

RESEARCH ARTICLE

Potential effects of future climate change on global reptile distributions and diversity

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Abstract

Aim: Until recently, complete information on global reptile distributions has not been widely available. Here, we provide the first comprehensive climate impact assessment for reptiles on a global scale.

Location: Global, excluding Antarctica.

Time period: 1995, 2050 and 2080.

Major taxa studied: Reptiles.

Methods: We modelled the distribution of 6296 reptile species and assessed potential global and realm-specific changes in species richness, the change in global species richness across climate space, and species-specific changes in range extent, overlap and position under future climate change. To assess the future climatic impact on 3768 range-restricted species, which could not be modelled, we compared the future change in climatic conditions between both modelled and non-modelled species.

Results: Reptile richness was projected to decline significantly over time, globally but also for most zoogeographical realms, with the greatest decreases in Brazil, Australia and South Africa. Species richness was highest in warm and moist regions, with these regions being projected to shift further towards climate extremes in the future. Range extents were projected to decline considerably in the future, with a low overlap between current and future ranges. Shifts in range centroids differed among realms and taxa, with a dominant global poleward shift. Non-modelled species were significantly stronger affected by projected climatic changes than modelled species.

Main conclusions: With ongoing future climate change, reptile richness is likely to decrease significantly across most parts of the world. This effect, in addition to considerable impacts on species range extent, overlap and position, was visible across lizards, snakes and turtles alike. Together with other anthropogenic impacts, such as habitat loss and harvesting of species, this is a cause for concern. Given the historical lack of global reptile distributions, this calls for a re-assessment of global reptile conservation efforts, with a specific focus on anticipated future climate change.

KEYWORDS

bioclimate, biodiversity, environmental niche model, global warming, ISIMIP, lizard, snake, species distribution model, species richness, turtle

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1 | INTRODUCTION

Emissions from anthropogenic activities have led to an increase in global surface temperature of *ca.* 1°C in the last 100 years. This has already led to changes in weather and the occurrence of climate extremes in every region across the globe (IPCC, 2021). Unless emissions are vastly reduced in the coming decades, global warming will continue and exceed 1.5–2°C compared with pre-industrial levels by the end of the 21st century (IPCC, 2021).

Climate change has already had adverse effects on biodiversity and ecosystem functioning, and these effects are likely to worsen as warming continues in the future (IPBES, 2019; IPCC, 2022). Impacts of climate change on ecological processes at scales ranging from genes to entire ecosystems can affect organisms, populations or entire communities and vary between physiological, morphological, phenological and distributional shifts (Bellard et al., 2012; Scheffers et al., 2016). In particular, changes in species abundance and distribution owing to climate change have already been observed frequently (Bowler et al., 2017; Lenoir et al., 2020), with many species shifting their range towards higher latitudes and elevations (Chen et al., 2011). However, some species also respond to climate change by idiosyncratic range shifts (Gibson-Reinemer & Rahel, 2015).

In the past, most assessments of the impact of climate change on vertebrate biodiversity have focused on endotherms (birds and mammals). Reptiles, although they account for one-third of global terrestrial vertebrate diversity, have largely been ignored (Pacifiçi et al., 2015), and previous assessments of climate change impacts on reptile species have either used only a subset of species (Newbold, 2018; Warren et al., 2018) or have not been of global extent (Araújo et al., 2006). Moreover, global biodiversity assessments often either consider overall effects on a single taxon (Baisero et al., 2020; Voskamp et al., 2021) or compare multiple taxa (Hof et al., 2018; Newbold, 2018; Thuiller et al., 2019; Warren et al., 2018), but only very rarely compare different taxonomic groups within one taxon (but see, e.g., Hof et al., 2011).

In the past, reptiles have also often been neglected when assessing global conservation priorities (Brooks et al., 2006). They are most diverse in arid and semi-arid regions, which suggests that their distributions are driven by ecological and evolutionary processes that differ from other vertebrate taxa, and these regions have previously been unrecognized as conservation priorities because other vertebrate taxa could be protected more efficiently elsewhere (Roll et al., 2017).

Although reptiles as a whole have been found to use similar habitats to mammals and birds (Cox et al., 2022), treating all reptile species as uniform might be problematic because reptile taxonomic groups (lizard, snakes and turtles) exhibit large differences in species richness hotspots (Roll et al., 2017) and habitat use, making them vulnerable to different anthropogenic impacts (Cox et al., 2022).

Given that reptiles are ectothermic, they are likely to be influenced strongly by climate warming, with some species already experiencing body temperatures above their physiological optima. This could indicate a higher vulnerability of these species to climate

warming in comparison to species from cold environments (Diele-Viegas & Rocha, 2018). Nonetheless, temperate species are also likely to be vulnerable, assuming that their physiological adaptations for living in cold environments might hinder their ability to cope with hotter climates (Monasterio et al., 2013). However, previous studies assessing the impacts of climate change on reptile species are biased towards certain species and taxonomic groups and certain zoogeographical realms (Diele-Viegas et al., 2020).

The aim of our research was to provide a detailed account of projected climate change impacts on global reptile distributions and diversity, looking at species-specific changes and at broad-scale geographical trends across and within different taxonomic groups. We assessed changes in reptile species richness globally, within each zoogeographical realm and across their respective climate space. For each species, we also quantified the change in range extent, range overlap and range distribution and again assessed differences across zoogeographical realms and taxonomic groups. Given that we cannot model range-restricted species, we also performed a more general assessment of species-specific changes in climate space across both modelled and non-modelled species.

2 | METHODS

2.1 | Species data

Until recently, global reptile distribution data were unavailable, but this has changed with the release of the global distribution database by the Global Assessment of Reptile Distributions (GARD) initiative (Roll et al., 2017) and, more recently, the release of the full set of International Union for Conservation of Nature (IUCN) reptile range maps (IUCN, 2022). We obtained global range maps for 10,064 reptile species from the GARD initiative (Roll et al., 2017). The range maps cover lizards, snakes, turtles, worm lizards, crocodiles and the tuatara, but in this paper, in an approach similar to that of Roll et al. (2017), we contrast only snakes, turtles and paraphyletic lizards (for simplicity, we subsequently refer to the latter as lizards).

Range maps were gridded to a 0.5° × 0.5° grid in World Geodetic System 1984 (WGS84), to align with the available climate data (see next subsection), considering any grid cell that intersected with a species range polygon as a presence. Given that range maps provide information on the presence of a species but not on its absence, pseudo-absence data for each species were generated by randomly selecting grid cells with no presence, taking a distance-weighted approach, whereby grid cells closer to the range edge were favoured over grid cells further away (see Hof et al., 2018). The number of absences was either equal to the number of presences for species with ≥1000 presences or 1000 absences for species with <1000 presences, because a minimum of 1000 absences considerably increases model performance (Barbet-Massin et al., 2012). For each species, we derived 10 replicate sets of pseudo-absences, to account for the variability in model accuracy because of the random sampling of pseudo-absence data. Barbet-Massin et al. (2012) found

that, depending on the number of pseudo-absences and model algorithm chosen, 5–12 replicates provide the best model quality. Given the relatively high number of pseudo-absences, 10 replicates should thus result in a high quality of our models. We created a separate model for each of these 10 sets, but the results were then averaged across the 10 sets.

2.2 | Climate data

Global bias-corrected daily climate (minimum temperature, maximum temperature and precipitation) data at a spatial resolution of 0.5° (WGS84) were obtained from the meteorological forcing dataset “Earth2Observe, WFDEI and ERA-Interim data Merged and Bias-corrected for ISIMIP” (EWEMBI; Lange, 2016) for current conditions (1980–2009) and from the Inter-Sectoral Impact Model Intercomparison Project phase 2b (ISIMP2b; Frieler et al., 2017) for future simulations (2036–2065 and 2066–2095). Future climate simulations were available from four global circulation models (GCMs; GFDL-ESM2M, HadGEM2-ES, IPSL-CM5A-LR and MIROC5) and for three representative concentration pathways (RCPs; RCP2.6, RCP6.0 and RCP8.5) under the Coupled Model Intercomparison Project Phase 5 (CMIP5). Future climate simulations depend strongly on the GCM used (Watterson, 2019). The four GCMs chosen by ISIMP2b capture a large range of plausible future climate projections from all the different GCMs available (Frieler et al., 2017), and the RCPs represent different emission scenarios depending on the ongoing and future trajectories of global CO₂ emissions (Van Vuuren et al., 2011).

Monthly means of each climate variable over the respective 30-year time periods, centred around 1995, 2050 and 2080, and for each future scenario (GCM and RCP) were used to calculate 19 bioclimatic variables (Supporting Information Appendix S1, Table S1.1) using the `biovars()` function of the “`dismo`” package (Hijmans et al., 2021) in R (R Core Team, 2021). Bioclimatic variables represent annual trends, seasonality and extreme or limiting environmental factors and are thus more biologically meaningful variables than temperature or precipitation alone.

2.3 | Species distribution models

Species distribution models (SDMs) are a common way of assessing species-specific responses to climate change (Guisan & Thuiller, 2005) but are also used to assess the impacts of climate change on biodiversity (Thuiller et al., 2005). SDMs statistically infer a relationship between the observed distribution of a species and the underlying environmental conditions (Elith & Leathwick, 2009) and can then be used to project current distributions into the future (Elith et al., 2010), assuming that the species maintains its climatic niche (Wiens & Graham, 2005). By doing this for multiple species, these projections can be combined to assess future changes in species richness (e.g., Hof et al., 2018).

We fitted SDMs using the presence/pseudo-absence data of a species as the response variable and the derived bioclimatic variables for current (1995) conditions as explanatory variables. The number and choice of explanatory variables used strongly influences the outcome of the SDMs (Petitpierre et al., 2017). We thus adopted a rigorous approach to variable selection. After pre-selecting the 10 most commonly used variables from the literature (see Porfirio et al., 2014), all potential combinations of three and four bioclimatic variables with a low Pearson correlation ($r \leq .7$) were used to model 10% of all species ($n = 987$), which were randomly selected, using a generalized additive model (GAM) approach (see Hof et al., 2018). The model performance of the different variable combinations was tested, and models for all species were fitted using the best-performing variable combination, which was temperature seasonality, maximum temperature of the warmest month, annual precipitation and precipitation seasonality (see Supporting Information Figure S1.1).

Projections based on SDMs vary considerably among model algorithms (Thuiller et al., 2019); therefore, we fitted two different modelling algorithms with good performance and discrimination capacity (Elith et al., 2010; Meynard & Quinn, 2007), an additive model (GAM) and a regression tree-based model [generalized boosted regression model (GBM)].

GAMs were fitted with a Bernoulli response, a logit link and thin-plate regression splines using the “`mgcv`” package (Wood, 2003, 2011) in R (R Core Team, 2021). GBMs were fitted with the “`gbm`” package (Greenwell et al., 2020) in R (R Core Team, 2021), and the optimal parameter settings for learning rate (0.01 and 0.001), tree complexity (1, 2 and 3) and number of trees (1000–10,000) for each species were identified by cross-validation (Bagchi et al., 2013).

Spatial autocorrelation in species distributions can bias parameter estimates and error probabilities (Kühn, 2007). Two different methods were used to account for spatial autocorrelation in the SDMs. Species with ≥ 50 presences were modelled using an ecoregion-blocking approach. Here, the world was divided into 10 blocks based on a representative subset of the climate space across each of the ecoregions of the world (Bagchi et al., 2013; Olson et al., 2001). Subsequently, 10 models per species were built, leaving out one block at a time, using the left-out block for model evaluation (Bagchi et al., 2013). For species with 10–49 presences, we split the data into 10 datasets by repeated random selection of 70% of the data, followed by using the left-out 30% for model evaluation. Species occurring in ≤ 10 grid cells ($n = 3602$; Table 1) were not modelled because the sampling size would be too low to produce meaningful results (Hernandez et al., 2006). Together with the 10 different pseudo-absence sets, this resulted in 100 models for each model algorithm and species.

The performance of the fitted SDMs was evaluated by calculating the overall area under the curve (AUC) for each species (the average AUC across the 10 blocks and the 10 sets of pseudo-absences). Models with an overall AUC $< .7$ were dropped ($n = 166$), which left us with SDMs for 6296 reptile species (Supporting Information Figure S1.2), which represents 62.6% of the total number of available

Taxonomic group	Lizard	Snake	Turtle	Total
Number of species with available data	6328	3414	322	10,064
Number of range-restricted species ($n < 10$, removed)	2536	1047	19	3602
Number of species with low model performance (area under the curve $< .7$, removed)	97	62	7	166
Total number of species modelled	3695	2305	296	6296
Percentage of available species modelled	58.4	67.5	91.9	62.6

TABLE 1 Number of species that were excluded from the species distribution models owing to their restricted range or low model performance.

species from GARD (Table 1). In addition to assessing the model fit of the individual models, we also compared the observed species richness with the projected current richness per grid cell (Supporting Information Figure S1.3) in order to assess the performance of all our models when looking at changes in species richness.

The same modelling approach has been adopted previously to assess the impacts of climate change on amphibians, birds and mammals; see Hof et al. (2018) and Biber et al. (2020). The former paper provides a more detailed explanation of the modelling methodology, and the latter gives a thorough account of the caveats and uncertainties associated with SDMs.

2.4 | Future projections

Future species distributions were projected using the future bioclimatic variables for the two future time periods (2050, 2080), each GCM (GFDL-ESM2M, HadGEM2-ES, IPSL-CM5A-LR and MIROC5), each RCP (RCP2.6, RCP6.0 and RCP8.5) and both model algorithms (GAM and GBM). Model results are presented as the ensemble mean across the four GCMs and two model algorithms considered.

Future projections of each species were limited to the extent of their original and the neighbouring ecoregions to prevent predictions of areas with analogous climatic conditions. Future projections were limited further by applying a species-specific dispersal buffer. For most species considered in this paper, species-specific dispersal distances are unknown (Nathan et al., 2012), hence we used species-specific dispersal buffers that were based on the diameter (d) of the largest range polygon of a species. We used three species-specific dispersal scenarios ($d/4$, $d/8$ and $d/16$; Supporting Information Figure S1.4) and provide a detailed comparison of these in the Supporting Information (Appendix S2). Here, we provide results under a medium dispersal scenario ($d/8$), which corresponds to a mean dispersal distance of 2.4 km/year.

2.5 | Impact analysis

The current and future probabilities of occurrence of the individual SDMs were thresholded into binary presence-absence data using species-specific thresholds according to the true skill

statistic (MaxTSS; Allouche et al., 2006; Supporting Information Figure S1.5d). Thresholded species occurrences were then used to calculate current and future species richness, as well as richness increase, decrease, change and relative change (as a percentage). Richness increase and decrease were identified by using the presence information of each individual species, then summing the number of species that occur newly in a given grid cell (species increase) or species that disappear from the respective grid cell (species decrease).

Summing the thresholded species occurrences frequently overestimates species richness (Calabrese et al., 2014), thus we also present the results using the sum of the raw non-thresholded probabilities of occurrence of each species in the Supporting Information (Appendix S3).

We calculated the projected species richness for each cell of a global grid of $0.5^\circ \times 0.5^\circ$ resolution globally and for each zoogeographic realm, as defined by Holt et al. (2013), for each time period. We then tested for significant changes in species richness over time using Student's paired t-tests with Holm correction. To assess how species richness and richness changes were related to the overall change in climatic conditions, we assessed both parameters against univariate temperature and precipitation, in addition to the interaction of temperature and precipitation conditions. To assess potential future climate effects on individual species, we quantified the percentage of change in range extent, the percentage of range overlap and the direction and distance in range shift. The percentage of change in range extent was calculated based on the projected current and future range extent of a species (Supporting Information Figure S1.5e). The percentage of range overlap was calculated by extracting the total area of spatial range overlap between the projected current and future range extent and dividing it by the projected current range extent (Supporting Information Figure S1.5f). To assess the magnitude of the range shift for each species, we derived the range centroid for both time periods and calculated the distance and direction of the projected range shift (Supporting Information Figure S1.5g).

Given that 37.4% of all reptile species for which data were available could not be modelled (largely owing to their restricted range extent; Table 1), we performed an additional analysis considering all 10,064 species for which data were available. We used the same four bioclimatic variables that we used for the SDMs to transform

the multidimensional climate data to a two-dimensional climate space using the first two axes of a principal components analysis (PCA). PCAs were performed for both current and future conditions, taking into consideration the same GCMs, RCPs and time periods as before. The explained variance of the first two PCA axes was >75% under all scenarios (Supporting Information Figure S1.6). For each scenario combination, we then calculated the Euclidean distance between the two PCA axes of current and future conditions to obtain a measure of climatic change (Supporting Information Figure S1.7). We then extracted the climatic distance for the gridded locations of each species and compared the climatic distance of modelled and non-modelled (range-restricted) species using a Student's unpaired t-test with Holm correction.

Where no specific groups (lizards, snakes or turtles) are mentioned, we present the results for all reptile species together. The Supporting Information (Appendix S4) presents group-specific results. Results are presented for the year 2080 under a medium representative concentration pathway (RCP6.0). A sensitivity analysis with regard to the variation across years and RCPs is shown in the Supporting Information (Appendix S5).

3 | RESULTS

3.1 | Spatial changes

Projected reptile richness (sum of thresholded SDM projections) based on a resolution of $0.5^\circ \times 0.5^\circ$ for current conditions varied between 0 at high latitudes and 251 in the tropics, with particular hotspots in Brazil, Cameroon and Indonesia (Figure 1a). Overall, reptile richness was dominated by lizard species ($n = 3695$), followed by snakes ($n = 2305$), while turtle species made only a slight contribution to the total number of modelled species ($n = 296$; Table 1; Figure 1b).

For future conditions, a large number of reptile species were projected to disappear, and at the same time, a large number of new species were projected to appear in Brazil and Australia, while other regions showed either a strong decrease or increase in species (Figure 1c,d). The greatest future decreases of species richness were projected east of the Caspian Sea and in South Africa (Figure 1c), while strong future increases were projected in the south-west of China and in the eastern USA (Figure 1d). Overall, the projected decrease in richness was greater than the increase in richness, which resulted in a net loss in species richness from 1995 to 2080 (Figure 1c-e). The largest net loss in species richness was projected for Brazil, Australia and South Africa, while the highest net gain was projected for south-west China and the western USA (Figure 1e). Relative change (as a percentage) was projected to be negative (in particular, for most of the Southern Hemisphere), whereas the high northern latitudes showed a strong positive relative change (Figure 1f).

Spatial patterns in the changes in species richness varied greatly across the three taxa, with lizards seeing both strong increases and

decreases in Australia, snakes showing a strong decrease in South America and turtles seeing a strong increase in the eastern part of North America (Supporting Information Figures S4.18 and S4.20). All three taxa showed a net gain in species richness in northern latitudes, while lizards showed the greatest net loss in parts of Australia, snakes in large parts of South America and turtles in parts of South America and southern Africa (Supporting Information Figures S4.19 and S4.21).

3.2 | Global and zoogeographical realm changes

Summed across all $0.5^\circ \times 0.5^\circ$ grid cells globally, species richness was projected to decline significantly ($p < .01$) from 1995 to 2080 globally, with a decline in mean reptile richness per grid cell from 58.4 ± 0.24 (SE) in 1995 to 53.39 ± 0.19 in 2080 (Figures 1b and 2a). Eight of 11 zoogeographical realms showed a significant decline in reptile richness by 2080 (Figure 2b-d,f-h,j,k), while the Nearctic and Palearctic realms showed a significant increase (Figure 2e,i) and the Sino-Japanese realm showed no significant change (Figure 2l).

Looking at the global averages of species richness for each 0.5° grid cell for the three reptile groups separately, snakes had the highest mean species richness ($\mu_{\text{mean}} = 30.4 \pm 0.15$), followed by lizard ($\mu_{\text{mean}} = 24.3 \pm 0.09$ SE) and turtle richness ($\mu_{\text{mean}} = 3.71 \pm 0.02$ SE; Figure 1b; Supporting Information Figure S4.17). Globally, similar to the total reptile richness, the individual taxonomic groups (lizards, snakes and turtles) all showed a significant decline in species richness, while there were slight differences across the individual realms (Supporting Information Figure S4.22-24). Lizards showed a significant increase in richness only in the Palearctic realm and no significant change in richness in the Sino-Japanese realm, while in all other realms they showed a significant decrease (Supporting Information Figure S4.22). Snake and turtle richness increased significantly in the Nearctic and Palearctic realms. Snake richness decreased significantly in all other realms apart from the Sino-Japanese one (Supporting Information Figure S4.23), while turtle richness significantly decreased in all other realms apart from the Saharo-Arabian and the Sino-Japanese ones (Supporting Information Figure S4.24).

3.3 | Biophysical changes

Reptile richness varied greatly across conditions with varying combinations of temperature and precipitation (Figure 3a-c). For 1995, reptile richness was projected to be highest in areas with a temperature of ca. 28.5°C , a precipitation of ca. 5500mm and when considering temperature and precipitation together in warm and moist regions (21°C and 3000mm; Figure 3c). The climatic conditions with the highest richness shifted to even more extreme (warmer and wetter) new climate conditions by 2080 (Figure 3a,b,d).

Looking at the change in species richness across the two-dimensional climate space, net change was positive at the upper precipitation limits across all temperatures and the very hot and

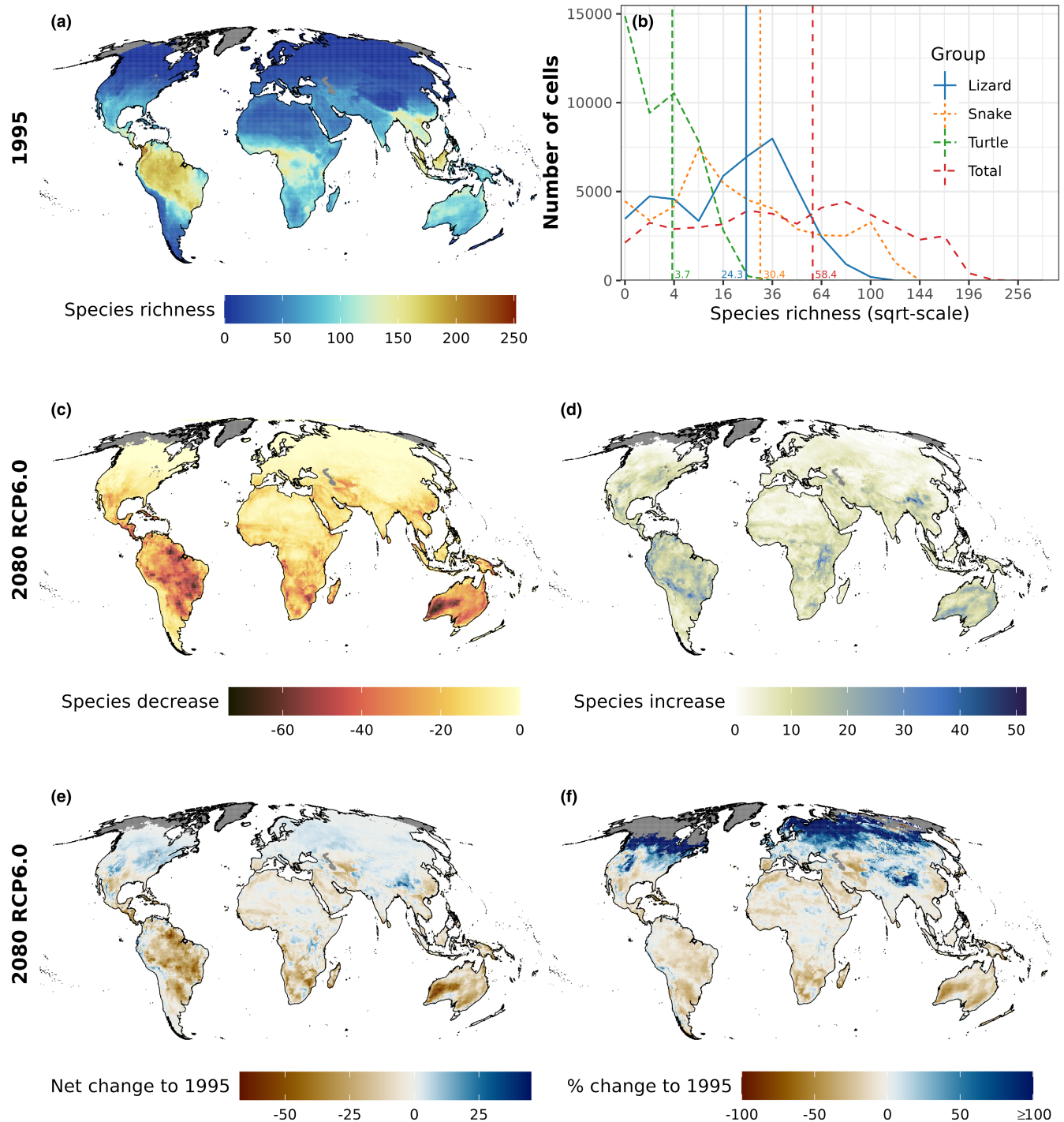


FIGURE 1 (a) Map of projected global terrestrial reptile species richness (1995), (b) frequency of species richness by taxonomic group (lizard, snake, turtle and total), with mean values indicated by vertical lines, and (c) increase, (d) decrease, (e) net change and (f) relative change (as a percentage) in reptile species richness for all modelled reptile species ($n = 6296$) for the year 2080 under a medium representative concentration pathway (RCP6.0) and a medium dispersal scenario ($d/8$). Results are presented as the ensemble mean across the four global circulation models (GCMs) and two model algorithms [generalized additive model (GAM) and generalized boosted regression model (GBM)] considered. All maps are based on $0.5^\circ \times 0.5^\circ$ grid cells, which have been projected to the Mollweide equal-area projection (EPSG:54009). Grey areas are regions for which no projections are available. Note that the colour scales differ among the individual panels.

very dry conditions and negative throughout the entire precipitation range, especially for the higher temperatures. Overall, the negative change was much greater and more pronounced than the positive net change (Figure 3e). The highest positive and

negative relative change values were clustered, and both occurred at the upper precipitation limits at low and medium temperatures (Figure 3f). A considerable percentage of the climate space (29.5%) was shifting towards new climatic conditions, for which no change

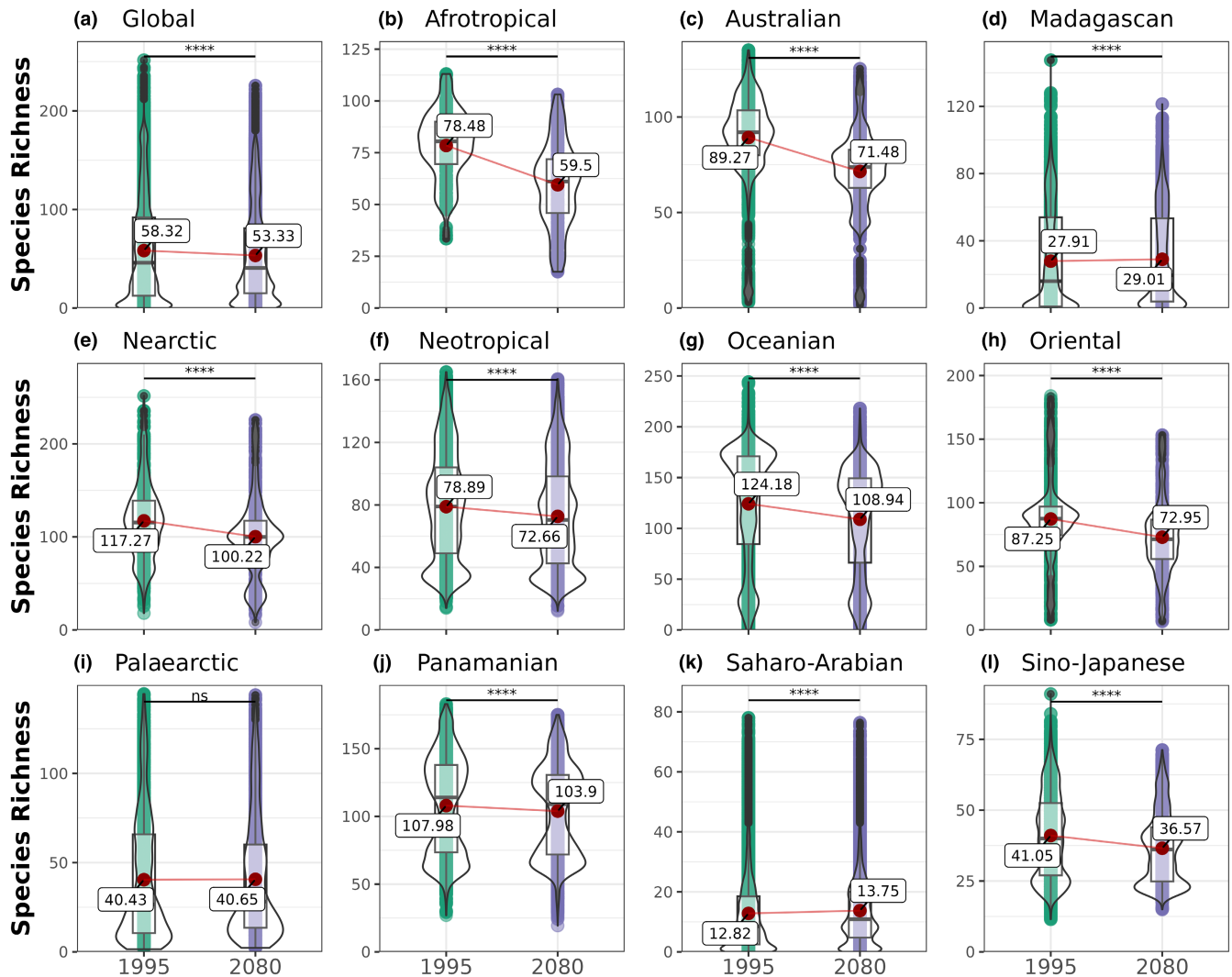


FIGURE 2 Terrestrial reptile species richness (a) across the globe and (b–l) for each zoogeographical realm (Afrotropical, Australian, Madagascan, Nearctic, Neotropical, Oceanian, Oriental, Palearctic, Panamanian, Saharo-Arabian and Sino-Japanese) over time (1995, 2080) based on all modelled reptile species ($n = 6296$). Results are presented as the ensemble mean across the four global circulation models (GCMs) and two model algorithms [generalized additive model (GAM) and generalized boosted regression model (GBM)] considered, under a medium representative concentration pathway (RCP6.0) and a medium dispersal scenario ($d/8$). The statistical difference between years was tested using Student's paired t -test with Holm correction ($*p < .05$; $**p < .01$; $***p < .001$; $****p < .0001$). Plots show the mean (red circle and label), median (black horizontal line), 25th to 75th percentiles (box), entire range of data (violin and data points) and density of values (width of violin). [Figure 5](#) provides a map outlining the different zoogeographical realms.

in species richness could be estimated, while only few discrete climatic conditions in addition to very cold and very dry conditions (4.75%) were lost ([Figure 3e,f](#)).

3.4 | Species-specific range changes

The range extent of most species ($n = 6021$) showed a considerable decrease ($\mu_{\text{mean}} = -27.7 \pm 0.16$ SE; [Figure 4a,c,e](#)). Lizard species showed the greatest decline ($\mu_{\text{mean}} = -31.8 \pm 0.22$ SE) in range extent ([Figure 4a](#)), followed by snakes ($\mu_{\text{mean}} = -22.6 \pm 0.25$ SE), while almost equal numbers of turtle species showed a decline ($n = 274$) and an increase ($n = 205$), with decreases being much more pronounced than increases ($\mu_{\text{mean}} = -17.5 \pm 0.72$ SE; [Figure 4e](#)). Almost half of the

modelled reptile species ($n = 3029$) showed a strong change in range position, demonstrated by a relatively low range overlap ($\leq 60\%$), which was consistent across all three groups ([Figure 4b,d,f](#)).

Most of the range centroids (58%) of all reptile species fell within the Neotropical ($n = 1133$), Afrotropical ($n = 1039$), Oriental ($n = 785$) and Australian ($n = 698$) realms. Turtle species had 50% of their range centroids in the Nearctic ($n = 58$), Oriental ($n = 53$) and Afrotropical ($n = 38$) realms, while lizards and snakes reflected the overall, total reptile patterns ([Figure 5d](#)). Range centroids were highly clustered within the different realms, which reflects the overall richness hotspots, and hardly any centroids were found in the high northern latitudes ([Figure 5d](#)). By 2080, species centroids were projected to shift by a mean \pm SE distance of 111 ± 0.9 km, primarily towards the south. Lizards showed a shift in all directions,

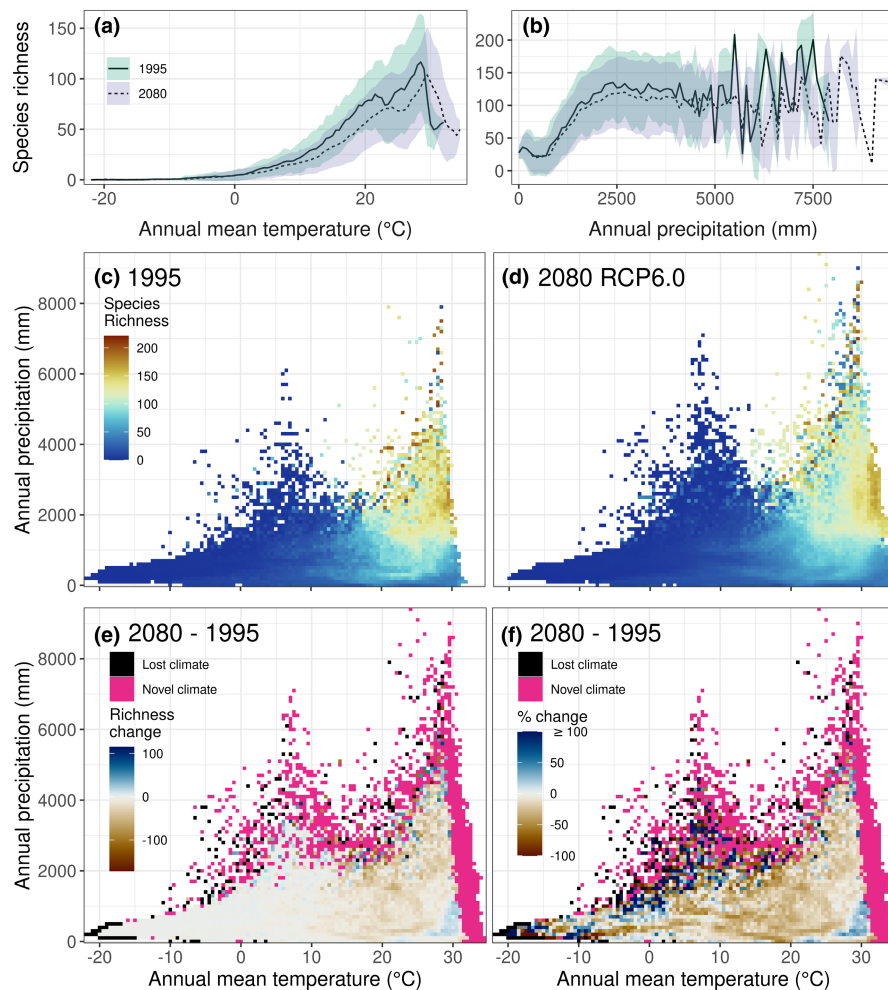


FIGURE 3 Univariate relationship of current (1995) and future (2080 RCP6.0) reptile species richness with (a) temperature and (b) precipitation; and the bivariate relationship of temperature and precipitation with reptile species richness for (c) 1995 and (d) 2080 RCP6.0; and the respective (e) net richness change and (f) relative richness change (as a percentage) under a medium dispersal scenario ($d/8$). Heat maps and lines show the mean and ribbons the standard deviation in variance across space, global circulation models (GCMs) and the two model algorithms [generalized additive model (GAM) and generalized boosted regression model (GBM)].

with a slightly greater number of species exhibiting a shift towards the south (Figure 5a), while snakes and turtles showed a more pronounced shift of species towards the north (Figure 5b,c). Turtle ranges shifted by the largest distances, followed by snakes (Figure 5a–c). The northern realms (Nearctic, Saharo-Arabian, Palearctic and Sino-Japanese) showed a dominant shift towards the north, while the southern realms (Neotropical, Afrotropical and Australian) showed a dominant shift towards the south. This was also reflected in the taxon-specific range shifts for the Northern and Southern Hemispheres (Supporting Information Appendix S6, Figure S6.37). The Panamanian, Madagascan and Oriental realms also showed a northerly shift, while the Oceanian realm showed a bi-directional shift to the north-west and south-east (Figure 5d; Supporting Information Appendix S6, Figure S6.38). Large realms had a greater percentage of species that shifted their range over a greater distance (Figure 5; Supporting Information Appendix S6, Figure S6.38).

3.5 | Non-modelled species

Using SDMs, 37.4% of reptile species for which data would have been available could not be modelled, owing to either a small sample

size or a low model performance (Table 1). We found that the species that could not be modelled showed a significantly greater ($p < .05$) mean climatic distance between current and future conditions than did the modelled species and thus occurred in areas that are projected to experience a greater change in climatic conditions. This pattern was consistent across all three taxa.

3.6 | Sensitivity analysis

Looking at the sum of occurrence probabilities, we found similar spatial patterns and a similar magnitude of change compared with the sum of thresholded occurrences (species richness) (Supporting Information Figures S4.18–S4.20). Projected richness values and their future changes were slightly higher assuming a larger dispersal ability ($d/4$), but on the whole, all results were consistent across the three dispersal scenarios considered (Supporting Information Figures S5.21–S5.26). Climate change impacts on future species richness increased over time, with greater effects seen for 2080 than for 2050 and with the greatest impacts being observed under a high emission scenario (RCP8.5) compared with the two lower scenarios (Supporting Information Figures S6.27–S6.38).

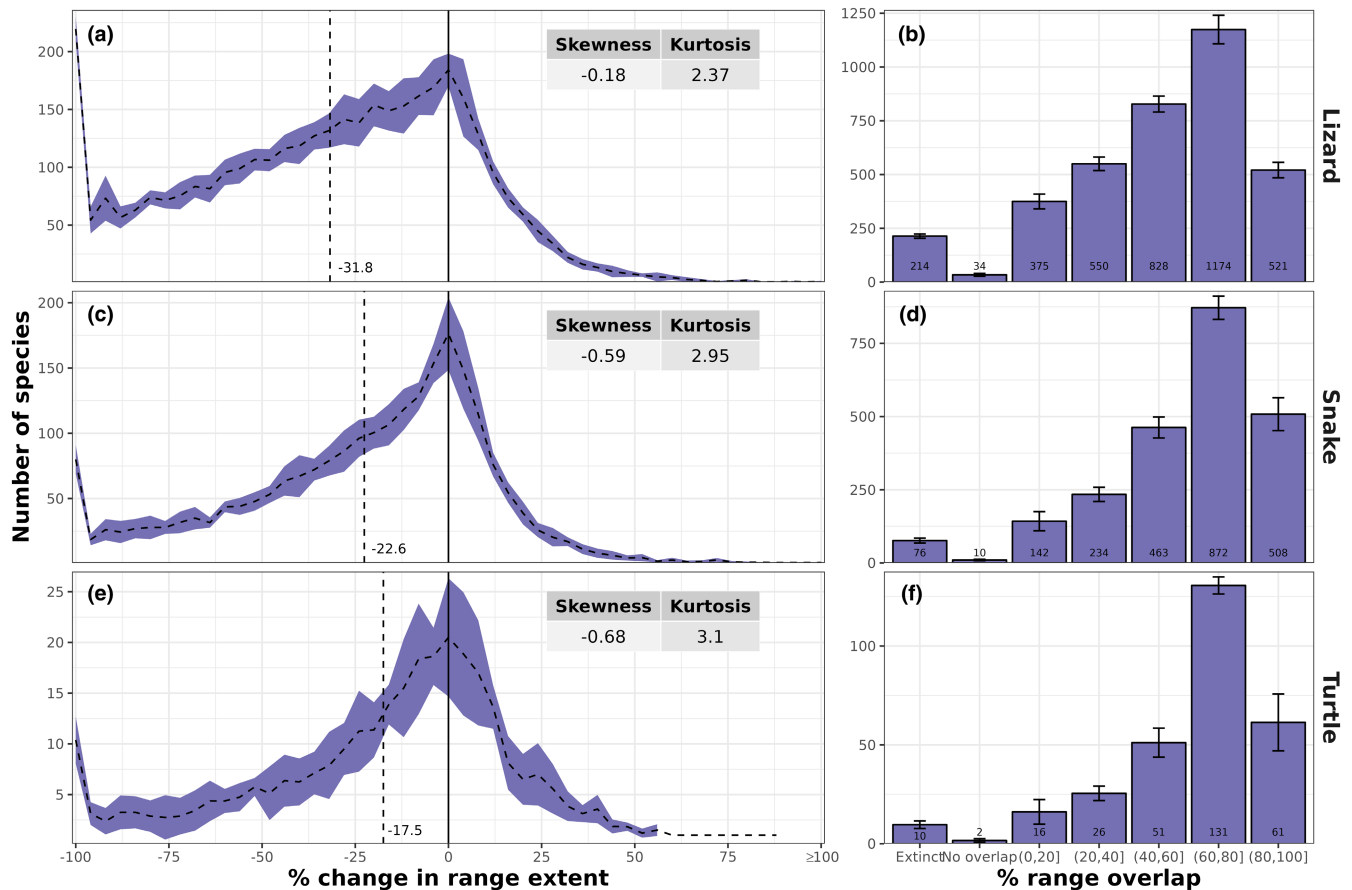


FIGURE 4 Frequency plots of the mean number of reptile species [(a) lizard, (c) snake and (e) turtle] and their potential future change (as a percentage) in range extent (total area of occupied grid cells) and the mean number of reptile species [(b) lizard, (d) snake and (f) turtle] per potential range overlap class (0–20, 20–40, 40–60, 60–80 and 80–100). Error margins/bars indicate the standard deviation across the four global circulation models (GCMs) and the two model algorithms [generalized additive model (GAM) and generalized boosted regression model (GBM)] used. Results are shown for 2080 under a medium representative concentration pathway (RCP6.0) and a medium dispersal scenario (d/8).

4 | DISCUSSION

Reptile richness was projected to decrease significantly across most parts of the world in the future (Figures 1 and 2). This effect was apparent for lizards, snakes and turtles alike, although regional and species-specific responses differed across the three groups (Supporting Information Figures S4.17–S4.21).

4.1 | Spatial changes

Reptile richness was projected to decrease in Brazil, Australia and South Africa (Figure 1c,e). These areas overlap significantly with the biotic convergence zones, areas with a high spatial concentration of lepidosaurians (i.e., snakes and lizards) identified by Diele-Viegas et al. (2020), which were also found to cover a large number of the lepidosaurian species vulnerable to climate change (Diele-Viegas et al., 2020). Huey et al. (2012) also found that ectotherms sharing climate vulnerability traits seem to be concentrated in lowland tropical forests. Combining climate-based

SDMs with information on land-use change, Newbold (2018) created future projections for 20,938 vertebrate species and found that Brazil will be strongly affected by vertebrate diversity loss owing to climate change and, together with Australia, is also likely to be strongly affected by future land-use changes, especially under a high-emission scenario (RCP8.5). Given that Brazil, in particular, not only hosts a high reptile richness (Roll et al., 2017; Figure 1a) but also has recently been found to host a large number of threatened reptile species (Cox et al., 2022), this highlights the responsibility of this mega-diverse country to protect reptile diversity. South-western China and the western USA were projected to show a net gain in reptile richness under climate warming (Figure 1e), but they also belong to those areas where most reptile species are threatened by habitat loss from agriculture and logging or the harvesting of species (Böhm et al., 2013). These projected losses owing to habitat change could potentially counteract any positive effects of climate warming.

The high variation that we found in changes in species richness across regions and taxa obviously reflect their original richness patterns. Species richness of amphibians, birds and mammals together is

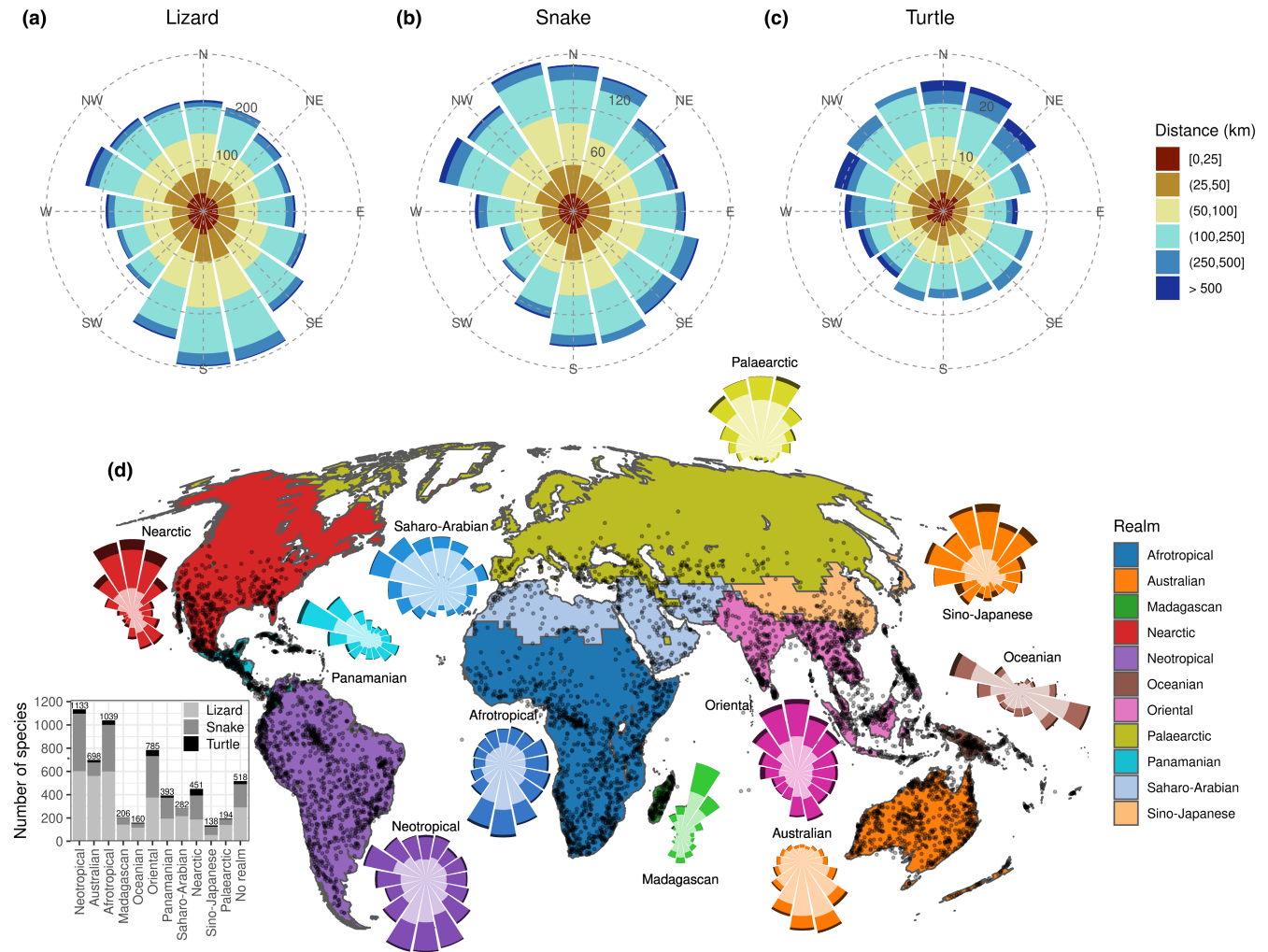


FIGURE 5 Cumulative direction and distance of potential range centroid changes per taxonomic group [(a) lizard, (b) snake and (c) turtle] and (d) range centroids (points on map) and the number of species and their directional shift in range centroid position per zoogeographical realm (inset polar plots). Results are presented as the ensemble mean across the four global circulation models (GCMs) and two model algorithms [generalized additive model (GAM) and generalized boosted regression model (GBM)] considered, for the year 2080 under a medium representative concentration pathway (RCP6.0) and a medium dispersal scenario ($d/8$). The inset bar chart shows the number of species that have their range centroid located in the respective realm. Numbers show the total number of species per realm, and the bars are shaded according to the three different taxonomic groups. Please note that a considerable number of species ($n = 518$) have their range centroid located outside of the zoogeographical realm boundaries and were therefore not associated with any realm and considered for the polar plots in Figure 5d.

a good spatial surrogate for species richness of all reptiles combined and of snake richness, but is not a good surrogate for lizard or turtle richness (Roll et al., 2017). Thus, it is not surprising that the areas with the highest decline in overall reptile richness (see Figure 1) overlap significantly with the areas of highest projected changes in vertebrate species richness (amphibians, birds and mammals) found by Hof et al. (2018), although global reptile richness is constrained largely by temperature, whereas global richness of all other vertebrate groups is constrained primarily by the availability of energy and water (Qian, 2010). Furthermore, historical shifts in geographical ranges and climatic niches have also demonstrated that niche shifts in endotherms are significantly faster than in ectotherms (Rolland et al., 2018).

4.2 | Global and zoogeographical realm changes

Globally, reptile richness was projected to decline significantly, from an average of *ca.* 58 to *ca.* 53 (9.4%) species per grid cell from 1995 to 2080 (Figure 2a). This projected percentage change in average future reptile richness (9.4%) is considerably lower than the decline in reptile richness attributable to climate warming predicted by Newbold (2018). Although Newbold (2018) also used SDMs to infer future changes in reptile richness, he used only a subset of reptile species for which IUCN range maps were available at that time. In addition, he also applied a much smaller dispersal buffer (0.5 km/year), which might indicate that our projections provide a rather optimistic scenario. Newbold (2018) also

found that reptiles, together with amphibians, are disproportionately sensitive to future human land use. Given the synergistic effect of future climate and land-use changes on biodiversity (Brook et al., 2008) and species populations (Williams et al., 2022), land-use change is likely to exacerbate the impacts of climate change on global reptile distribution and diversity.

Changes in reptile richness differed among zoogeographical realms, but species richness declined significantly across most realms over both time periods (Figure 2b–d,f–h,j,k). Lizards, snakes and turtles all showed similar declines in species richness globally and across most realms, but differed slightly across individual realms. This is in line with a previous study covering various realms from tropical to temperate regions, which found that 60% of assessed lepidosaurian species ($n = 1114$) were vulnerable to changes in climate (Diele-Viegas et al., 2020). Diele-Viegas et al. (2020) also found that the Afrotropical, Nearctic and Sino-Japanese realms were the three realms where lepidosaurians were most vulnerable to climatic change, whereas lepidosaurians in the Madagascan and Oceanian realms were least vulnerable. In contrast, we found no significant decline in projected total reptile richness for the Sino-Japanese realm (Figure 2l), although individual subgroups were projected to show a significant decline in species richness from 1995 to 2050 (Figures S4.22–S4.24). Both the Madagascan and Oceanian realms were also projected to decrease significantly in species richness including all reptile species (Figure 2d,g) and all three subgroups (Figures S4.22–S4.24). However, given that the Madagascan realm, specifically, boasts >90% of endemic reptile species and genera (Glaw & Vences, 2007) and that both realms are composed of island territories, which are usually considered highly vulnerable to climate change and might also be affected by future sea-level rise and erosion (Diele-Viegas et al., 2020), our estimates might still underestimate potential climate change impacts in these realms. Interestingly, turtle richness seemed to be least affected by climate change, when looking at the different realms (Figure S4.24), although a recent review has deemed turtles to be the vertebrate group with the risk of highest extinction, because turtles are greatly affected by habitat loss, human consumption and pet trading (Stanford et al., 2020).

4.3 | Biophysical changes

Reptile richness differed significantly with temperature and precipitation, with the highest richness being observed in warm and moist conditions. Under future climate change scenarios, the climatic conditions with high species richness were projected to shift to even more extreme (warmer and wetter) conditions (Figure 3). This gives cause for concern, given that tropical forest and desert lizards already live in environmental conditions that are close to their thermal limits (Sinervo et al., 2010) and that desert and temperate lizard species have been found to be less able to regulate their temperature in order to deal with heat stress than tropical species (Anderson et al., 2022). Reptiles cannot regulate

their body temperature internally, hence they are strongly dependent on using solar energy captured by the environment to regulate their body temperature (Huey, 1982). This might lead to overheating when temperatures go beyond the critical limit of a species, which makes reptiles particularly susceptible to climatic changes (Sinervo et al., 2018). However, this might be compensated by other biological processes that help species to buffer the effects of climate change (i.e., genomic and phenotypic plasticity; Rodríguez et al., 2017), in addition to behavioural and physiological adaptation (Sunday et al., 2014). Overall, the persistence of reptile species would be much more affected by climate cooling than warming, but it has been suggested that increasing droughts, which will be a consequence of continued warming, pose a significant future threat to European reptiles (Araújo et al., 2006). It is likely that climate warming will have an additional impact on reptiles that have temperature-dependent sex determination. Altered sex ratios will not only result in a higher extinction risk for local populations, but, together with a reduction in nesting sites owing to habitat destruction and fragmentation, will also affect the dispersal and potential range expansion of a species. Therefore, it could also have an impact on population demography and size unless temperature shifts in sex determination or female nest-site choice evolve in pace with rising temperatures (Boyle et al., 2016; Gibbons et al., 2000).

4.4 | Species-specific range changes

The range extents of most species were projected to decrease considerably, with lizard species showing the greatest decline (Figure 4a). Furthermore, most reptiles also showed a strong decline in range overlap, which was consistent across all three groups (Figure 4). This is in line with results published by Warren et al. (2018), who found that projected future range losses of >50% occur in 8–52% of considered reptile species by 2100 depending on the climate scenario considered, although this study included only a fraction of all reptile species ($n = 1850$) and no species dispersal was considered.

In comparison to other terrestrial vertebrate groups (especially birds and mammals), reptiles have small geographical ranges, which also indicates narrower niche requirements. This is likely to make them more susceptible not only to future climate change (Newbold, 2018), but also to other threats, such as habitat loss or invasive species (Böhm et al., 2013; Cox et al., 2022). Reptiles are a paraphyletic class with a diverse range of body forms, habitat affinities and functional roles (Pincheira-Donoso et al., 2013), which will probably result in their responses to changes in climate and habitat being equally varied. In addition, cascading effects generated by disease, invasive species, habitat loss and climate change might lead to declines of sympatric species and a faster deterioration of ecosystem structure than anticipated for climate change alone (Zipkin et al., 2020).

The majority of reptile species showed projected shifts towards the south, which were driven largely by range shifts in lizards (Figure 5).

Comparing the Northern and Southern Hemispheres (Supporting Information Figure S6.37), we found a clear overall poleward shift in species ranges across all three groups, which has also been found previously in various other taxonomic groups (Chen et al., 2011). Turtle ranges were projected to shift farthest, followed by snakes (Figure 5). The relatively short range shift distances in lizard species are probably attributable to the fact that lizards have the smallest range extents across the three groups (Roll et al., 2017), which, given that our dispersal buffers are based on range extent, also resulted in smaller dispersal distances for lizards compared with the two other groups (Supporting Information Figure S1.4). This is, however, obviously somewhat counter-intuitive and in stark contrast to generally perceived differences in mobility characteristics (e.g., movement speed) among lizards, snakes and turtles. Although it is hard to tackle this problem in a globally and taxonomically comprehensive study, such as ours, it underlines the need for more efforts in collecting data on real, empirically quantified dispersal distances in order to consider them in SDMs and large-scale biogeographical analyses.

4.5 | Non-modelled species

Range-restricted (non-modelled) species were projected to experience a significantly larger shift in climatic distance than modelled species (Figure 6), indicating that range-restricted species are also likely to be strongly affected by climate change. This highlights once

more that sample size restrictions of SDMs are likely to downplay the effects of climate change on narrow-ranging and threatened species (Platts et al., 2014). Hof et al. (2018) also found significant impacts of changes in climate and land use on range-restricted vertebrate species, excluding reptiles. However, similar to the latter study, we looked only at climate anomalies (Euclidean distance between current and future climatic conditions) as a metric of climate change, whereas different metrics have been found to indicate contrasting patterns of climate change on a global scale (Garcia et al., 2014). In addition to effects of climate change, habitat modification has been found to have a greater impact on range-restricted reptile species and on species with a small clutch size (Doherty et al., 2020). Range-restricted reptile species are also often evolutionarily unique (Murali et al., 2021) and have been found to overlap least with current conservation priority areas (Cox et al., 2022; Roll et al., 2017).

4.6 | Sensitivity analysis

Our results were strongly dependent on the dispersal assumption, time period and emission scenario (RCP) considered (Supporting Information Appendices S5 and S6). As expected, the overall patterns and richness changes were more pronounced in a later time period and for scenarios representing higher levels of greenhouse gas emissions, because these reflect potential futures with a higher level of climate warming. Thuiller et al. (2019) have previously assessed the uncertainty originating from

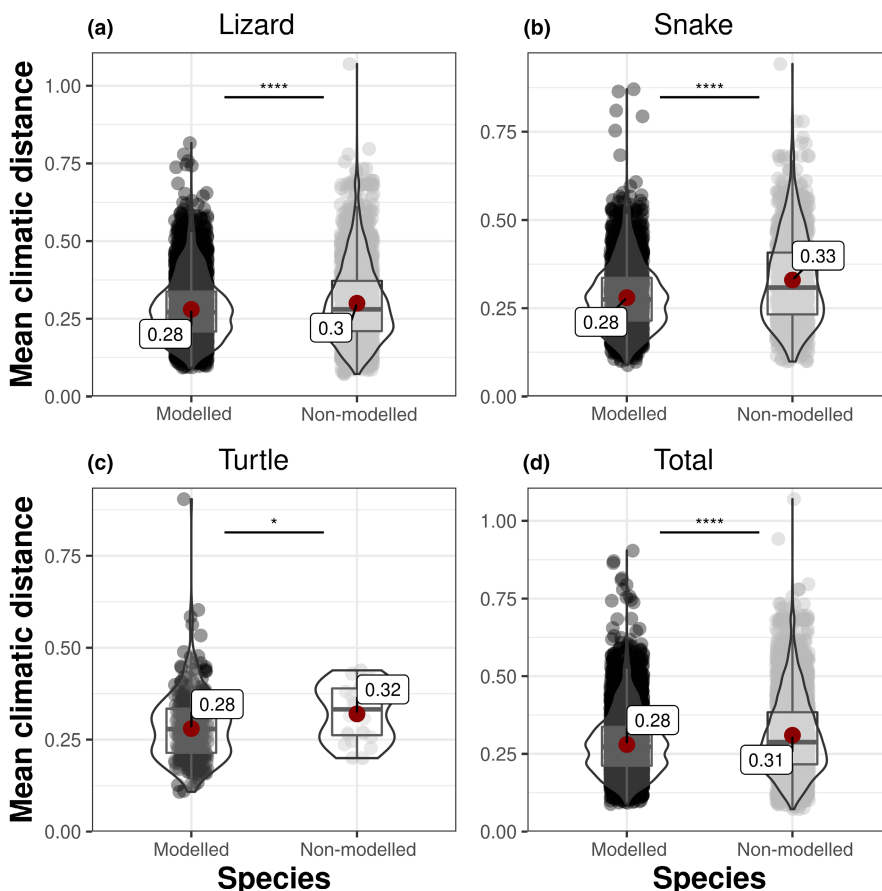


FIGURE 6 Mean climatic distance for modelled and non-modelled species, split by taxonomic group [(a) lizard, (b) snake, (c) turtle and (d) total]. The statistical difference between modelled and non-modelled species was tested using Student's unpaired *t*-test with Holm correction (* $p < .05$; ** $p < .01$; *** $p < .001$; **** $p < .0001$). Plots show the mean (red point and label), median (black horizontal line), 25th to 75th percentiles (box), entire range of data (violin and data points) and density of values (width of violin). The results are shown as the ensemble mean across the four global circulation models (GCMs) for the year 2080 under a medium representative concentration pathway (RCP6.0).

dispersal, model algorithm, GCM and RCP on the future biodiversity scenario of amphibians, birds and mammals and found that the model algorithm and RCP have the greatest influence.

On the contrary, greater dispersal distances imply that reptile species are able to move greater distances in order to track their optimal climatic niche and thus provide more optimistic potential changes in species occurrence and richness patterns. Reptile-specific studies have considered either no dispersal at all (Araújo et al., 2006; Warren et al., 2018) or a dispersal rate of 0.5 km/year (Newbold, 2018). We used species-specific dispersal buffers with an average of 2.4 km/year (Supporting Information Figure S1.4). Although these buffers might be optimistic, they are based on the transparent rationale of a range size-dependent dispersal buffer (i.e., species with a small range size have a smaller dispersal buffer than species with a large range size), which avoids the unlikely assumption of uniform dispersal distances across species. Given that our model results and the underlying climate scenarios are based on a 0.5° grid size (ca. 50 km × 50 km), small differences in dispersal distance do not have a strong impact on our results (Supporting Information Appendix S2). Nevertheless, these considerations again highlight the challenges in sensibly accounting for the influence of dispersal in global climate impact assessments on species distributions and diversity.

The projected changes in species distributions help us to investigate potential changes in global reptile richness patterns and in highlighting potential hotspots of the impacts of climate change. They also allow a comparison of climate change vulnerability across taxonomic groups and help to identify areas where conservation efforts might be needed most urgently (Voskamp et al., 2022). However, SDMs are always simplifications, and the resulting projections need to be interpreted with caution.

To improve SDMs, in future studies researchers should try to consider additional factors, such as biotic interactions (Schleuning et al., 2020) and the reshuffling of species communities (Voskamp et al., in prep), which might lead to a change in competitive balance (Ockendon et al., 2014), altered predator–prey relationships (Harley, 2011) or changes in functional diversity (Stewart et al., 2022) and thus the provision of ecosystem functions and services (Pecl et al., 2017). Although the above factors might improve projections of the impact of climate change in the future, such modelling studies will never reflect the truth, because the response of a species to climate change will be influenced strongly by behaviour, diel rhythm, thermoregulatory potential and microclimatic conditions (Anderson et al., 2022). This complexity highlights the need for integrative approaches when investigating the responses of species to climate change (Hof, 2021).

5 | CONCLUSION

Our study shows that reptiles are likely to be impacted by future climate change, both globally and within most zoogeographical realms. These impacts are projected to have a considerable effect on the extent and location of the geographical ranges of species. Thus, to

prevent large-scale declines in reptile species, it is of key importance not only to lower CO₂ emissions in order to stop on-going climate change, but also to maintain adequate habitats of sufficient size and quality, especially grassland and savanna habitats (Roll et al., 2017). Furthermore, it is necessary to establish new protected areas that will help to prevent the extinction of particularly vulnerable species (i.e., by establishing high-elevation climate refugia within current species ranges; Sinervo et al., 2018).

AUTHOR CONTRIBUTIONS

M.F.B., A.V. and C.H. conceived the ideas; M.F.B. and A.V. performed the analyses; M.F.B. wrote the paper, with significant input of A.V. and C.H.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest

DATA AVAILABILITY STATEMENT

GARD range maps are available from: <https://doi.org/10.5061/dryad.83s7k>. EWEMBI and ISIMIP2b climate data are available from: <https://data.isimip.org/10.5880/pik.2019.004> and <https://data.isimip.org/search/query/ISIMIP2b%20Input/tree/ISIMIP2b/Input/Data/climate/atmosphere/>. The code for creating the species distribution models can be found at: https://github.com/christianhof/BioScen1.5_SDM. The code and data for the performed data analysis and the presented figures can be found on Dryad (doi: 10.5061/dryad.rn8pk0pgb; Biber et al., 2023).

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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