Potential future climate change effects on global reptile distribution and diversity

Matthias F. Biber[1,*], Alke Voskamp[2], Christian Hof[1]

[1]Technical University of Munich, Terrestrial Ecology Research Group, Department for Life Science Systems, School of Life Sciences, 85354 Freising, Germany

[2]Senckenberg Biodiversity and Climate Research Centre (SBiK-F), 60325 Frankfurt, Germany

Running head: Global reptiles under climate change

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 reptile distributions at a global scale.

Location: Global, excluding Antarctica

Time period: 1995, 2050, 2080

Major taxa studied: Reptiles

Methods: We performed species distribution models for 6296 reptile species and assessed potential global as well as realm-specific changes in species richness, the change in global species richness across climatic space and species-specific changes in distribution and range extent and overlap, under future climate change. To assess the future climatic impact of 3768 non-modeled species, we compared the future change in climatic conditions between both modeled and non-modeled species.

Results: Reptile richness was projected to decline significantly over time, globally but also for most zoogeographic realms, with the strongest decrease in Brazil, Australia and South Africa. Species richness was highest in warm, but moist regions, which were projected to shift further to climate extremes in the future. Extents of occurrence were projected to decline considerably in the future, with a low overlap between projected current and future ranges. Shifts in range centroids differed among realms and taxa, with a dominating global poleward shift. Non-modeled species were significantly stronger affected by climatic changes than modeled species.

Main conclusions: Reptile richness was projected to decrease significantly across most parts of the world with ongoing future climate change. This effect is visible across lizards, snakes and turtles alike and has considerable impact on species' extent of occurrence (EOO) and range distribution. Together with other anthropogenic impacts, such as habitat loss and harvesting, this

is cause for concern. Given the historical lack of information on global reptile distributions, this calls for an re-assessment of global conservation efforts towards reptile species, with specific focus on anticipated future climatic changes.

KEYWORDS: species distribution model, turtle, snake, lizard, ISIMIP, bioclim, global warming, environmental niche model

Introduction

Emissions from anthropogenic activities have lead to an increase in global surface temperature of around 1°C in the last 100 years. This has already led to changes in weather and 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 to 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 proceeds in future (IPBES, 2019; IPCC, 2022). Climate change impacts on ecological processes scales 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). Especially changes in species abundance and distribution due to climate change have already been frequently observed (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).

Species distribution models (SDMs) are a common way of assessing species-specific responses to climate change (e.g. Engelhardt *et al.* (2020)), but also to assess climate change impacts on biodiversity (Thuiller *et al.*, 2005). SDMs statistically infer a relationship between the observed distribution of a species to the underlying climatic 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 (Hof *et al.*, 2018; Newbold, 2018; Thuiller *et al.*, 2019).

In the past most climate change impact assessments on vertebrate biodiversity have focused on endotherms (birds & mammals). Reptiles, though accounting for a third of global terrestrial vertebrate diversity, have been largely ignored (Pacifici *et al.*, 2015). Previous studies that assessed climate change impacts on reptiles species, have either only used a subset of species (Warren *et al.*, 2018; Newbold, 2018) or have not been of global extent (Araújo *et al.*, 2006). Until recently, this was largely due to the unavailability of global reptile distribution data, 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 the release of the full set of IUCN reptile range maps (IUCN, 2022).

Global biodiversity assessments further 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; Warren *et al.*, 2018; Thuiller *et al.*, 2019), but only very rarely compare different taxonomic groups within one taxon (but see, for example Hof *et al.* (2011)). This may

be problematic as pooling all species may obscure the evolutionary and biogeographic history of major lineages, and from a global conservation perspective ignores the fact that hotspots of total reptile richness hardly overlap with those of lizard or turtle richness (Roll *et al.*, 2017).

Here, we tried to fill the gaps outlined above, by providing a detailed account of projected climate change impacts on global reptile distributions and diversity, looking at species-specific changes as well as broad-scale geographic trends across and within different taxonomic groups. We assessed changes in reptile richness globally, within each zoogeographic realm and across their respective climate space. For each species, we further quantified the change in extent of occurrence (EOO), range overlap and range distribution and again assessed differences across zoogeographic realms and taxonomic groups. Given that we cannot model range restricted species, we also performed a more general assessment of species-specific changes in climatic space across both modeled and non-modeled species.

Methods

Species data

We obtained global range maps of 10,064 reptile species from the Global Assessment of Reptile Distributions (GARD, https://doi.org/10.5061/dryad.83s7k). Roll *et al.* (2017) provide a detailed description of the methodology used for deriving the range maps. The range maps cover lizards, snakes, turtles, worm lizards, crocodiles and the tuatara, but in this paper, similar to (Roll *et al.*, 2017), we only contrast snakes, turtles and paraphyletic lizards (the latter of which we subsequently refer to as lizards for simplicity).

Range maps were gridded to a 0.5° x 0.5° grid in WGS84, considering any cell that intersected with the range polygon, and pseudo-absence data for each species were generated by randomly selecting absences using a distance-weighted approach (see Hof *et al.*, 2018). The number of absences was either equal to the number of presences or 1000 absences for species with less than 1000 presences. For each species we derived 10 sets of pseudo-absences, which were modeled separately.

Climate data

Global bias-corrected daily climate (minimum temperature, maximum temperature and precipitation) data at a spatial resolution of 0.5° (WGS84) was 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 & 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). Monthly means of each climatic variable over the respective 30-year time periods, centered around 1995, 2050 and 2080, and for each future scenario (GCM & RCP) were used to calculate 19 bioclimatic variables using the 'dismo' package (Hijmans *et al.*, 2021) in R (R Core Team, 2021). We used the same model selection approach as described in Hof *et al.* (2018) and fitted our models using the best-performing combination of four explanatory variables, which was temperature seasonality, maximum temperature of the warmest month, annual precipitation and precipitation seasonality.

Species Distribution Models (SDMs)

Projections based on SDMs vary considerably among the model algorithm considered, for this we fitted two modeling algorithms with a good performance and discrimination capacity (Meynard & Quinn, 2007; Elith *et al.*, 2010), an additive (Generalized Additive Model (GAM)) and a regression tree based model (Generalized Boosted Regression Models (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 (1000-10000) 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 equal or more than 50 presences were modeled using an ecoregion-blocking approach. Here the world was divided into 10 blocks, based on a representative subset of the climatic space of each of the world's ecoregions (Olson *et al.*, 2001), and 10 models were built leaving out one block at a time, using the left out block for model evaluation (Bagchi *et al.*, 2013). For range-restricted species (10 - 49 presences), we split the data into 10 datasets by repeatedly randomly selecting 70% of the data, using the left-out 30% for model evaluation. Species occurring in less than 10 grid cells were not modeled (N = 3602, Table 1).

The performance of the fitted SDMs was evaluated by calculating the overall AUC for each species (the average AUC across the 10 blocks and the 10 sets of pseudo-absences). Models with an overall AUC smaller than 0.7 were dropped (N = 166), which left us with SDMs for 6296 reptile species (see Fig. S1.1 in Appendix S1 in Supporting Information), which represents 62.6 % of the total number of available species by GARD (Table 1).

The same modeling approach has been used previously to assess climate change impacts on birds, amphibians and reptiles, see Hof *et al.* (2018) and Biber *et al.* (2020). The former provides a more detailed explanation of the modeling methodology, while the latter gives a thorough account of the caveats and uncertainties associated with species distribution models.

Future projections

Future species distributions were derived by predicting the models using the future bioclimatic variables of the two future time periods (2050, 2080) and the respective future scenario (GCM & RCP). Future projections of each species were limited to their original and the extent of their neighboring ecoregions, to avoid predictions to areas with analogue climatic conditions. Future projections were further limited by applying a species-specific dispersal buffer. For most species considered here species-specific dispersal distances are still unknown (Nathan *et al.*, 2012), hence we used species-specific dispersal buffers, which 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, d/16, see Fig. S1.2 in Appendix S1) and provide a detailed comparison of these in the Supporting Information (see Appendix S4), but below provide the results under the medium dispersal scenario d/8, with a mean dispersal distance of 2.4 km per year.

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). Thresholded species occurrences were then used to calculate current and future species richness, as well as richness increase, decrease, change and relative change (%). Richness increase and decrease was identified by using the presence information of each individual species and then summing up the number of species that newly occur in a given grid cell (species increase) or species that disappear from the respective grid cell (species decreae).

As stacked thresholded data frequently overestimates species richness, we also present the results using the stacked raw probabilities of occurrence, as suggested by Calabrese *et al.* (2014), of the individual SDMs without thresholding where applicable, in the Supporting Information (see Appendix S3).

We calculated the overall mean projected species richness globally and for each zoogeographic realm, as defined by Holt *et al.* (2013), for each time period and tested for significant changes in species richness over time using a paired t-test with Holm correction. To assess how species richness and changes in species richness are related to the overall change in climatic conditions, we assessed both across univariate temperature and precipitation as well as the interaction of temperature and precipitation conditions. To assess potential future climate effects on individual species, we quantified the proportion of change in EOO and the proportion of range overlap for species. And to assess the geographic change between each current and future species range, we calculated the range centroid for current and future conditions of each species and then identified the distance and direction of change between current and future range centroids.

Given that 37.4% of reptile species for which data was available could not be modeled (largely due 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 4 bioclimatic variables used for the SDMs to transform the multidimensional climate data in a two-dimensional climate space using the first two axes of a principal component analysis (PCA). PCAs were performed for both current and future conditions, considering the same GCMs, RCPs and time periods as before (Fig. S1.3). For each scenario combination, we then calculated the Euclidean distance between the two PCA-axes of current and future conditions, to get a measure of climatic change (Fig. S1.4). We then extracted the climatic distance for the gridded locations of each species and compared the climatic distance of modeled and non-modeled species using a non-paired t-test with Holm correction.

Where no specific groups (lizards, snakes, turtles) are mentioned, we present the results for all reptile species together. Results are presented as the ensemble mean, across the four GCMs and two model algorithms considered, for the year 2080 under a medium representative concentration pathway (RCP6.0). A sensitivity analysis with regards to the variation across years and RCPs is shown in the Supporting Information (see Appendix S4).

Results

Projected reptile richness for current conditions varied between 0 (high latitudes) and 251 in the tropics, with particular hotspots in Brazil, Cameroon and Indonesia (Fig. 1a). Overall, reptile

richness was dominated by lizard species (N = 3695), followed by snakes (N = 2305), while turtle species only contributed marginally to the total number of modeled species (N = 296, Table 1). Looking at the spatial configuration of species richness across the three groups, snakes had the highest mean species richness (μ_{mean} = 30.4 ± 0.15), followed by lizard (μ_{mean} = 24.3 ± 0.09 SE) and turtle richness (μ_{mean} = 3.71 ± 0.02 SE), while the mean total richness was 58.4 ± 0.24 (SE; Fig. 1b, Fig. S2.5, Appendix S2). A large number of reptile species was 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 species decrease or increase (Fig. 1 c,d). The strongest future species decreases were projected east of the Caspian Sea and in South Africa (Fig. 1 c), while strong future increases were predicted in the south-west of China and in the eastern United States (Fig. 1 d). Overall, species decrease was stronger than species increase, which resulted in a stronger negative net change in species richness from 1995 to 2080 (Fig. 1c,d,e). The lowest negative net change in species richness was observed in Brazil, Australia and South Africa, while the highest positive net change was projected for south-west China and the western United States (Fig. 1 e). Relative change (%) was projected to be negative in particular for most of the southern hemisphere, while the high northern latitudes showed a strong positive relative change (Fig. 1 f).

Spatial patterns in species richness changes varied strongly 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 eastern North America (Fig. S2.6). All three taxa showed a positive net change in species richness in northern latitudes (Fig. S2.7), while lizards decreased in parts of Australia (Fig. S2.7 a,b), snakes in large parts of South America (Fig. S2.7 c, d) and turtles showed a strong negative net change in parts of South America and southern Africa (Fig. S2.7 f).

Globally reptile richness was projected to decline significantly ($p < 0.01$) from 1995 to 2080, with a decline in mean reptile richness from 58.4 ± 0.24 (SE) in 1995 to 53.39 ± 0.19 (SE) in 2080 (Fig. 2 a). 8 out of 11 zoogeographic realms showed a significant decline in reptile richness by 2080 (Fig. 2 b, c, d, f, g, h, j, k), while the Nearctic and Palearctic realm showed a significant increase (Fig. 2 e, i) and the Sino-Japanese realm showed no significant change (Fig. 2 l).

The different taxonomic groups (lizards, snakes and turtles) showed changes in global species richness that were similar to all reptiles, while there were slight differences across the individual realms. Lizards only showed a significant increase in richness 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 (Fig. S2.8). Snake and turtle richness increased significantly in the Nearctic and Palearctic realm. Snake richness decreased significantly in all other realms apart from the Sino-Japanese one, while turtle richness significantly decreased in all other realms apart from the Saharo-Arabian and the Sino-Japanese one (Fig. S2.9, S2.10).

Reptile richness strongly differed across conditions of varying combinations of temperature and precipitation (Fig. 3 a,b,c). For 1995 reptile richness was projected to be highest in areas with a temperature around 28.5°C, a precipitation of about 5500 mm and when considering temperature and precipitation together in warm, but moist regions (21°C & 3000 mm, Fig. 3 c). The climatic conditions with the highest richness shifted to even more extreme (warmer & wetter) novel climate conditions by 2080 (Fig. 3 a,b,d).

Looking at the species richness change across the 2-dimensional climate space, net change was positive at the upper precipitation limits across all temperatures and the very hot and very dry conditions and negative throughout the entire precipitation range especially for the higher temperatures. Overall the negative change was much stronger and more pronounced than the positive net change (Fig. 3 e). The highest positive and negative relative change values were clustered, both occurred at the upper precipitation limits at low and medium temperatures (Fig. 3 f). A considerable proportion of the climate space (29.5 %) was shifting towards novel climatic conditions, for which no change in species richness could be estimated, while only few discrete climatic conditions as well as very cold & very dry conditions (4.75 %) got lost (Fig. 3 e,f).

The EOO of most species (n = 6021) showed a considerable decrease (μmean = -27.7 ± 0.16 SE, Fig. 4 a,c,e). Lizard species showed the strongest decline (μmean = -31.8 ± 0.22 SE) in EOO (Fig. 4 a), followed by snakes (μmean = -22.6 ± 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 (μmean = -17.5 ± 0.72 SE, Fig. 4 e). Almost half of the modeled reptile species (n = 3029) showed a strong change in range position, demonstrated by a relatively low range overlap (<= 60 %), which was consistent across all three groups (Fig. 4 b,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 realm (n = 698). Turtle species had 50 % of their range centroids in the Nearctic (n = 58), Oriental (n = 53) and Afrotropical realm (n = 38), while lizards and snakes reflected the overall, total reptile, patterns (Fig. 5 d). 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 (Fig.5 d). By 2080 species centroids were projected to shift by a mean distance of 111 km ± 0.9 SE mostly towards a southerly direction. Lizards showed a shift towards all directions, with a slight trend in the number of species towards the South (Fig. 5 a), while snakes and turtles show a more pronounced shift of species towards the North (Fig. 5 b, c). Turtle ranges shifted by the largest distances, followed by snakes (Fig. 5 a-c). The northern realms (Nearctic, Saharo-Arabian, Paleartic und Sino-Japanese) showed a dominant shift towards the North, while the southern realms (Neotropical, Afrotropical and Australian) showed a dominant shift towards the South. The Panamanian, Madagascan and Oriental realms also showed a northerly shift, while the Oceanian realm showed a bi-directional shift to the Northwest and Southeast (Fig. 5 d, Fig. S2.11). Large realms had a larger proportion of species that shifted their range for a larger distance (Fig. S2.11).

37.4 % of reptile species, for which data would have been available, could not be modeled using SDMs, either due to a small sample size or a low model performance (Table 1). We found that the species that could not be modeled showed a significant higher mean climatic distance between current and future conditions compared to the modeled species and thus occurred in areas that experience a stronger change in climatic conditions. This pattern was consistent across all three taxa (Fig. 6).

Looking at the sum of occurrence probabilities, we found similar spatial patternsand a similar magnitude in change (Fig. S3.13 - S3.15). Projected richness values and their future changes were slightly larger under a larger dispersal ability (d/4), but overall all results were consistent across the three dispersal scenarios considered (Fig. S4.16 - S4.21). Climate change impacts on future species richness increased over time, with stronger effects seen for 2080 than 2050, and

the strongest impacts being observed under a high emission scenario (RCP8.5) compared to the two lower scenarios (Fig. S5.22 - S5.32).

Discussion

Reptile richness was projected to decrease significantly across most parts of the world in the future (Fig. 1 & 2). This effect was visible across lizards, snakes and turtles alike, although regional and species-specific responses differed across the three groups (Fig. S2.7 - S2.10).

Reptile richness is projected to decrease in Brazil, Australia and South Africa, and to increase in south-western China and the western United Sates (Fig. 1 e). These areas overlap strongly with the biotic convergence zones identified for the conservation of Lepidosaurians (Diele-Viegas *et al.*, 2020). Brazil in particular is not only characterized by a high reptile richness (Roll *et al.* (2017), Fig. 1 a), but also hosts a large proportion of threatened reptile species (Böhm *et al.*, 2013). Furthermore, most protected areas within Brazil are only of low conservation status (IUCN Categories V - VI) and the stricter ones underrepresent a large proportion of the Brazilian biophysical environment (Baldi *et al.*, 2019). While the areas that were projected to show an increase in reptile richness with climate warming, i.e. south-west China and the western United States, partially overlap with the areas that have the largest proportion of reptile species, they are also the ones most threatened by habitat loss from agriculture and logging or harvesting (Böhm *et al.*, 2013).

Species richness changes varied strongly across different regions and different taxa, with lizards seeing a strong species increase and decrease in Australia, snakes seeing a strong decrease in species richness in South America and turtles seeing a strong increase in the eastern part of the United States (Fig. S2.7). All three taxa saw a positive net change in the northern latitudes (Fig. S2.7), while lizards saw a decrease in parts of Australia (Fig. S2.7 a,b), snakes in large parts of South America (Fig S.2.7 c,d) and turtles saw a strong relative net change in parts of Australia and northern Africa (Fig S2.7 f). These differences across groups are also reflected in their original richness patterns. Species richness of amphibians, birds and mammals together is a good spatial surrogate for species richness of all reptiles combined and of snakes, but not 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 Fig. 1) strongly overlap 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 largely constrained by temperature, while global richness of all other vertebrate groups is mostly constrained by the availability of energy and water (Qian, 2010). Historical shifts in geographical ranges and climatic niches further showed that niche shifts in endotherms are significantly faster than in ectotherms (Rolland *et al.*, 2018). Newbold (2018) further found that Brazil is strongly affected by vertebrate diversity loss due 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).

Globally reptile richness was projected to decline significantly, from about 58 to 53 (9.4 %) species on average per grid cell from 1995 to 2080 (Fig. 2 a). This estimate is slightly lower than the reptile richness decline predicted by Newbold (2018). One explanation for this difference could be that Newbold (2018) only used a subset of species but they also applied a much smaller dispersal buffer, which might indicate that our projections provide a rather optimistic scenario. Newbold (2018) further found that reptiles together with amphibians are disproportionately

sensitive to future human land-use. Given the synergistic effect of future climate and land-use change on biodiversity (Brook *et al.*, 2008) as well as species population s (Williams *et al.*, 2022), land-use change might further exacerbate climate change impacts on global reptile distribution and diversity.

Changes in reptile richness differed among zoogeographic realms, but species richness declined significantly across most realms over both time periods (Fig. 2 b,c,d,f,g,h,j,k). Lizards, snakes and turtles all showed similar declines in global species richness and across most realms, but slightly differed 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). We found that only the Oceanian and Madagascan realms did not show a consistent decline in species richness, which partially corresponds with the results of Diele-Viegas *et al.* (2020), who found that the Madagascan and Oceanian realm were the ones where Lepidosaurians were the least vulnerable to climatic change. However, given that the Madagascan realm boasts over 90% of endemic reptile species and genera (Glaw & Vences, 2007) and that both realms are completely 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 in fact underestimate potential climate change impacts in these realms.

Reptile richness differed strongly across temperature and precipitation, with the highest richness being observed in warm, but moist conditions. Under future climate, the climatic conditions with high species richness were projected to shift to even more extreme (warmer & wetter) conditions (Fig. 3). Reptiles cannot regulate their body temperature internally, so are strongly dependent on solar energy captured by the environment to regulate their body temperature (Huey, 1982). This might lead to overheating when temperatures reach beyond a species' critical limit, which makes them particularly susceptible to climatic changes (Sinervo *et al.*, 2018). However, this might be compensated by other biological processes that help species to buffer climate change effects, i.e. genomic and phenotypic plasticity (Rodríguez *et al.*, 2017) as well as behavioral and physiological adaptation Sunday *et al.* (2014). Overall, the persistence of reptile species would be much more affected by climate cooling than warming, but increasing droughts, which will be a consequence of continued warming, have been suggested to pose a significant future threat to European reptiles (Araújo *et al.*, 2006). Climate warming will likely have an additional impact on reptiles that have temperature-dependent sex determination. Altered sex ratios will not only result in a higher extinction risk of local populations, but, together with a reduction in nesting sites due 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 evolves in pace with rising temperatures (Boyle *et al.*, 2016; Gibbons *et al.*, 2000).

The EOO of most species considerably decreased, with lizard species showing the strongest decline (Fig. 4 a). Most reptiles further showed a strong decline in range overlap, which was consistent across all three groups (Fig. 4). This is in line with results by Warren *et al.* (2018), who found that range losses of more than 50% occur in 35% of considered reptile species, although this study included only a fraction of all reptile species and dispersal was not considered.

Terrestrial reptiles have narrow niche requirements and small ranges, compared to other vertebrate groups, which makes them more susceptible to threats such as habitat loss or invasive species (Böhm *et al.*, 2013). 21 % of reptilian species are currently threatened with extinction (IUCN, 2022), while adequate baseline data to inform conservation actions is often missing (Roll *et al.*, 2017). 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 by climate change alone (Zipkin *et al.*, 2020).

The majority of reptile species showed a shift towards the South, which was largely driven by range shifts in lizards. Turtle ranges overall shifted farthest, followed by snakes (Fig. 5). This is likely due to the fact that lizards have the smallest range sizes across the three groups (Roll *et al.*, 2017), which in our case also resulted in smaller dispersal distances (Fig. S1.3).

Range restricted (non-modeled) species are projected to experience significantly higher shift in climatic distance than modeled species (Fig. 6), indicating that range-restricted species are disproportionately affected by climate change. This highlights once more that sample size restrictions of SDMs downplay climate change effects on narrow-ranging and threatened species (Platts *et al.*, 2014). Hof *et al.* (2018) also found significant impacts of climate and land-use changes on range-restricted vertebrate species, excluding reptiles. However, similar to the latter study we only look at climate anomalies (Euclidean distance between current and future climatic conditions) as a metric of climate change, while different metrics have been found to show contrasting climate change patterns on a global scale (Garcia *et al.*, 2014). In addition to climate change effects, habitat modification has been found to have a more negative effect on small-ranging reptile species, as well as species with a small clutch size (Doherty *et al.*, 2020). While habitat modification would be an additional factor worthwhile to consider in future impact assessments, this would go beyond the scope of this study.

Our results were strongly dependent on the dispersal, time period and emission scenario (RCP) considered, but the overall patterns and richness changes were consistent throughout (see Supporting Information). Previous studies have highlighted differences among dispersal, time period and RCP across various vertebrate taxa (Thuiller *et al.*, 2019), but also specifically for reptiles (Araújo *et al.*, 2006; Newbold, 2018; Warren *et al.*, 2018). Reptile-specific studies have either considered no dispersal at all (Araújo *et al.*, 2006; Warren *et al.*, 2018) or a dispersal rate of 0.5 km per year (Newbold, 2018). We use a slightly higher biologically informed dispersal scenario, with an average of 2-5 km per year, which might be overly optimistic. The considered dispersal distances are species-specific and thus strongly depend on the range size of each species. Given that our model results as well as the underlying climate scenarios are based on a 0.5° grid size, small differences in the dispersal distances considered here did not have a strong impact on our results (see Appendix S4).

The projected changes in species distributions help to investigate potential changes in global reptile richness patterns and to highlight hotspots of climate change impacts. They also allow to compare climate change vulnerability across taxonomic groups. However, these projections are far from reality and have to be interpreted with caution. Future studies should try to consider additional factors, such as biotic interactions (Davis *et al.*, 1998) 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).

Conclusion

In addition to climate and land-use changes, reptile species are threatened by habitat loss and degradation, invasive species, environmental pollution, disease and biological resource use (e.g., hunting and timber harvesting) (Gibbons *et al.*, 2000, Chapple2021).

Existing protected areas, sites of biodiversity significance and global conservation schemes do not effectively protect reptiles, particularly lizards and turtles (Roll *et al.*, 2017) and 61% of the world's skinks do not overlap at all with protected areas (Chapple *et al.*, 2021). The climatic space of protected areas is projected to shift considerably with future climate warming (Elsen *et al.*, 2020), though even if existing nature reserves would adequately represent reptiles now, they might be inadequate to preserve biodiversity in the future.

Our study shows that reptiles are likely to be considerably impacted by future climate change, globally but also within most zoogeographic realms. These impacts are projected to have a considerable effect on species' extent of occurrence and range position. Thus, to prevent large scale declines in reptile species it is detrimental to lower CO_2 emissions in order to stop on-going climate change but also to maintain adequate habitats of sufficient size and quality, especially of grassland and savanna habitats (Roll *et al.*, 2017). Furthermore it is necessary to establish new protected areas that 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).

References

Allouche, O., Tsoar, A. & Kadmon, R. (2006) Assessing the accuracy of species distribution models: Prevalence, kappa and the true skill statistic (TSS). *Journal of Applied Ecology*, **43**, 1223–1232.

Araújo, M.B., Thuiller, W. & Pearson, R.G. (2006) Climate warming and the decline of amphibians and reptiles in europe. *Journal of Biogeography*, **33**, 1712–1728.

Bagchi, R., Crosby, M., Huntley, B., Hole, D.G., Butchart, S.H., Collingham, Y., Kalra, M., Rajkumar, J., Rahmani, A., Pandey, M. & others (2013) Evaluating the effectiveness of conservation site networks under climate change: Accounting for uncertainty. *Global Change Biology*, **19**, 1236–1248.

Baisero, D., Visconti, P., Pacifici, M., Cimatti, M. & Rondinini, C. (2020) Projected global loss of mammal habitat due to land-use and climate change. *One Earth*, **2**, 578–585.

Baldi, G., Schauman, S., Texeira, M., Marinaro, S., Martin, O.A., Gandini, P. & Jobbágy, E.G. (2019) Nature representation in south american protected areas: Country contrasts and conservation priorities. *PeerJ*, **7**, e7155.

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W. & Courchamp, F. (2012) Impacts of climate change on the future of biodiversity. *Ecology Letters*, **15**, 365–377.

Biber, M.F., Voskamp, A., Niamir, A., Hickler, T. & Hof, C. (2020) A comparison of macroecological and stacked species distribution models to predict future global terrestrial vertebrate richness. *Journal of Biogeography*, **47**, 114–129.

Böhm, M., Collen, B., Baillie, J.E., Bowles, P., Chanson, J., Cox, N., Hammerson, G., Hoffmann, M., Livingstone, S.R., Ram, M. & others (2013) The conservation status of the world's reptiles. *Biological conservation*, **157**, 372–385.

Bowler, D.E., Hof, C., Haase, P., Kröncke, I., Schweiger, O., Adrian, R., Baert, L., Bauer, H.-G., Blick, T., Brooker, R.W. & others (2017) Cross-realm assessment of climate change impacts on species' abundance trends. *Nature ecology & evolution*, **1**, 1–7.

Boyle, M., Schwanz, L., Hone, J. & Georges, A. (2016) Dispersal and climate warming determine range shift in model reptile populations. *Ecological Modelling*, **328**, 34–43.

Brook, B.W., Sodhi, N.S., & Bradshaw, C.J.A. (2008) Synergies among extinction drivers under global change. *Trends in Ecology & Evolution*, *23*, 453–460.

Calabrese, J.M., Certain, G., Kraan, C. & Dormann, C.F. (2014) Stacking species distribution models and adjusting bias by linking them to macroecological models. *Global Ecology and Biogeography*, **23**, 99–112.

Chapple, D.G., Roll, U., Böhm, M., Aguilar, R., Amey, A.P., Austin, C.C., Baling, M., Barley, A.J., Bates, M.F., Bauer, A.M. & others (2021) Conservation status of the world's skinks (scincidae): Taxonomic and geographic patterns in extinction risk. *Biological Conservation*, **257**, 109101.

Chen, I.-C., Hill, J.K., Ohlemüller, R., Roy, D.B. & Thomas, C.D. (2011) Rapid range shifts of species associated with high levels of climate warming. *Science*, **333**, 1024–1026.

Davis, A.J., Jenkinson, L.S., Lawton, J.H., Shorrocks, B. & Wood, S. (1998) Making mistakes when predicting shifts in species range in response to global warming. *Nature*, **391**, 783–786.

Diele-Viegas, L.M., Figueroa, R., Vilela, B. & Rocha, C. (2020) Are reptiles toast? A worldwide evaluation of lepidosauria vulnerability to climate change. *Climatic Change*, **159**, 581–599.

Doherty, T.S., Balouch, S., Bell, K., Burns, T.J., Feldman, A., Fist, C., Garvey, T.F., Jessop, T.S., Meiri, S. & Driscoll, D.A. (2020) Reptile responses to anthropogenic habitat modification: A global meta-analysis. *Global Ecology and Biogeography*, **29**, 1265–1279.

Elith, J., Kearney, M. & Phillips, S. (2010) The art of modelling range-shifting species. *Methods in Ecology and Evolution*, **1**, 330–342.

Elith, J. & Leathwick, J.R. (2009) Species distribution models: Ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics*, **40**, 677–697.

Elsen, P.R., Monahan, W.B., Dougherty, E.R. & Merenlender, A.M. (2020) Keeping pace with climate change in global terrestrial protected areas. *Science advances*, **6**, eaay0814.

Engelhardt, E.K., Neuschulz, E.L. & Hof, C. (2020) Ignoring biotic interactions overestimates climate change effects: The potential response of the spotted nutcracker to changes in climate and resource plants. *Journal of Biogeography*, **47**, 143–154.

Frieler, K., Lange, S., Piontek, F., Reyer, C.P., Schewe, J., Warszawski, L., Zhao, F., Chini, L., Denvil, S., Emanuel, K. & others (2017) Assessing the impacts of 1.5°c global warming–simulation protocol of the inter-sectoral impact model intercomparison project (ISIMIP2b). *Geoscientific Model Development*, **10**, 4321–4345.

Garcia, R.A., Cabeza, M., Rahbek, C. & Araújo, M.B. (2014) Multiple dimensions of climate change and their implications for biodiversity. *Science*, **344**, 1247579.

Gibbons, J.W., Scott, D.E., Ryan, T.J., Buhlmann, K.A., Tuberville, T.D., Metts, B.S., Greene, J.L., Mills, T., Leiden, Y., Poppy, S. & others (2000) The global decline of reptiles, déjà vu amphibians: Reptile species are declining on a global scale. Six significant threats to reptile populations are habitat loss and degradation, introduced invasive species, environmental pollution, disease, unsustainable use, and global climate change. *BioScience*, **50**, 653–666.

Gibson-Reinemer, D.K. & Rahel, F.J. (2015) Inconsistent range shifts within species highlight idiosyncratic responses to climate warming. *PloS One*, **10**, e0132103.

Glaw, F. & Vences, M. (2007) *A field guide to the amphibians and reptiles of madagascar*, Vences & Glaw.

Greenwell, B., Boehmke, B., Cunningham, J. & Developers, G. (2020) *Gbm: Generalized boosted regression models*,.

Harley, C.D. (2011) Climate change, keystone predation, and biodiversity loss. *Science*, **334**, 1124–1127.

Hijmans, R.J., Phillips, S., Leathwick, J. & Elith, J. (2021) *Dismo: Species distribution modeling*,.

Hof, C., Araújo, M.B., Jetz, W. & Rahbek, C. (2011) Additive threats from pathogens, climate and land-use change for global amphibian diversity. *Nature*, **480**, 516–519.

Hof, C., Voskamp, A., Biber, M.F., Böhning-Gaese, K., Engelhardt, E.K., Niamir, A., Willis, S.G. & Hickler, T. (2018) Bioenergy cropland expansion may offset positive effects of climate change mitigation for global vertebrate diversity. *Proceedings of the National Academy of Sciences*, **115**, 13294–13299.

Holt, B.G., Lessard, J.-P., Borregaard, M.K., Fritz, S.A., Araújo, M.B., Dimitrov, D., Fabre, P.-H., Graham, C.H., Graves, G.R., Jønsson, K.A. & others (2013) An update of wallace's zoogeographic regions of the world. *Science*, **339**, 74–78.

Huey, R.B. (1982) *Temperature, physiology, and the ecology of reptiles*. *Biology of the reptilia*, Citeseer.

IPBES (2019) Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the intergovernmental science-policy platform on biodiversity and ecosystem services. *IPBES secretariat, Bonn, Germany*.

IPCC (2021) Climate change 2021: The physical science basis. Working group i contribution to the sixth assessment report of the intergovernmental panel on climate change. *Cambridge University Press*.

IPCC (2022) Climate change 2022: Impacts, adaptation and vulnerability. Working group II contribution to the sixth assessment report of the intergovernmental panel on climate change. *Cambridge University Press*.

IUCN (2022) The IUCN red list of threatened species. Available at https://www.iucnredlist.org/resources/spatial-data-download. *Cambridge University Press*.

Kühn, I. (2007) Incorporating spatial autocorrelation may invert observed patterns. *Diversity and Distributions*, **13**, 66–69.

Lange, S. (2016) EartH2Observe, WFDEI and ERA-interim data merged and bias-corrected for ISIMIP (EWEMBI).

Lenoir, J., Bertrand, R., Comte, L., Bourgeaud, L., Hattab, T., Murienne, J. & Grenouillet, G. (2020) Species better track climate warming in the oceans than on land. *Nature Ecology & Evolution*, **4**, 1044–1059.

Meynard, C.N. & Quinn, J.F. (2007) Predicting species distributions: A critical comparison of the most common statistical models using artificial species. *Journal of Biogeography*, **34**, 1455–1469.

Munoz, M.M., Stimola, M.A., Algar, A.C., Conover, A., Rodriguez, A.J., Landestoy, M.A., Bakken, G.S. & Losos, J.B. (2014) Evolutionary stasis and lability in thermal physiology in a group of tropical lizards. *Proceedings of the Royal Society B: Biological Sciences*, **281**, 20132433.

Nathan, R., Klein, E., Robledo-Arnuncio, J.J. & Revilla, E. (2012) *Dispersal kernels*, Oxford University Press Oxford, UK.

Newbold, T. (2018) Future effects of climate and land-use change on terrestrial vertebrate community diversity under different scenarios. *Proceedings of the Royal Society B*, **285**, 20180792.

Ockendon, N., Baker, D.J., Carr, J.A., White, E.C., Almond, R.E., Amano, T., Bertram, E., Bradbury, R.B., Bradley, C., Butchart, S.H. & others (2014) Mechanisms underpinning climatic impacts on natural populations: Altered species interactions are more important than direct effects. *Global Change Biology*, **20**, 2221–2229.

Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V., Underwood, E.C., D'amico, J.A., Itoua, I., Strand, H.E., Morrison, J.C. & others (2001) Terrestrial ecoregions of the world: A new map of life on EarthA new global map of terrestrial ecoregions provides an innovative tool for conserving biodiversity. *BioScience*, **51**, 933–938.

Pacifici, M., Foden, W.B., Visconti, P., Watson, J.E., Butchart, S.H., Kovacs, K.M., Scheffers, B.R., Hole, D.G., Martin, T.G., Akçakaya, H.R. & others (2015) Assessing species vulnerability to climate change. *Nature Climate Change*, **5**, 215–224.

Pecl, G.T., Araújo, M.B., Bell, J.D., Blanchard, J., Bonebrake, T.C., Chen, I.-C., Clark, T.D., Colwell, R.K., Danielsen, F., Evengård, B. & others (2017) Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science*, **355**, eaai9214.

Platts, P.J., Garcia, R.A., Hof, C., Foden, W., Hansen, L.A., Rahbek, C. & Burgess, N.D. (2014) Conservation implications of omitting narrow-ranging taxa from species distribution models, now and in the future. *Diversity and distributions*, **20**, 1307–1320.

Qian, H. (2010) Environment–richness relationships for mammals, birds, reptiles, and amphibians at global and regional scales. *Ecological Research*, **25**, 629–637.

R Core Team (2021) *R: A language and environment for statistical computing*, R Foundation for Statistical Computing, Vienna, Austria.

Rodríguez, A., Rusciano, T., Hamilton, R., Holmes, L., Jordan, D. & Wollenberg Valero, K.C. (2017) Genomic and phenotypic signatures of climate adaptation in an anolis lizard. *Ecology and evolution*, **7**, 6390–6403.

Roll, U., Feldman, A., Novosolov, M., Allison, A., Bauer, A.M., Bernard, R., Böhm, M., Castro-Herrera, F., Chirio, L., Collen, B. & others (2017) The global distribution of tetrapods reveals a need for targeted reptile conservation. *Nature Ecology & Evolution*, **1**, 1677–1682.

Rolland, J., Silvestro, D., Schluter, D., Guisan, A., Broennimann, O. & Salamin, N. (2018) The impact of endothermy on the climatic niche evolution and the distribution of vertebrate diversity. *Nature Ecology & Evolution*, **2**, 459–464.

Scheffers, B.R., De Meester, L., Bridge, T.C., Hoffmann, A.A., Pandolfi, J.M., Corlett, R.T., Butchart, S.H., Pearce-Kelly, P., Kovacs, K.M., Dudgeon, D. & others (2016) The broad footprint of climate change from genes to biomes to people. *Science*, **354**, aaf7671.

Sinervo, B., Miles, D.B., Wu, Y., MÉNDEZ-DE LA CRUZ, F.R., Kirchhof, S. & Qi, Y. (2018) Climate change, thermal niches, extinction risk and maternal-effect rescue of toad-headed lizards, phrynocephalus, in thermal extremes of the arabian peninsula to the qinghai—tibetan plateau. *Integrative zoology*, **13**, 450–470.

Stewart, P.S., Voskamp, A., Santini, L., Biber, M.F., Hof, C., Willis, S.G. & Tobias, J.A. (2022) Global impacts of climate change on avian functional diversity. *Ecology Letters*.

Sunday, J.M., Bates, A.E., Kearney, M.R., Colwell, R.K., Dulvy, N.K., Longino, J.T. & Huey, R.B. (2014) Thermal-safety margins and the necessity of thermoregulatory behavior across latitude and elevation. *Proceedings of the National Academy of Sciences*, **111**, 5610–5615.

Thuiller, W., Guéguen, M., Renaud, J., Karger, D.N. & Zimmermann, N.E. (2019) Uncertainty in ensembles of global biodiversity scenarios. *Nature Communications*, **10**, 1–9.

Thuiller, W., Lavorel, S., Araújo, M.B., Sykes, M.T. & Prentice, I.C. (2005) Climate change threats to plant diversity in europe. *Proceedings of the National Academy of Sciences*, **102**, 8245–8250.

Tingley, R., Meiri, S. & Chapple, D.G. (2016) Addressing knowledge gaps in reptile conservation. *Biological Conservation*, **204**, 1–5.

Voskamp, A., Baker, D.J., Stephens, Philip A, Howard, C., Butchart, S.H. & Willis, S.G. (in prep) Impacts of climate change on the world's terrestrial bird assemblages.

Voskamp, A., Butchart, S.H., Baker, D.J., Wilsey, C.B. & Willis, S.G. (2021) Site-based conservation of terrestrial bird species in the caribbean and central and south america under climate change. *Frontiers in Ecology and Evolution*, **9**, 234.

Warren, R., Price, J., Graham, E., Forstenhaeusler, N. & VanDerWal, J. (2018) The projected effect on insects, vertebrates, and plants of limiting global warming to 1.5°c rather than 2°c. *Science*, **360**, 791–795.

Wiens, J.J. & Graham, C.H. (2005) Niche conservatism: Integrating evolution, ecology, and conservation biology. *Annual Review of Ecology, Evolution, and Systematics*, **36**, 519–539.

Williams, J.J., Freeman, R., Spooner, F. & Newbold, T. (2022) Vertebrate population trends are influenced by interactions between land use, climatic position, habitat loss and climate change. *Global change biology*, **28**, 797–815.

Wood, S.N. (2011) Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society (B)*, **73**, 3–36.

Wood, S.N. (2003) Thin-plate regression splines. *Journal of the Royal Statistical Society (B)*, **65**, 95–114.

Zipkin, E.F., DiRenzo, G.V., Ray, J.M., Rossman, S. & Lips, K.R. (2020) Tropical snake diversity collapses after widespread amphibian loss. *Science*, **367**, 814–816.

Data Accessibility Statement

GARD range maps are available from https://doi.org/10.5061/dryad.83s7k. EWEMBI and ISIMIP2b climate data are available from https://esg.pik-potsdam.de/search/isimip/?product=input. The code for the species distribution models can be found at **https://github.com/xxxx/xxxx**, whereas the code and data for the performed data analysis and the presented figures, can be found at **https://github.com/xxxx/xxxx**.

Tables

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

Taxonomic group	Lizard	Snake	Turtle	Total
No. of species with available data	6328	3414	322	10064
No. of range restricted species (N < 10, removed)	2536	1047	19	3602
No. of species with low model performance (AUC < 0.7, removed)	97	62	7	166
Total number of species modeled	**3695**	**2305**	**296**	**6296**
Percentage of available species modeled	58.4 %	67.5 %	91.9 %	62.6 %

Figures

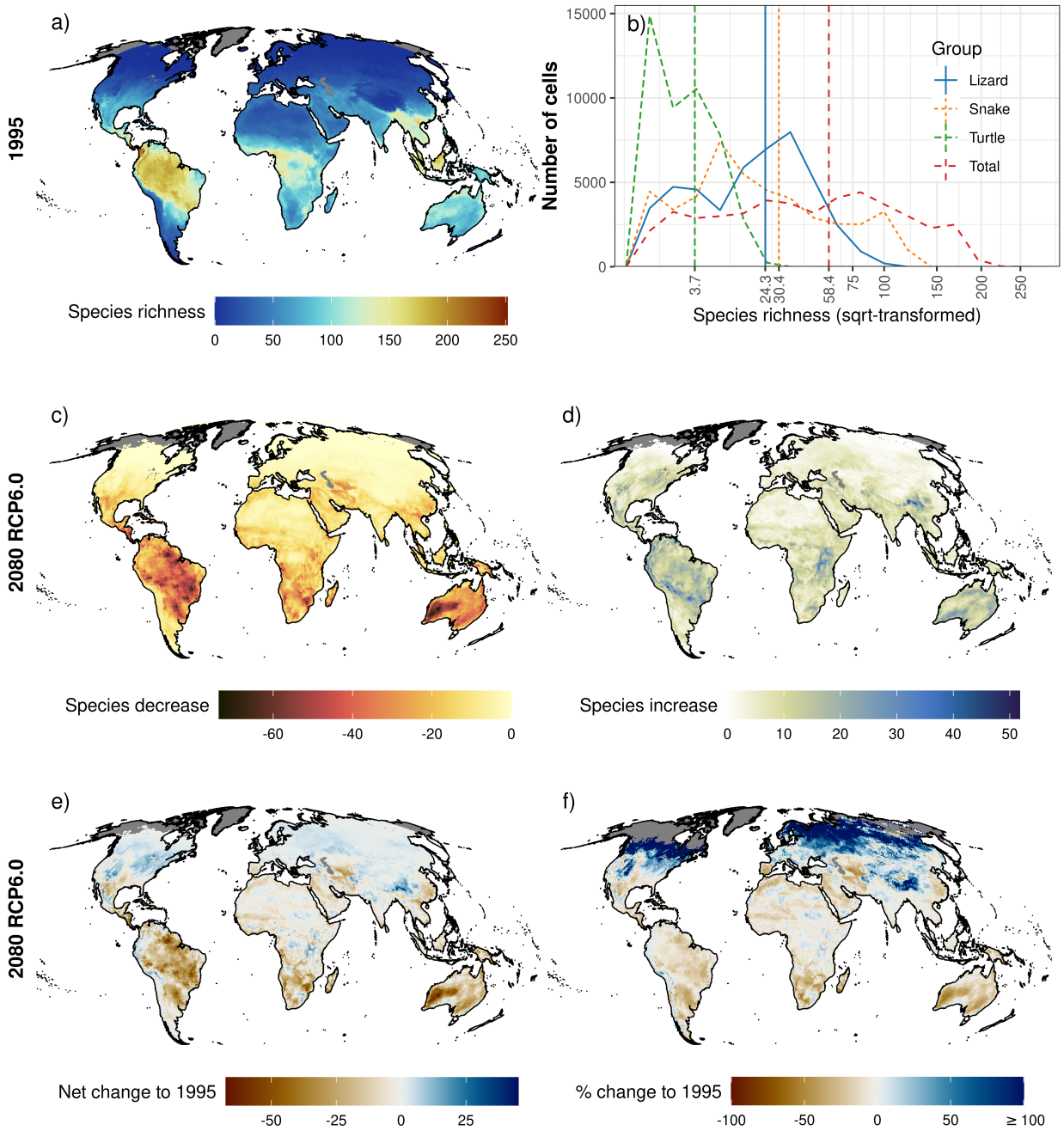

Figure 1. a) Map of projected global terrestrial reptile species richness (1995), b) frequency of species richness by taxonomic group (lizard, snake, turtle and total) and c) increase, d) decrease, e) net change and f) relative change (%) in reptile species richness under the representative concentration pathways RCP6.0 and dispersal scenario d/8 for the time period 2080. All maps are in Mollweide equal-area projection (EPSG:54009). Grey areas are regions for which no projections are available. Note that the colour scales differ between the individual panels.

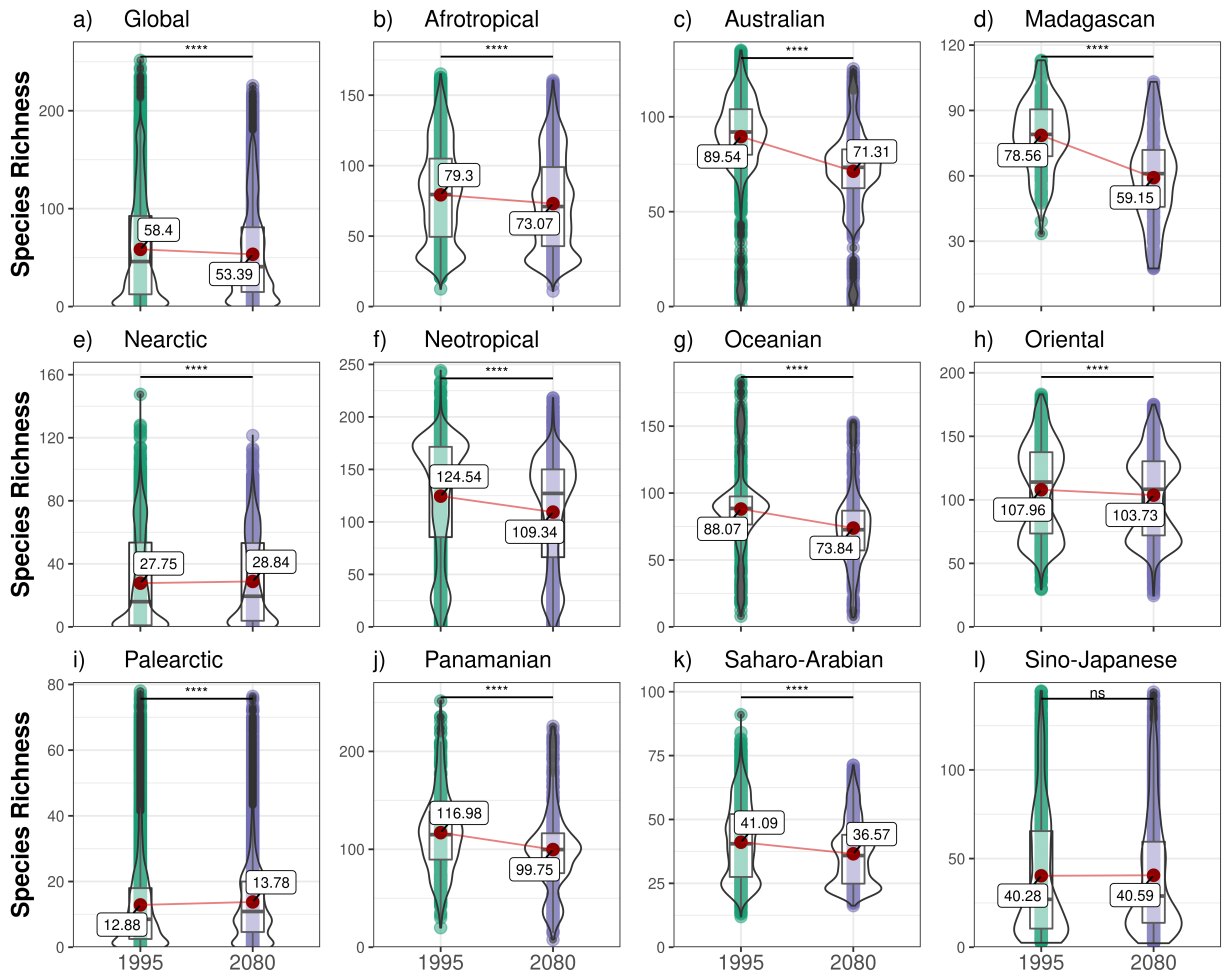

Figure 2. Terrestrial reptile species richness across the globe and for each zoogeographic realm (Afrotropical, Australian, Madagascan, Nearctic, Neotropical, Oceanian, Oriental, Palearctic, Panamanian, Saharo-Arabian & Sino-Japanese) over time (1995, 2080) under the representative concentration pathways RCP6.0 and the dispersal scenario d/8. Statistical difference between years was tested using a paired Student's t-test with Holm correction ($p < 0.05$ = *, $p < 0.01$ = **, $p < 0.001$ = ***, $p < 0.0001$ = ****). Plots show mean (red point & label), median (black horizontal line), 25th to 75th percentiles (box), entire range of data (violin & data points) and density of values (width of violin). Figure 5 provides a map outlining the different zoogeographic realms.

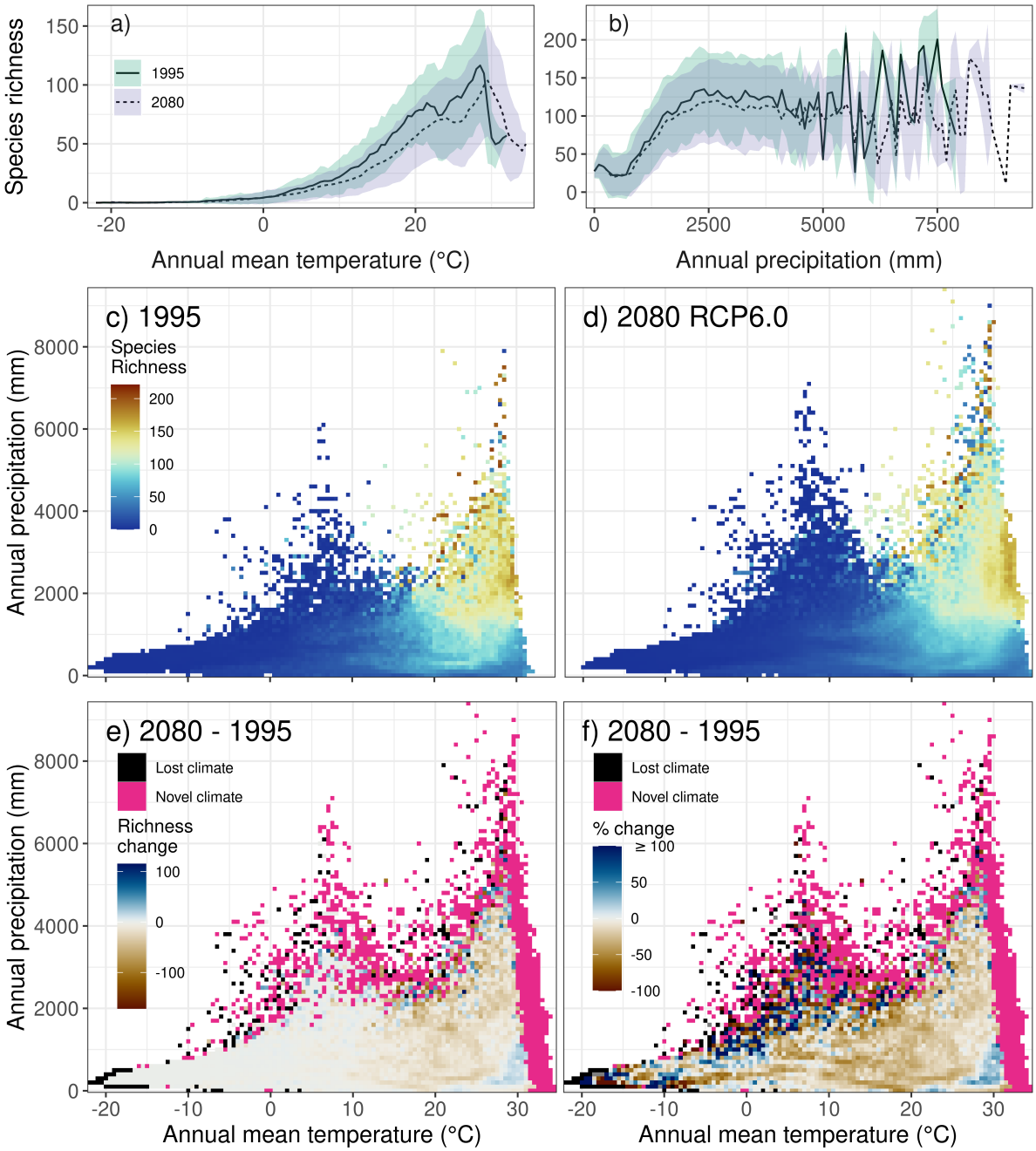

Figure 3. Univariate relationship of current (1995) and future (2080 RCP6.0) reptile species richness with a) temperature, b) precipitation and the bivariate relationship of temperature and precipitation with reptile species richness for c) 1995 and d) 2080 RCP6.0 and the respective e) net richness change and f) relative richness change (%) under the dispersal scenario d/8. Lines show the mean and ribbons the standard deviation in variance across space, global circulation model and algorithm.

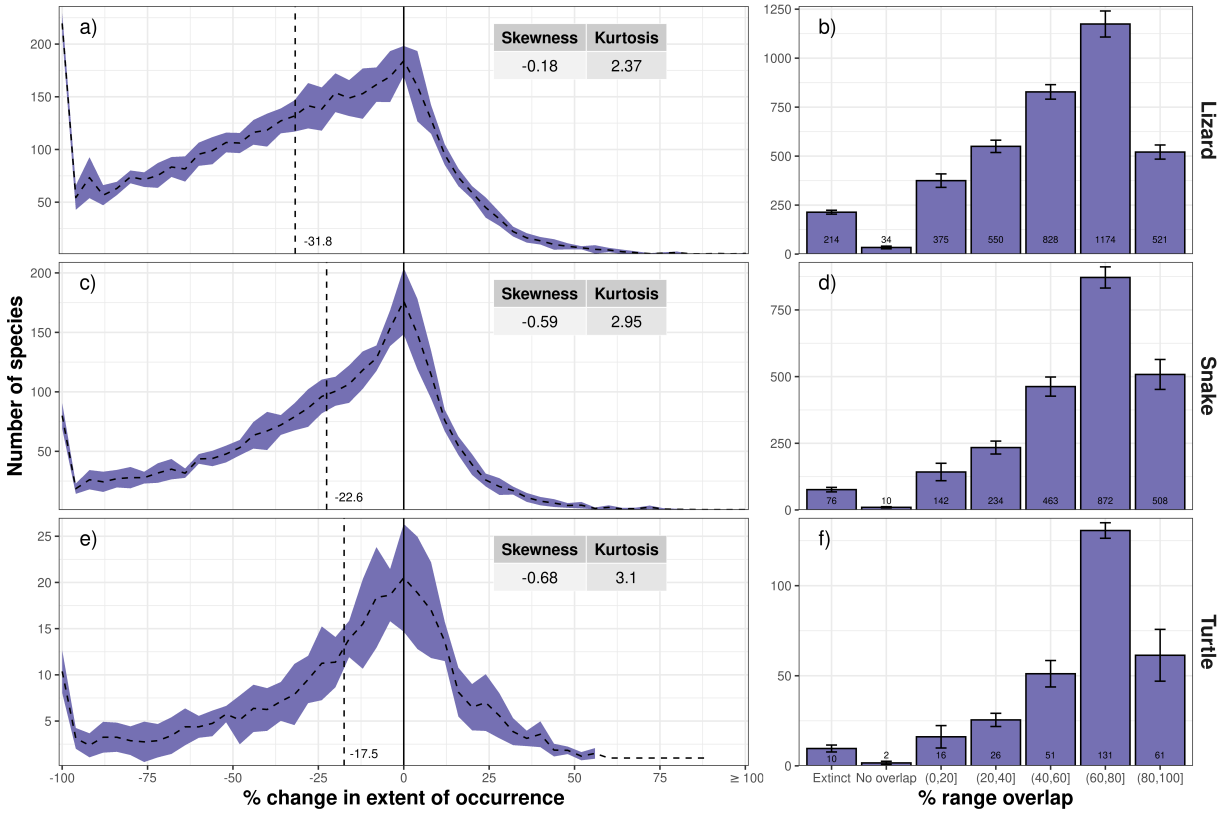

Figure 4. Frequency plots of the mean number of reptile species (a) lizard, b) snake, c) turtle) and their potential future change (%) in extent of occurrence (EOO) and the mean number of reptile species (d) lizard, e) snake, f) turtle) per potential range overlap class (0-20, 20-40, 40-60, 60-80, 80-100). Error margins/bars show standard deviation across the different global circulation models and model algorithms used. Both shown for 2080 under the representative concentration pathway RCP6.0 and the dispersal scenario d/8.

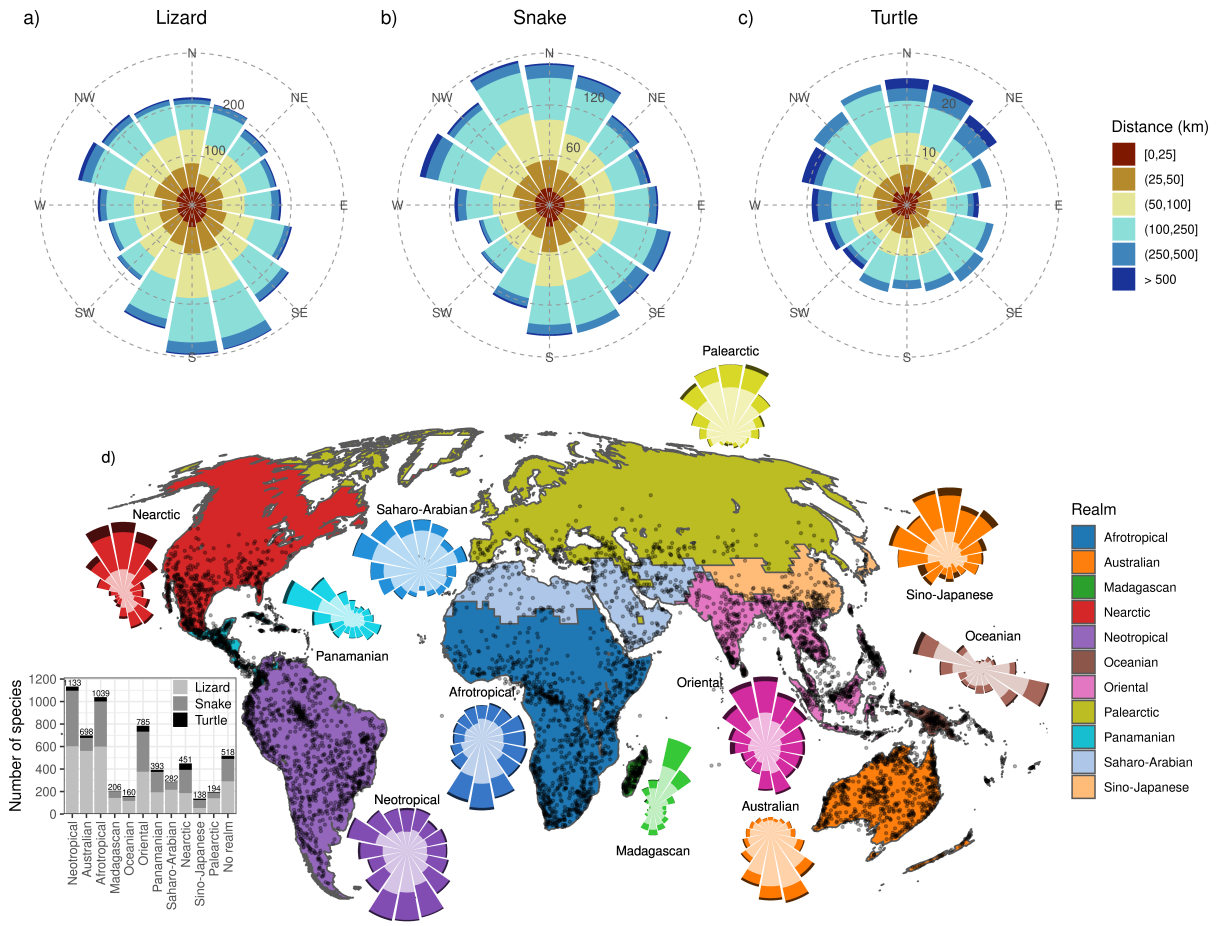

Figure 5. Cumulative direction and distance of potential range centroid changes per taxonomic group (b) lizard, c) snake, d) turtle) and d) range centroids (points on map) and the number of species and their directional shift in range centroid position per zoogeographic realm (inset polar plots) for 2080 under the representative concentration pathway RCP6.0 and the dispersal scenario d/8. Please note that some range centroids did not fall inside the zoogeographic realm boundaries and thus were not associated with an realm (n = 477).

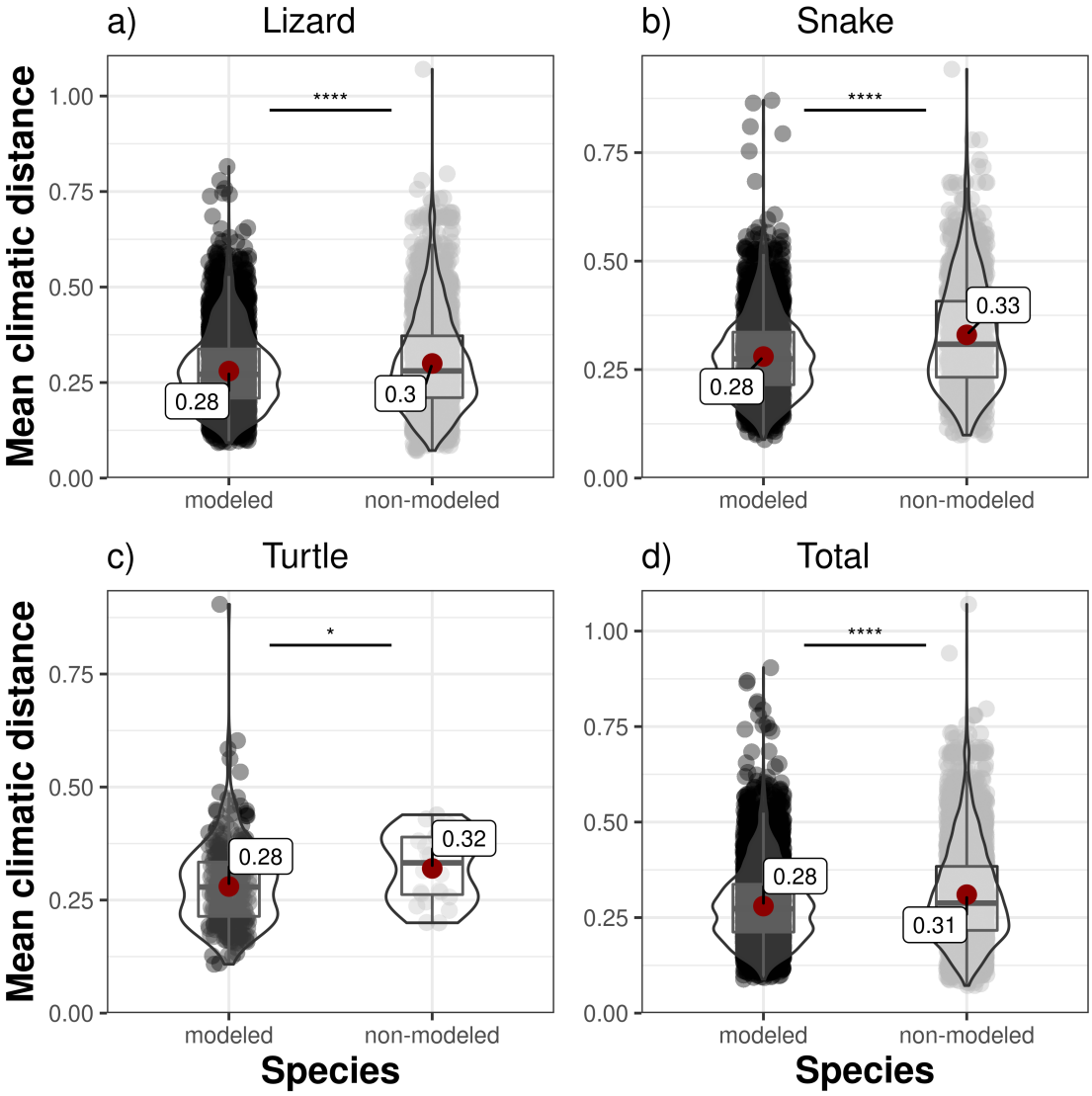

Figure 6. Mean climatic distance for modeled and non-modeled species, split by taxonomic group (a) lizard, b) snake, c) turtle and d) total). Statistical difference between modeled and non-modeled species was tested using a Student's t-test with Holm correction ($p < 0.05$ = *, $p < 0.01$ = **, $p < 0.001$ = ***, $p < 0.0001$ = ****). Plots show mean (red point & label), median (black horizontal line), 25th to 75th percentiles (box), entire range of data (violin & data points) and density of values (width of violin). Results are shown for 2080 under the representative concentration pathway RCP6.0.