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Projected Increases in Climate Extremes Across Global Vertebrate Diversity Hotspots

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ABSTRACT

Climate change intensifies periods of climate extremes globally, threatening biodiversity. Vertebrates vulnerable to climate extremes are identified by the International Union for Conservation of Nature, though future changes in these species' exposure remain unclear. Using CMIP6 climate models under four shared socioeconomic pathways, we projected changes in extreme drought, heat, and precipitation frequencies between 1974–2014 and 2050–2090 for 1634 terrestrial vertebrates considered threatened by climate extremes, focusing on 33 vertebrate diversity hotspots. Results indicate substantial exposure increases, with tropical regions facing the largest relative increases in extreme heat and drought. Hotspots with fewer vertebrates considered vulnerable to climate extremes often face larger increases in climate extremes, suggesting vertebrate vulnerability within numerous hotspots is understudied. These results highlight the need to widely incorporate climate projections into conservation assessments, and for targeted research on the effects of climate extremes on tropical vertebrates, which may have lower tolerances to climatic change than temperate counterparts.

1 | Introduction

Climate extremes, such as anomalous drought, heat, and precipitation, are becoming more frequent, severe, and widespread due to anthropogenic climate change, posing serious threats to human societies and jeopardizing natural ecosystems and their wildlife (IPCC 2021). Wildlife may be affected directly through physiological stressors such as heat stress, hypothermia, or dehydration, and indirectly when climate extremes alter vertebrate habitat in ways impeding reproduction or survival (Blaustein et al. 2010). Such vulnerabilities can increase vertebrate extinction risks, particularly when they compound with other environmental stressors, including habitat destruction, disease, or pollution (Blaustein et al. 2010). Projecting the potential geographic distribution and frequencies of future climate extremes is critical for assessing their future effects on vertebrate species.

Climate change effects on wildlife are often studied with a focus on the greatest projected mean changes in climatic conditions (Diffenbaugh and Giorgi 2012). However, wildlife may be more vulnerable to changes in the frequency of climate extremes than to a shift in central tendency (Murali et al. 2023; Román-Palacios and Wiens 2020). Further, the ultimate impact on vertebrate populations also depends on a species' inherent vulnerability to the type of climate anomaly, which is linked to its evolutionary history. The climate stability hypothesis states that vertebrates in tropical regions have evolved under relatively stable climate conditions and are therefore more vulnerable to climatic changes (Janzen 1967); with evidence for this hypothesis found across endo-nd ectothermic vertebrates (Gutiérrez-Pesquera et al. 2016; Khaliq et al. 2014).

The International Union for Conservation of Nature (IUCN) assigns conservation threats underlying a species' conservation status as threatened or nonthreatened, and these include climate-related threats such as storms and flooding, drought, and temperature extremes (IUCN 2024). While these categories are useful for conservation planning, they rely on expert opinion, making them susceptible to subjectivity and bias (Trull et al. 2018; Hayward 2009). Thus, the number of species categorized as threatened by climate change, including climate extremes, may be underestimated, especially for species with limited historical exposure to such stressors (Harfoot et al. 2021; Trull et al. 2018; Ameca y Juárez et al. 2013). The spatial overlap between areas projected to experience notable increases in exposure to climate extremes and the ranges of vertebrates identified as threatened by climate extremes is currently unknown.

To address this knowledge gap, we examined changes in frequencies with which terrestrial vertebrates considered by IUCN to be threatened by extreme drought, heat, and storms and flooding are projected to be exposed to climate extremes in the second half of the 21st century. Using climate models from CMIP6, we analyzed climate extreme projections under four shared socioeconomic Pathways (SSP1-2.6, SSP2-4.5, SSP3-7.0, and SSP5-8.5) and identified exposure changes for four Global Climate Models (GCMs). These GCMs represent a range of future outcomes, from mild warming with increased precipitation to extreme heat and severe drought. We focused on 33 hotspots that collectively harbor most of the world's vertebrate diversity, testing the spatial intersection of changing climate extremes and species with corresponding threat assignments.

2 | Methods

2.1 | Hotspot and Species Range Data

The IUCN uses threat classifications to list factors underlying the extinction risk of species resulting in a particular conservation status (Hayward 2009). To obtain a subset of vertebrates of particular interest regarding changes in the frequency of climate extremes, we extracted ranges of terrestrial year-round resident vertebrates (IUCN-code: Extant—resident; $n=1634$) in the classes of amphibians, birds, mammals, and reptiles from the IUCN database considered threatened by drought ($n=1143$), storms and flooding ($n=531$) and temperature extremes ($n=392$; IUCN 2024). Our analysis focused on projected increases in drought exposure for drought-threatened vertebrates and on increases in extreme heat for those considered threatened to temperature extremes, while the threat category of storms and flooding most closely related to projected increases in extreme precipitation. We summarized results across 33 global hotspots of terrestrial vertebrate diversity defined by Jenkins et al. (2013). These represent a modified version of the 25 Myers' flora-based biodiversity hotspots, which range between −45° S and 45° N and comprise 85% of global diversity in bird, mammal, and amphibian species, while also having high spatial overlap with global reptile diversity (Biber et al. 2023). The most notable additions by Jenkins et al. (2013) are hotspots in parts of the Amazon Basin and northeastern coastal South America, the Eastern Afromontane hotspot adjacent to the already existing hotspot in eastern Africa, as well as hotspots for the Himalaya region, forested eastern Australia, Tasmania, Papua Island, and most of Japan. Other Myers' hotspots were downsized, such as the California Floristic Province hotspot which was reduced to a smaller 'Oregon hotspot', and some were removed, such as the Mediterranean Basin and Caucasus hotspots. We adapted names of the original Myers' hotspots and named additional hotspots corresponding to their general geographic location (Figure 1).

2.2 | Climate Data

We analyzed frequency changes in three types of climate extremes: extreme heat, drought, and extreme precipitation. The Copernicus Climate Atlas (C3S 2024) uses climate stripes to quantify variability among GCMs. To capture the range of potential future scenarios, we used these climate stripes for the entire globe, excluding the Antarctic and areas without landmass, to identify GCMs that project the lowest, middle, or highest amounts of change in monthly means of daily maximum temperature and monthly means of daily precipitation between 1974–2014 and 2050–2090. Despite the exclusion of seas and the Antarctic landmass we will refer to our study area as 'global', as it includes virtually all terrestrial vertebrate diversity. We identified four GCMs representing the greatest global increases between 1974–2014 and 2050–2090 in temperature ("Hot"; ACCESS-CM2), median increases in precipitation and temperature ("Middle"; EC-Earth3-veg-LR), lowest increases in temperature which also represented greatest increases in precipitation ("Cold–wet"; INM-CM4-8), and greatest decreases in precipitation ("Dry"; GFDL-ESM4). For each variable under each GCM, we downloaded CMIP6 monthly climate projections for a recent historical (1973–2014) and future (2049–2090) period (C3S 2021). We reprojected all data to the coarsest common resolution, which was $2° \times 1.5°$. We extracted future period data under four different shared socioeconomic pathways (SSP1-2.6, SSP2-4.5, SSP3-7.0, and SSP5-8.5), whereby SSP1-2.6 is the pathway with the fewest greenhouse gas emissions, thus lowest global mean temperature increase, and SSP5-8.5 implies the highest emissions (Rogelj et al. 2018).

Projected changes in frequencies of climate extremes were calculated using precipitation and temperature data for four modeled historical climates, one per GCM, and sixteen modeled future climate scenarios (hereafter; future scenarios)—four GCMs under each of the four SSPs.

2.3 | Climate Data Calculations

We used the Standardized Precipitation Index (SPI) to calculate past and future extreme drought and precipitation (McKee et al. 1993), whereby SPI values represent the deviation of accumulated precipitation from a historical average. Negative SPI values indicate drier conditions, and positive values indicate wetter conditions than the reference period. Using rolling time windows, monthly SPI values represent accumulated precipitation over a given number of months preceding the target month. We

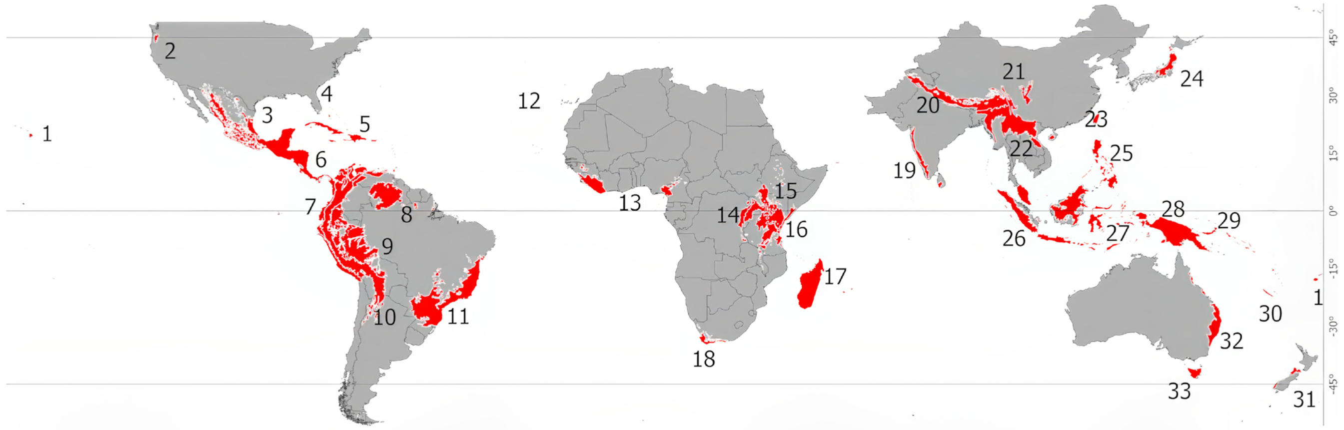

FIGURE 1 | The 33 global hotspots of terrestrial vertebrate diversity, based on Jenkins et al. (2013), which together are a modified version of the 25 Myers' flora-based biodiversity hotspots. These hotspots range between about −45° S and 45° N and comprise 85% of global terrestrial vertebrate diversity. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

calculated SPI values on a 12-month timescale, as effects of anomalous precipitation or drought conditions on wildlife can occur on, or increase with, longer timescales (Cady et al. 2019; Prugh et al. 2018). We calculated SPI using the ‘SPEI’ package (Beguería et al. 2014) in R (R Core Team 2025), with 1973–2014 specified as the historical reference period to obtain SPI values for historical climates ranging 1974–2014 and future climates ranging 2050–2090. Precipitation data from 1973 and 2049 were used to calculate accumulated precipitation for 1974 and 2050 SPI values, respectively. We used monthly means of daily maximum temperature for historical climates (1974–2014) and future climates (2050–2090) to calculate past and future frequencies of heat extremes.

2.4 | Calculation of Changes in Climate Extreme Frequencies

To define temperature and precipitation extremes, we used the historical 10th or 90th percentile of climate variables, as has been used by the Intergovernmental Panel on Climate Change (Seneviratne et al. 2012). For each GCM we stacked historical monthly SPI rasters and calculated the 10th percentile of the stacks to obtain extreme drought thresholds and the 90th percentiles of historical SPI and temperature values to obtain extreme precipitation and heat thresholds, respectively. For each future scenario, we calculated the sum of months exceeding the historical extremity threshold of the corresponding GCM. For each combination of the four GCMs and SSPs, we subtracted historical counts from future counts of climate extremes to obtain 16 rasters of projected frequency changes in climate extremes between 1974–2014 and 2050–2090.

For all ranges of resident terrestrial vertebrates the IUCN considers threatened by drought, storms and flooding, or temperature extremes, we calculated projected exposure changes in the frequencies of extreme drought, extreme precipitation, and extreme heat, respectively, averaged across each species' range. Similarly, we extracted average frequency changes for each climate extreme for the 33 vertebrate hotspots. We also counted how many ranges of climate extreme-threatened vertebrates intersected with vertebrate hotspots.

3 | Results

3.1 | Increases in Frequencies of Climate Extremes for Threatened Vertebrates

Out of 1643 vertebrate species IUCN considers threatened by a climate extreme, 70% have drought as a conservation threat, and 66% are amphibians (Figure 2). Of vertebrates considered threatened by extreme temperatures or storms and floods, 55% and 37% are also drought-threatened, respectively. In total, 2066 threats are assigned across 1643 vertebrate species. Of the 1143 drought-threatened vertebrates, 74% occur in at least one hotspot, as do 87% of the 531 vertebrates threatened by storms and flooding, and 71% of the 392 vertebrates threatened by extreme temperatures. The projected increases in frequencies of climate extremes were similar for mammals, birds, amphibians, and reptiles (Figure 2).

In terms of extreme drought, 20%–40% (depending on the GCM) of drought-threatened vertebrates are projected to face extreme drought increases of up to 100% under SSP1-2.6. Under SSP5-8.5, many additional vertebrates may be exposed to increases over 100%, with up to 20% being exposed to increases in extreme drought over 300% (Figure 2). For extreme precipitation, 20%–50% of storm- and flood-threatened species would experience increases up to 100% under SSP1-2.6, with the number of affected species remaining relatively stable while percentages of increase rise proportionally across SSPs. Increases in extreme heat for temperature-threatened vertebrates would be of a higher magnitude, affecting all vertebrates under all climate scenarios. Up to 60% of species are projected to experience increases ranging 100%–200% under SSP1-2.6, while under SSP5-8.5, 40%–90% of species would see increases over 300%.

Vertebrate hotspots with few climate extreme-threatened vertebrates are often hotspots with the greatest predicted increases in exposure to climate extremes (Figure 3; Figure S1). For example, the Mesoamerica and Caribbean islands hotspots consistently have relatively high numbers of climate extreme-threatened vertebrates, whereas areas such as the Cape Floristic, Papua Island, and Sundaland hotspots have larger predicted changes in extreme heat and precipitation frequencies, but few species considered vulnerable to climate extremes.

Averaged across future scenarios, 29 of 33 vertebrate hotspots are projected to have greater increases in extreme heat frequency

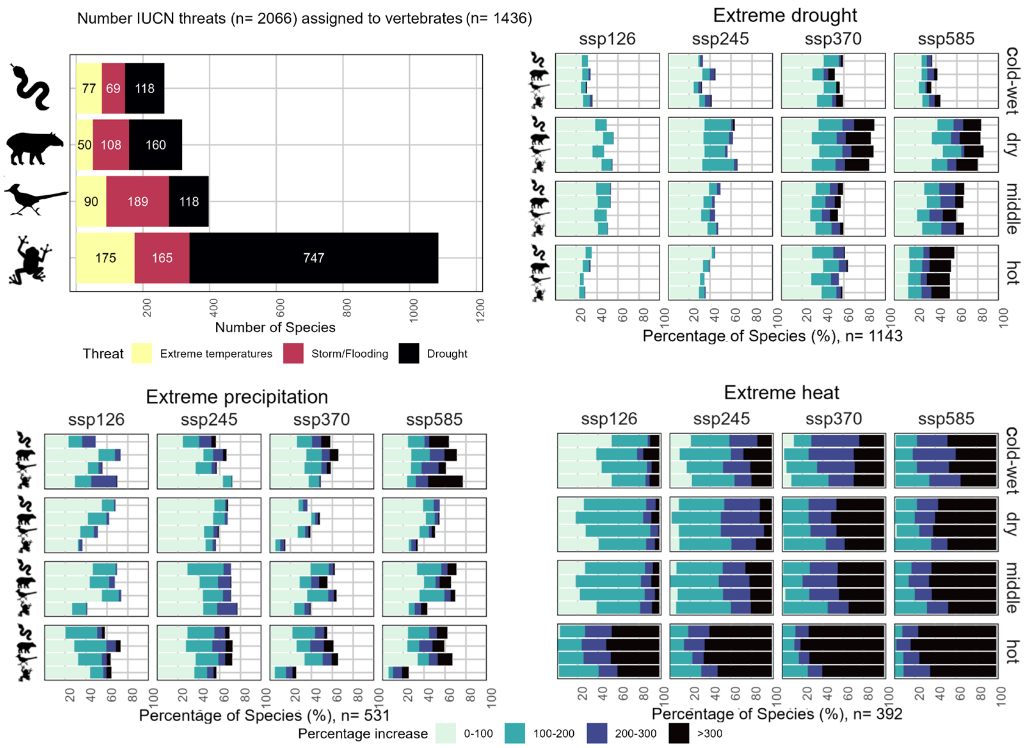

FIGURE 2 | Percentage of vertebrate species to be exposed to increases in the frequency of extreme drought (top-right), precipitation (bottom-left), and heat exposure (bottom-right). For each threat, only terrestrial vertebrates classified by the IUCN as vulnerable to drought, storms and flooding, extreme temperatures, respectively, are represented (top-left).

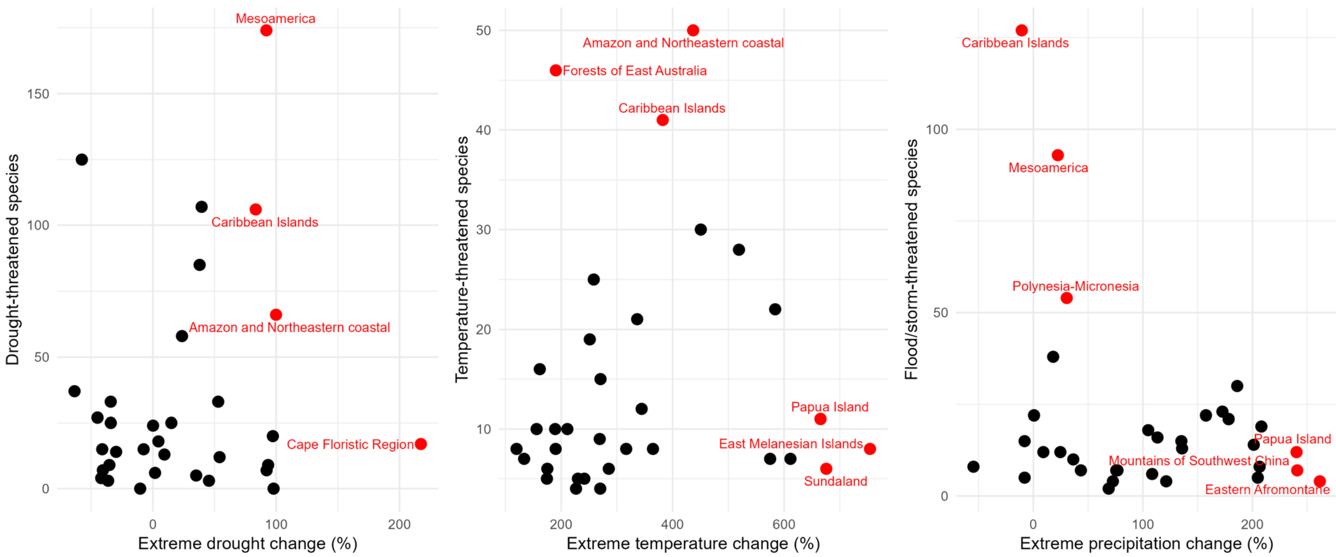

FIGURE 3 | The number of terrestrial vertebrates with a particular climate extreme as IUCN-assigned conservation threat, along with the predicted change in exposure to the corresponding climate extreme, averaged across all global climate models and shared socioeconomic pathways. Results are summarized for the 33 global vertebrate diversity hotspots, with notable examples of affected hotspots as red circles, along with their respective names, and other hotspots as black circles.

compared to the global average, with projected changes near the equator being about twofold the global average (Figure 4). Above-average increases in extreme drought frequencies are projected for 22 of 33 hotspots, with peaks around −25° S and 25° N. Vertebrate hotspots around the equator would see the greatest increases in extreme precipitation frequencies, though this would be above the global average for only 7 of 33 hotspots.

4 | Discussion

Increases in the frequency, intensity, and duration of climate extremes will strongly impact natural ecosystems and their wildlife (IPCC 2021), and our analysis highlights gaps in the scientific understanding of vulnerability to climate extremes. Though projected increases in climate extremes are similar across vertebrate classes, nearly half of 1634 species with an IUCN-assigned threat related to climate extremes are drought-threatened amphibians. However, other vertebrate groups may be similarly vulnerable to extreme drought (Maxwell et al. 2019). Similarly, nondrought climate extremes warrant increased attention: though the number of vertebrates assigned extreme temperatures as a conservation threat is three times lower, projected changes in extreme heat exceed those in extreme drought for all vertebrate hotspots. The frequency with which historical heat extremes are surpassed will be highest in tropical regions due to their low annual temperature variability (Orlowsky and Seneviratne 2012), while these regions also face above-average increases in year-long extreme drought. This has important implications for biodiversity conservation because the tropics hold the majority of vertebrate diversity. While in absolute terms projected changes in average climate variables are larger in temperate regions than in the tropics (C3S 2024; Diffenbaugh and Giorgi 2012), tropical vertebrates often have narrower climatic tolerances and a more specialized ecological niche, thus may be less resilient to increasing climatic extremes compared to their temperate counterparts (Gutiérrez-Pesquera et al. 2016; Khaliq et al. 2014; Janzen 1967). Additionally, tropical climates are driven by seasonal precipitation patterns that are becoming increasingly unstable under climate change (Feng et al. 2013). Such intra-annual climatic variability may further stress vertebrates facing more frequent extremely dry or wet years (Brawn et al. 2024). Though the tropics are expected to have below-average increases in extreme precipitation, such events may nevertheless drive habitat degradation through flooding and erosion (Oliver and Morecroft 2014). Finally, extreme precipitation in combination with extreme heat may cause compounding stressors in the form of increased physiological stress or phenological mismatches (Kissel et al. 2019). Our findings highlight climate extremes as underestimated threats to vertebrate diversity, particularly in numerous understudied hotspots of vertebrate diversity. Most IUCN-assigned conservation threats for vertebrates relate to habitat loss from land-use change, and threats related to climate extremes appear underrepresented given the high projected increases in climate extremes vertebrates face. Certain vertebrate hotspots projected to have the largest increases in climate extreme frequencies, particularly in southeastern Asia and in Africa, hold relatively few vertebrates currently considered threatened by these phenomena. For instance, projected heat and drought increases in Madagascar and the Indian Ocean islands are above-average, though fewer than 4% of vertebrates here have extreme drought or heat assigned as a threat, which is remarkably low compared to numbers for more localized threats like habitat destruction from mining (9%) or urbanization (20%). Similarly, nearly 12% of amphibians in the Amazon and Northeastern coastal hotspot in South America have a climate extreme-related threat, compared to <1% of amphibians in the Northwestern South America hotspot, despite similar projected increases in extreme heat and drought, and larger projected increases in extreme precipitation

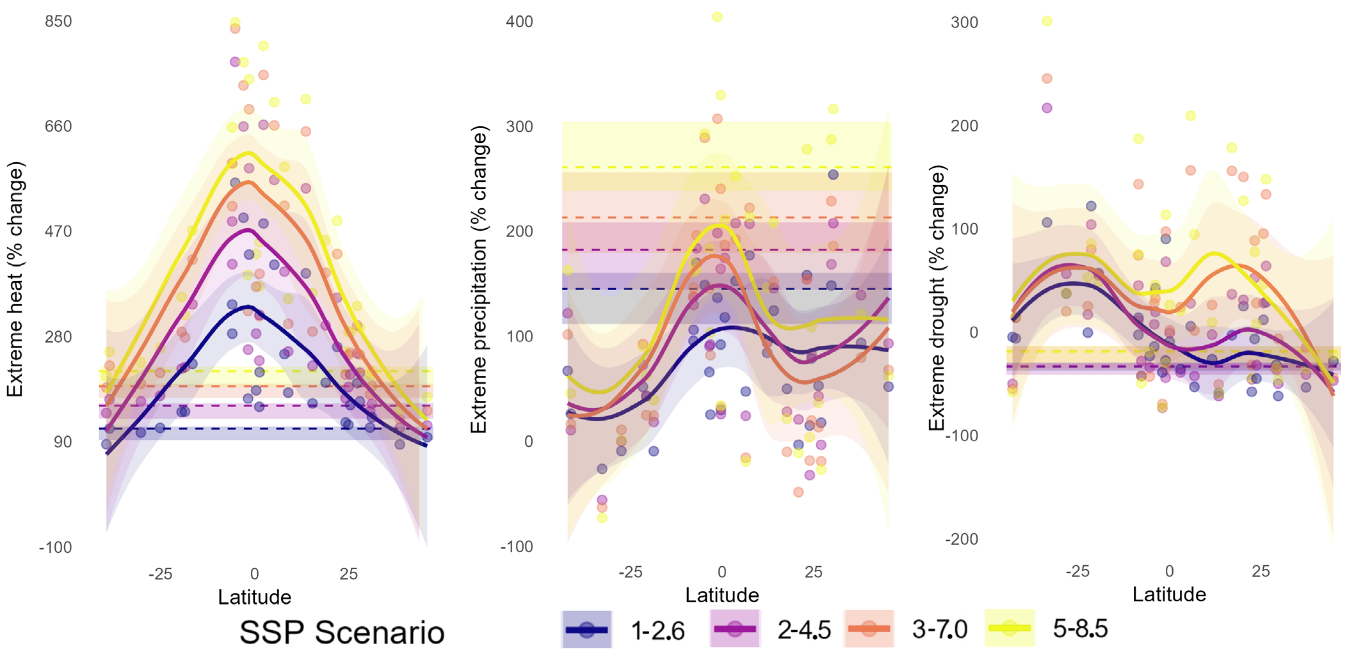

FIGURE 4 | Predicted changes in climate extremes frequencies across 33 vertebrate diversity hotspots. Solid lines represent percentage changes for hotspots, and horizontal lines represent global averages. Projected changes are shown for each shared socioeconomic pathway, with shaded areas showing the 25–75 confidence intervals across four global climate models.

for Northwestern South America. An IUCN-threat for extreme precipitation does not exist, and while the threat 'storms and flooding' most closely relates to extreme precipitation, vertebrates assigned to this threat are likely to be affected by extreme precipitation in various ways and to various degrees. For example, the Caribbean Islands hotspot is predicted to have a small decrease in extreme precipitation, and the high number of Caribbean vertebrate species considered threatened by storms and floods may relate more to threats of sea level rise (Appendix S1 and S2). Our analysis excludes nonresident vertebrates, primarily migratory birds, to maintain consistency in exposure estimates. We used 10th and 90th percentiles of historical climate data to quantify extremes, though a variety of definitions of climate extremes exist (Seneviratne et al. 2012) which undoubtedly have differing ecological implications. We used SPI, rather than SPEI (Standardized Precipitation-Evaporation Index), to calculate drought. SPEI has the advantage of accounting for the influence of temperature-related parameters by including potential evapotranspiration. However, here, we simultaneously analyzed changes in high temperatures, which drives evapotranspiration. Exposure to extremely negative SPEI values and high temperatures would therefore represent related phenomena, whereas SPI allowed us to project extreme drought and wetness solely based on precipitation and not directly related to projections of extreme heat. Additionally, SPI and SPEI have historically been strongly correlated, with correlations > 0.95 across most of our study area (Nwayor and Robeson 2024). Finally, this analysis estimates changing frequencies in climate extremes averaged across large regions, and full species ranges, ignoring variability within such regions or species ranges. These estimates serve as a baseline to prioritize areas or taxa to study exposure and vulnerability to climate extremes on a higher spatial resolution (van den Bosch et al. 2024). Widespread integration of future climate scenarios into conservation assessments is key to mitigating the impacts of climate extremes on vertebrate biodiversity. Tropical regions, holding the highest vertebrate diversity, are projected to be the first to experience climates continuously exceeding historical variability (Mora et al. 2013), while the number of tropical vertebrates considered threatened by climate extremes may currently be underestimated (Harfoot et al. 2021), particularly because tropical vertebrates may have narrower climatic tolerances than temperate species. Identifying biodiversity hotspots where large increases in climate extremes coincide with low numbers of species identified as vulnerable to such threats points toward knowledge gaps. Filling these gaps through targeted research and monitoring will allow us to better target efforts to mitigate biodiversity loss as the climate changes. Improving our understanding of vertebrate tolerances to climatic extremes could help more accurately assess their vulnerability to future threats. Such knowledge could be used to prioritize areas where proactive management can create refugia from climate extremes. For example, through conserving or restoring wetlands, which mitigate the effects of extreme drought and mitigate flooding caused by extreme precipitation (Wu et al. 2023). Finally, our analysis reveals the magnitude of projected increases in climate extremes is strongly determined by the socioeconomic pathway (SSP) under consideration. Similarly, under less sustainable socioeconomic pathways, catastrophic wildlife habitat loss and fragmentation are expected in biodiversity hotspots (Jantz et al. 2015). Such impacts would compound with threats posed by increasing climate extremes (Ameca et al. 2024), underscoring the importance of addressing greenhouse gas emissions and transitioning to a sustainable socioeconomic pathway as the primary methods of mitigating biodiversity loss.

Author Contributions

M. van den Bosch: conceptualization, data curation, formal analysis, methodology, visualization, writing – original draft, writing – review and editing. **J. K. Costanza:** conceptualization, data curation, methodology, writing – review and editing. **R. A. Peek:** conceptualization, methodology, writing – review and editing. **Z. L. Steel:** conceptualization, funding acquisition, methodology, project administration, supervision, writing – review and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data and code that support the findings of this study are openly available in Dryad at https://doi.org/10.5061/dryad.sn02v6xf9. Species range maps were obtained from the IUCN Red List at https://www.iucnredlist.org/search, while CMIP6 temperature and precipitation data were obtained from the Copernicus Climate Change Service (C3S) at https://doi.org/10.24381/cds.c866074c.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.