impacts in biodiversity that are not compensated by lower climate change impacts. Under this low-emission scenario, larger proportions of species distributions and a higher number of small-range species may become impacted by the combination of land-use and climate change than under the high-emission scenario, largely a result of bioenergy cropland expansion. Our findings highlight the need to carefully consider both climate and land-use change when projecting biodiversity impacts. We show that biodiversity is likely to suffer severely if bioenergy cropland expansion remains a major component of climate change mitigation strategies. Our study calls for an immediate and significant reduction in energy consumption for the benefit of both biodiversity and to achieve the goals of the Paris Agreement.

global change | species distribution modeling | species richness | macroecology | ISIMIP

Anthropogenic climate change is one of the greatest challenges the world is facing. According to the latest assessment report of the Intergovernmental Panel on Climate Change (IPCC), the likely global average temperature increase between the baseline period of 1986–2005 and 2081–2100 varies between 0.3 and 4.8 °C, with stronger increases on land compared with the ocean surface (1). The projected temperature changes vary considerably depending on the respective greenhouse gas emission scenario (representative concentration pathways, RCPs) used for the climate model simulations, and with higher greenhouse gas concentration scenarios further warming is expected beyond the end of the century. Under the low-level emission scenario RCP2.6, the global mean temperatures might stabilize at a level that is ~1.6 °C warmer in 2100 than during 1850–1900, while under a medium- to high-level emission scenario, such as RCP6.0, temperatures will continue to increase even beyond 2100, reaching a level of around 3 °C higher than the preindustrial period. Due to the expected severe consequences of even the medium climate change scenarios (2), the international community is striving to restrict warming to a minimum level: the basis of the Paris Agreement. This Agreement, outcome of the Climate Summit in

Paris in December 2015, aims for “holding the increase in the global average temperature to well below 2 °C above pre-industrial levels and pursuing efforts to limit the temperature increase to 1.5 °C above pre-industrial levels, recognizing that this would significantly reduce the risks and impacts of climate change” (3). The Agreement entered into force in November 2016 and by November 2018 it had been signed by 197 and ratified by 184 countries.

To date, most assessments of the potential impacts of climate change have focused on medium- to high-level emission scenarios, while the impacts of low-emission scenarios have been only a minor component of climate-impact research (4–6). This is mainly because the vast majority of researchers have anticipated warming levels greater than 2 °C, due to the limited efforts to date to reduce the consumption of fossil fuels and thereby greenhouse gas emissions (7). With the Paris Agreement, the evaluation of potential impacts resulting from a low-emission scenario has become a priority on the research agenda, even though limiting global warming to 1.5 °C remains a great challenge.

Due to its unprecedented velocity, current anthropogenic climate change has been identified as a major threat to global

Significance

Understanding how land-use and climate change interact is of major importance to project the future of biodiversity. We assessed how the global species richness of vertebrates may become affected by these two threats, especially under a scenario following the Paris Agreement, which aims to limit global warming to 2 °C or even 1.5 °C. We found that combined effects of climate and land-use change will be most severe under such a scenario, due to the massive expansion of bioenergy cropland for climate change mitigation. While our findings suggest that the Paris goals will reduce direct climate change impacts on biodiversity, biodiversity will suffer as severely as under a high-level emission scenario if bioenergy remains a major component of climate change mitigation strategies.

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biodiversity (8, 9). Numerous studies have documented changes of species' abundances, phenologies, and geographical distributions in response to climate change (10–12). In addition to this empirical work, an increasing number of studies have explored the potential impacts of future climate change on species, ecosystems, and biodiversity, using various methodological approaches (13–15). The potential implications on species, as summarized in the last IPCC report (2), include poleward and uphill range shifts, changes in abundance, global extinctions, and loss of genetic diversity (16). To date, the low-emission scenarios outlined by the IPCC and agreed upon in Paris have not been a research focus in terms of climate change impacts on biodiversity; instead, most studies have emphasized the severe implications of the high-emission scenarios (17, 18; but see refs. 19–21).

Aside from climate change, biodiversity faces numerous additional anthropogenic threats. In general, land-use and land-cover change, accompanied by the destruction, degradation, and fragmentation of natural habitats, have been the most important drivers of past biodiversity change (8, 22). However, it is now widely acknowledged that climate and land-use change interact, additively or synergistically, to affect biodiversity (23–27). Despite this, studies that consider the interacting effects of both threats remain scarce (e.g., refs. 20 and 28) and are, with very few exceptions (21), not available for low-emission scenarios.

The ambitious goal of reducing the global average temperature increase to less than 2 °C may lead to complex interactions between land-use and climate change (29–31). Many climate mitigation scenarios rely on large-scale bioenergy deployment, among which bioenergy crops are an important component (32–34). Recent land-cover projections for the RCP2.6 emission scenario suggest an increase in the area of bioenergy cropland of more than 600 Mha worldwide until 2100. This equates to more than 4% of the global land area. In contrast, under RCP6.0, the simulated increase in bioenergy cropland is only marginal (5).

Although the expansion of bioenergy cropland is a relatively recent phenomenon, impacts on biodiversity are already apparent. Depending on the prior land use, the effects are mostly negative, especially in tropical regions, where both flora and fauna become impoverished in oil-palm plantations used for bioenergy production relative to natural forests (35, 36). In temperate regions, the replacement of other crops by maize for bioenergy production has negatively affected populations of many farmland birds and mammals (37–39). Although bioenergy crops have an important role in climate change mitigation (32, 40) and may reduce direct impacts from climate change on biodiversity, increasing bioenergy cultivation may accelerate the expansion of high-intensity land use, with potentially severe negative consequences for biodiversity (33, 41).

In summary, it is very likely that the impacts of climate change and of land-use changes resulting from mitigation efforts aimed at combating climate change will influence future biodiversity. However, there are, to the best of our knowledge, no integrated assessments that: (i) consider both of these factors jointly, (ii) are broad in their taxonomic and comprehensive in their spatial coverage, and (iii) explicitly compare low- and high-emission scenarios. Furthermore, the few studies that do try to integrate data on both climate and land-use change have not used harmonized sets of climate and land-use projections (24, 25, 28), but relied on data from disparate scenarios, each of which will have different underlying assumptions (42).

Here, we aim to overcome these deficiencies by evaluating the potential future impacts of climate and land-use change on global species richness of terrestrial vertebrates using consistent climate and land-use impact projections from the Inter-Sectoral Impact Model Intercomparison Project (ISIMIP) (5, 43). We stack climate-based species distribution models to derive species richness estimates for the world's amphibians, birds, and mammals. We then combine these with projections of land-use change to identify areas of high threat intensity (high climate or land-use change) and investigate whether these areas overlap in the future. Furthermore, we assess which proportions of species distributions

are affected by the different threats, and quantify the number of threatened range-restricted species. We focus on two emission scenarios, and study differences in bioenergy cropland and other land-use types (nonbioenergy cropland, pastures). Under the low-emission scenario (RCP2.6) we expect weaker direct effects of climate change and, due to a dramatic increase of bioenergy cropland, stronger impacts of land-use change compared with the high-emission scenario (RCP6.0).

Results

Geographical Patterns of Projected Changes in Species Richness and Land-Use Change. Under a no-dispersal assumption (i.e., assuming that species will not be able to shift their distributions), areas of highest projected climate-driven changes in species richness are located in South America and on New Guinea (reaching potential losses of up to 150 species) (Fig. 1 and *SI Appendix, Fig. S1*). Areas with potential losses of between 20 and 70 species are scattered across all continents. The two emission scenarios (RCP2.6, RCP6.0) are similar regarding the geographical patterns of potential richness change. However, changes are projected to become more pronounced under the high-emission scenario (RCP 6.0). Under a basic dispersal assumption (*Methods* and *SI Appendix, SI Materials and Methods*), changes in projected species richness become less severe in some regions,

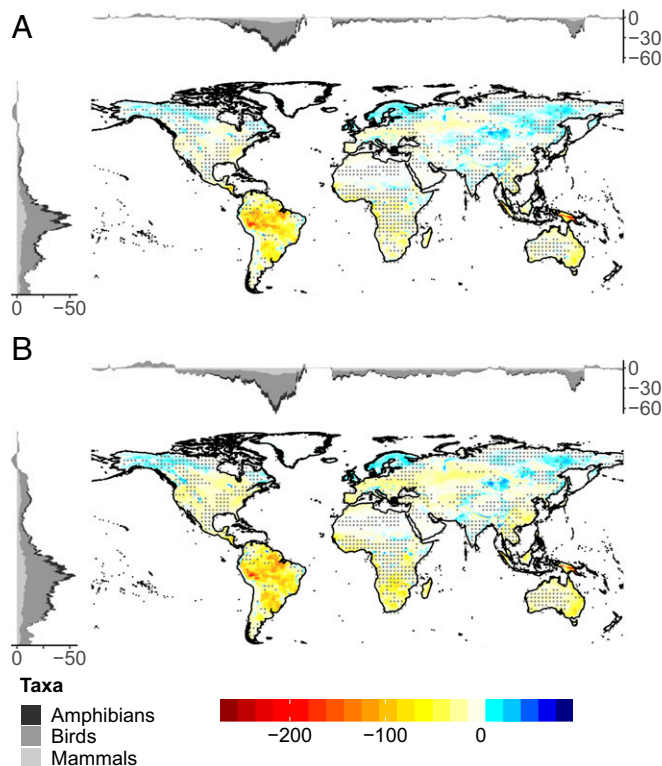


Fig. 1. Spatial patterns of climate-driven change in projected species richness (number of species) for the year 2080 compared with 1995 assuming no dispersal. Results are shown for the two emission scenarios: RCP2.6 (A) and RCP6.0 (B). Barcharts to the left and to the top indicate the change in projected species richness per latitudinal and longitudinal band of 0.5°, separated for the three different vertebrate taxa. Change in species richness was calculated as the difference between 1995 and 2080 in stacked probabilities of occurrence obtained from climate-based SDMs and averaged across two model types and four different GCMs. For a basic dispersal scenario, see *SI Appendix, Figs. S2 and S3*. Stipplings indicate areas with a coefficient of variation (CV) among summed probabilities across eight model type × GCM combinations of less than 10% (see *SI Appendix, Fig. S2* for details). For a version of this figure that highlights the model agreement on the sign of change rather than the CV, see *SI Appendix, Fig. S1*.

and species richness is even projected to increase at high latitudes or altitudes (*SI Appendix, Figs. S2 and S3*). Nevertheless, with few exceptions, the geographical patterns of projected species losses are similar between the two dispersal assumptions. While there was considerable variation among the changes in species richness projected by different species distribution model (SDM) algorithms and global climate models (GCMs), the areas of high potential change in species richness showed comparatively high levels of model agreement (Fig. 1 and *SI Appendix, Figs. S1–S5*; see *SI Appendix, SI Materials and Methods* for further details on species-richness estimates and model validation). The geographical patterns of projected land-use change vary considerably among the two emission scenarios (Fig. 2 and *SI Appendix, Fig. S6*), mainly due to differences in the extent of bioenergy cropland. While under RCP2.6 the percentage cover of bioenergy cropland increases strongly, the projected increase in bioenergy cropland is negligible under RCP 6.0 (see *SI Appendix, SI Results and Discussion* for more details on projected land-use changes).

Spatial Pattern of Threats and Their Overlap. The overall area where species richness is projected to become impacted by either of the threats or any of their combinations does not differ between the low- and the high-emission scenario, except for amphibians, where the area is higher under the low-emission scenario (Fig. 2 and *SI Appendix, Table S1*). Under RCP2.6, vertebrate species richness may become impacted by high-intensity climate and land-use change in about 36% of the world's terrestrial area [amphibians: 35.9 ± 3.94 (SD); birds: 36.2 ± 4.45 , mammals: 36.8 ± 4.97]; under RCP6.0, this figure is also projected to be about 36% (amphibians: 33.6 ± 3.05 ; birds: 37.4 ± 7.92 , mammals: 38.1 ± 7.68) (Fig. 2 and *SI Appendix, Table S1*). The main differences between the RCP2.6 and RCP6.0 emission scenario lies in the individual extent of climate and land-use change threat. Whereas climate change threat is projected to become more extensive under the high-emission scenario, threat from land-use change may become more extensive

under the low-emission scenario. This high level of land-use change threat under the low-emission scenario is mainly due to the large projected increase in bioenergy cropland. Focusing on the overlap between projected impacts from climate change and cropland change (both bioenergy and nonbioenergy), RCP2.6 shows a larger area of potential impact: for these threat combinations, about 5.2% [amphibians: 5.9 ± 0.63 (SD); birds: 4.6 ± 0.84 ; mammals: 5.0 ± 0.86] of the global land area is projected to become impacted under RCP2.6, but only 3.2% (amphibians: 3.1 ± 0.36 ; birds: 3.3 ± 0.65 ; mammals: 3.3 ± 0.69) under RCP 6.0 (*SI Appendix, Table S1*). All of these values decline slightly when a basic dispersal of species is incorporated, but the differences remain consistent (*SI Appendix, Fig. S8 and Table S1*). Areas where nonbioenergy cropland change is projected to overlap with direct climate change impacts are larger under RCP6.0, as are areas where projected changes to pastures overlap with climate change impacts (Fig. 2 and *SI Appendix, Table S1*). The patterns of threat overlap also vary across space, depending on the taxonomic group, the emission scenario, and the land-use type (see Fig. 2 for details). Overall, most areas with high levels of projected climate and land-use change impacts coincide in the tropics. Southwestern South America (mainly the Pampas, Atlantic Forest, and Cerrado regions), Central America, large parts of tropical Africa, and also of south and southeast Asia, including Indonesia and New Guinea, are projected to become highly impacted from different threat combinations, independent of the taxon or the emission scenario.

The Species Perspective. Overall, a slightly larger number of species, of 15,448 species included in the SDM analyses, will potentially be affected by climate threat alone under RCP6.0 [$14,989 \pm 142$ (SD)] than under RCP2.6 ($14,855 \pm 129$), while a much larger number of species will potentially be affected by bioenergy cropland changes alone under RCP2.6 ($10,346 \pm 370$) than under RCP6.0 ($2,054 \pm 279$). Looking at the effects of climate threat and bioenergy cropland expansion (individually and combined), a slightly larger

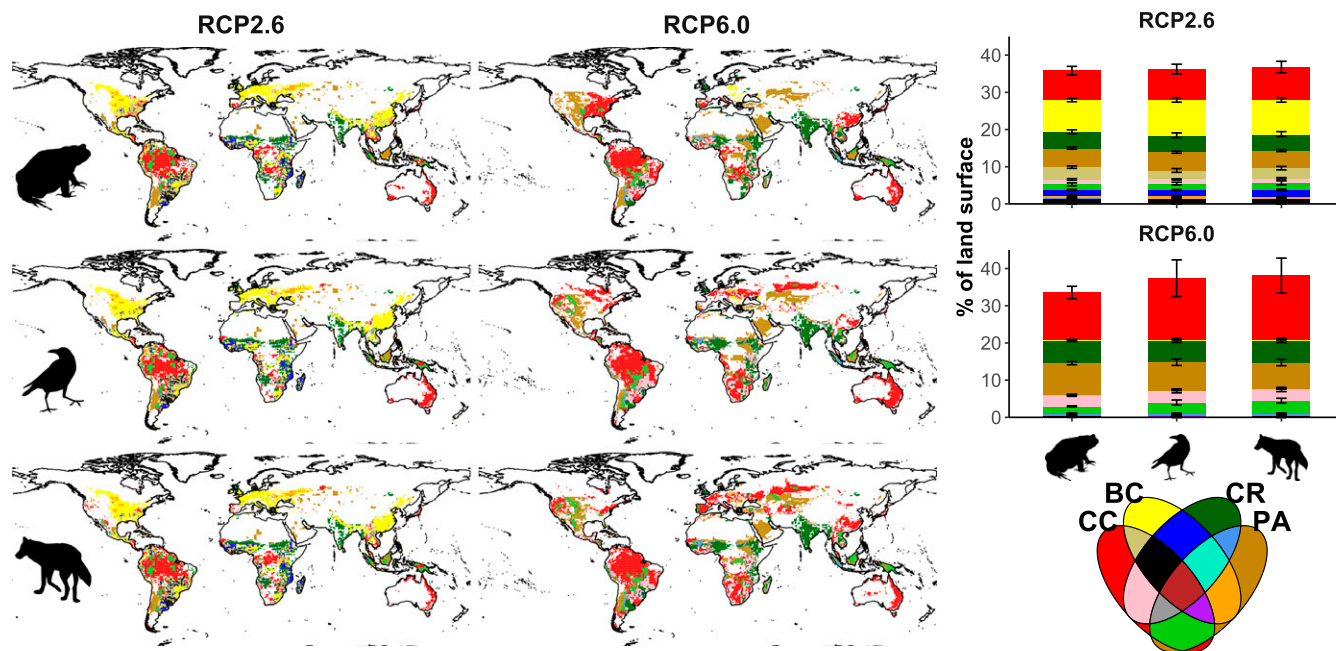


Fig. 2. Spatial distribution and overlap of threat from climate and land-use change for 2080, assuming no dispersal (for a basic dispersal scenario, see *SI Appendix, Fig. S8*). The individual colors indicate the different threats (BC, bioenergy cropland; CC, climate change; CR, nonbioenergy cropland; PA, pastures) and the overlap between each of the threats (see Venn diagram for the color code). Results are shown individually for the three taxa and the two emission scenarios. The map shows the distribution of the threats that are defined for each variable as the (global) top quartile of cells with the highest mean change across RCPs, model types, and GCMs for climate change threat and the top quartile of cells with the highest mean change across RCPs and GCMs for land-use change threat (see *Methods* for further details). For the bar chart, threat areas were identified individually for each of the eight model types \times GCM combinations for climate change threat and for each of the four GCMs for land-use change threat; the bar chart columns show the mean across these eight (four) combinations, with error bars indicating the SDs.

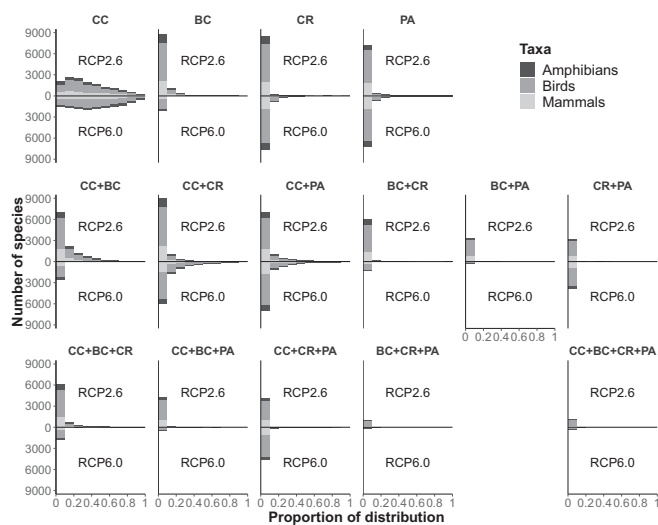


Fig. 3. Mean number of species and the proportion of their distribution which is projected to become affected by climate and/or land-use threat under the two emission scenarios for 2080, assuming no dispersal. Species ranges can be affected by four different threats (BC, bioenergy cropland; CC, climate; CR, nonbioenergy cropland; PA, pastures) or a combination of multiple threats. Results are based on an ensemble mean across the two model types and the four GCMs for the projected climate change impacts, as well as an ensemble mean across the four GCMs for the projected land-use change impacts.

number of species will potentially be affected under RCP2.6 ($15,309 \pm 92$) than under RCP6.0 ($14,994 \pm 140$) (Fig. 3). When investigating the extent to which species distributions are projected to become exposed to different threats, the differences between the emission scenarios, mainly driven by bioenergy cropland changes, are even stronger (Fig. 3). For example, many more species may become directly impacted by climate change individually across larger proportions of their ranges ($\geq 50\%$) under RCP6.0 ($6,063 \pm 634$) than under RCP2.6 ($3,884 \pm 575$). In contrast, under RCP2.6, 1,623 (± 540) species are projected to experience a threat by bioenergy cropland alone within 10% or more of their current distribution, while under RCP6.0, only 3 (± 2) species are projected to experience substantial impacts from bioenergy expansion (Fig. 3).

For the small-range species, similar numbers of species are projected to become exposed to any threat at a high-intensity level under both emission scenarios [RCP2.6 = $4,396 \pm 113$ (SD), RCP6.0 = $4,338 \pm 78$] (SI Appendix, Fig. S9). However, while more species ($1,995 \pm 130$) may become potentially impacted by climate change alone under RCP6.0 than under RCP2.6 ($1,269 \pm 118$), a much larger number of species ($2,310 \pm 68$) occurs in areas where bioenergy cropland is projected to increase under RCP2.6 than under RCP6.0 (107 ± 22) (alone or in combination with other threats) (SI Appendix, SI Results and Discussion and Fig. S9).

Discussion

Our analysis demonstrated that the combined potential impacts of future climate and land-use change for global vertebrate species richness, measured as the area potentially impacted by either of the threats or their combinations, reach similar levels for the low- and the high-emission scenario. Furthermore, larger proportions of species distributions and more species with very small distributional ranges are likely impacted by multiple threats in the future under the low-emission scenario RCP2.6. For this scenario, a strong increase in bioenergy cropland may cause detrimental effects on biodiversity, which are not likely to be compensated by the slight reduction in direct impacts of climate change (compared with the RCP6.0 scenario). Overall, our findings suggest that a climate change mitigation strategy that largely relies on bioenergy crops may lead to impacts on biodiversity at least over similar

geographical extents and for more of the species with the smallest geographical distributions under RCP2.6 than under RCP6.0.

The projected high impact of cropland change on biodiversity, under an extensive climate change mitigation strategy, is in line with numerous studies investigating local conflicts between biofuel expansion and biodiversity (31, 44). Areas with high potential for bioenergy crops tend to overlap with areas of high biodiversity, as well as potential future climate refugia (29, 45). Subsequently, trade-offs between the protection of wildlife habitats, biodiversity hotspots, and other areas of conservation interest and the expansion of biofuel cropland, to mitigate climate change, are frequently unavoidable (46, 47). Although the impact of biofuel cropland expansion on biodiversity depends on a variety of factors as the regional context, location, previous habitat type, as well as the type of bioenergy cropland (48), impacts have been found to be negative across a variety of locations and scales (29, 35, 37, 38).

As we expected, the discrepancy between the low- and high-emission scenarios in the high-threat areas is mainly due to differences in land-use change, and here mainly to the projected change in bioenergy cropland (Fig. 2 and SI Appendix, Figs. S6 and S7). In fact, the maps depicting the different land-use types (SI Appendix, Fig. S6) suggest a shift from pastures to bioenergy cropland in the tropics, and a switch from nonbioenergy to bioenergy cropland in temperate regions and eastern Asia. While we cannot precisely identify the areas where pastures or natural areas are turned into bioenergy cropland, we assume that a potential shift from pastures (which also include extensively used rangeland) to bioenergy cropland (for which we expect a higher cultivation intensity) will be particularly detrimental for biodiversity (38).

Furthermore, under the low-emission scenario, many regions with extensive bioenergy cropland expansion coincide both with global hotspots of biodiversity and areas where species richness is projected to strongly decline because of direct impacts of climate change (Fig. 2). Impacted hotspots include the Atlantic Forest and the Cerrado in South America, Mesoamerica, and parts of western and eastern Africa. While projected changes in nonbioenergy cropland or pastures may also severely threaten species richness, especially under the high-emission scenario (Fig. 2), the extent of the area of any threat and of the area where different threats overlap is particularly large for the combination of bioenergy cropland and climate change (SI Appendix, Table S1).

This geographical pattern is mirrored by the species-based perspective; here the two scenarios showed the most pronounced differences in the high number of species likely becoming exposed to bioenergy cropland change across large proportions of their distributions under RCP2.6. Potentially even more worrying is the observation that under this low-emission scenario almost half of the smallest-range species (which could not be modeled using SDMs) occur in those areas where bioenergy cropland is projected to strongly increase (as single threat or as overlap with other threats). Most of these species are range-restricted amphibians occurring in Central America, the tropical Andes or the Atlantic Forest in South America, around Mount Cameroon in Africa or on Madagascar (SI Appendix, Fig. S14), all of which are areas of highest conservation priority not only for amphibians. While it remains a challenge to better integrate these small-range species into SDMs (49), it is important not to ignore such species, even if the only viable approaches are simplistic. The fact that the vast majority of threatened species are also small-range species (50) makes them even more vulnerable to high intensities of land-use and climate change.

Potential decreases of species richness due to direct impacts of climate change were larger under the high-emission scenario. However, regions with significant levels of potential species loss emerge already under the low-emission scenario. The relatively small differences between the scenarios and their consistent spatial patterns are probably due to the fact that even though by 2080 the scenarios differ in the global average warming by about 1°C (RCP2.6: $+1.64^\circ$; RCP6.0: $+2.6^\circ$; both compared with the 1995 reference period), the climatic variables used for our SDM

analysis show considerable changes also under the low-emission scenario (*SI Appendix*, Figs. S12 and S13). This appears to be sufficient to cause significant changes in species' probabilities of occurrence and thus in projected species richness (Fig. 1).

When comparing the patterns of changes in projected species richness between the two dispersal scenarios, direct impacts from climate change appear to decrease slightly when assuming that species can, to some degree, track areas that become climatically suitable (*SI Appendix*, Figs. S2, S3, and S8). Even though our assumptions are simplified, the differences between the no-dispersal and a basic dispersal assumption highlight the importance of dispersal as a potential pathway to respond to climate change (51, 52). In a world of multiple interacting anthropogenic threats to biodiversity, responses via dispersal are, however, impeded by the effects of land-use change, in particular habitat fragmentation (24). Thus, identifying regions that may gain species dispersing from elsewhere or that contain potential dispersal corridors (e.g., ref. 53) and assessing to which extent these regions may be exposed to high levels of land-use change should be a high priority for global conservation efforts.

Our study reveals clear trends that do not appear to be subject to large effects of model uncertainty (Figs. 1 and 2 and *SI Appendix*, Figs. S6, S7, and S18) and we invested considerable effort to account for uncertainties that potentially confound SDM results, such as pseudoabsence selection, spatial autocorrelation, or naive assumptions about unlimited dispersal (*SI Appendix*, *SI Materials and Methods*). However, several data-related and methodological issues need to be borne in mind when interpreting our findings (*SI Appendix*, *SI Results and Discussion*). Consequently, a study like ours can only outline broad trends by relying on simplified assumptions and has to refrain from locality- or species-specific interpretation of the results.

In a world of anthropogenic global change, interactive effects among different threats can be expected, including synergies and trade-offs (33, 54). These interactions may vary under different scenarios of global warming: weaker direct impacts of climate change may be overruled by stronger effects of the mitigation efforts needed to combat global warming. Our analysis suggests that a low-emission scenario does not necessarily decrease the combined negative effects of climate and land-use change on biodiversity compared with a high-emission scenario, a finding consistent for both the geographic and the species-based perspectives (Figs. 2 and 3). Importantly, the strong effects under the low-emission scenario are in fact due to efforts for climate change mitigation, namely to the massive expansion of bioenergy cropland. Averaging across the four GCMs we used for the low-emission scenario (RCP2.6) results in a global mean temperature increase of approximately 1.6 °C until 2080 compared with our 1995 baseline, which corresponds to an average warming level of approximately 2.1 °C compared with preindustrial conditions (1). Keeping the warming level below 2 °C or even 1.5 °C likely requires even more mitigation efforts, such as additional expansion and intensification of bioenergy agriculture, with consequences for biodiversity that may be even more severe than those suggested by our analysis.

From a biodiversity perspective, the overarching goals of the Paris Agreement (3) are very much worth pursuing, as climate change remains one of the largest threats for global biodiversity. However, biodiversity is likely to suffer severely if bioenergy cropland expansion continues to play a major role in climate change mitigation efforts. Our findings highlight the urgent need to carefully consider biodiversity when expanding bioenergy cropland. On a more general note, an immediate and significant reduction in energy consumption to reduce the need for fossil fuel and bioenergy production appears to be challenging (34), but the ideal strategy for both protecting biodiversity and achieving the Paris goals.

Methods

SDMs. We obtained species distribution data for amphibians, mammals, and from refs. 55 and 56. Climatic data were obtained from the ISIMIP project (5, 57) (see *SI Appendix*, *SI Materials and Methods* for further details on all data used). We used two types of SDMs, generalized boosted regression models (GBM) and generalized additive models (GAM), to model the relationship between the bioclimatic variables and current species' distributions. These two widely used

models were selected due to their good performance compared with other modeling approaches (58–60) and to provide a contrast between an additive model (GAM) and a classification and regression tree-based modeling approach (GBM) (see *SI Appendix*, *SI Materials and Methods* for details on the approaches used, model validation, pseudoabsence selection, and spatial autocorrelation). Species' probabilities of occurrence were projected for current (1995) and future (2080) conditions under the assumption of different dispersal scenarios (see *SI Appendix*, *SI Material and Methods* for the definition of the respective 30-y time periods and details on the dispersal scenarios). Projections of species current and future probabilities of occurrence varied between the different SDM/GCM combinations. To document this variation, we calculated the coefficient of variation among the eight different estimates of projected species richness, based on summed probabilities of occurrence, for each grid cell (*SI Appendix*, Figs. S4 and S5). We also calculated the variation of the changes in mean probability of occurrence, across a species range, among all species for each of the different SDM/GCM combinations (*SI Appendix*, Figs. S10 and S11).

Land-Use Data. To represent land-use, we used ISIMIP2b simulations of current and future land-use associated with the relevant RCPs and GCMs based on the MAGPIE and REMIND-MAGPIE model (61–63), using the assumptions of population growth and economic development as described in Frieler et al. (5). Land-use change models accounted for climate impacts (e.g., on crop yields) and were driven with the same climate input as the SDMs. The ISIMIP land-use scenarios provide percentage cover of six different land-use types (urban areas, rainfed crop, irrigated crop, pastures, as well as rainfed and irrigated bioenergy crops) at a spatial resolution of 0.5° × 0.5°. We averaged annual land-use data for each of the two different time periods (1995 and 2080), across the four GCMs, and combined irrigated and rainfed crop categories into a single crop category.

Climate and Land-Use Threat. We assessed the potential threats to biodiversity from climate and land-use change from a geographical perspective (summarized for each of the three taxa amphibians, birds, and mammals) and from a species perspective.

For the geographical perspective, climate threat was quantified as the change in projected species richness per taxon, calculated as the differences in summed probabilities of occurrence between 1995 and 2080 from the SDMs (Fig. 1 and *SI Appendix*, Fig. S17). For each time period the projected probabilities of occurrence of every species were summed, without prior thresholding and transfer to presence-absence matrices, to avoid the general overestimation of species richness (64). For each taxon, we then calculated the mean projected species richness change across the four different GCMs and the two SDMs. Land-use threat per grid cell was quantified as the mean change in percentage cover across the four GCMs between 1995 and 2080 for each of the three land-use types (bioenergy cropland, nonbioenergy cropland, pastures) (*SI Appendix*, Fig. S6).

To identify areas of high threat intensity from climate and land-use change for vertebrate species richness (high threat, hereafter), we used a spatial threshold approach (23). As high-threat areas, we identified the 25% of all grid cells globally with the highest loss in projected species richness (summed probability of occurrence) as obtained by the SDMs or with the highest increase in percentage cover of the respective land-use type. To allow for a better comparison between the RCPs (RCP2.6 and RCP6.0), GCMs, and model algorithms (GAM, GBM), we first pooled all values for the respective threat and for each grid cell from all these categories and then calculated one 25% cut-off value for each of the four threats and each taxon based on these pooled datasets. We stress that by applying this approach we did not consider the scenarios separately, but combined all grid cells of both scenarios and identified the 25% of cells with the highest negative threat levels for this combined dataset. For example, as the overall increase in bioenergy cropland area is extremely low in RCP6.0, but very high in RCP2.6, this leads to a much larger number of high-threat grid cells in RCP2.6. We highlighted high-threat areas separately for climate change only and land-use change only (the latter separately for bioenergy cropland, nonbioenergy cropland, and pastures), as well as for areas of threat overlap (i.e., for any combination of the four different threats) (Fig. 2 and *SI Appendix*, Fig. S10) separately for each taxon and under the no-dispersal and basic dispersal assumptions.

To assess future potential threats from the species perspective, we quantified the proportion of the current range of each species which is projected to overlap with any given threat (see above for the threat definition). While we excluded species with a range smaller than 10 grid cells from the SDM analysis, we still included these species in our study by assessing the spatial overlap of their ranges with areas of projected high climate and land-use change (see *SI Appendix*, *SI Materials and Methods* for details).

Data Accessibility. The IUCN distribution data are available (55, 56). ISIMIP climate and land-use data are available from the ISIMIP node of the ESG

server (<https://esg.pik-potsdam.de/search/isimip/?product=input>). The model output of the SDMs is publicly available as part of the Terrestrial Biodiversity Sector of ISIMIP (https://esg.pik-potsdam.de/search/isimip/?sector=Terrestrial_Biodiversity). All analyses were done using the statistical software package R. R code of the analysis is available at https://github.com/christianhof/BioSzen1.5_SDM.

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