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Climate change scenarios forecast increased drought exposure for terrestrial vertebrates in the contiguous United States



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Anthropogenic climate change is altering patterns of extreme weather events across the planet, with far-ranging consequences for biodiversity. Increases in the frequency, duration, and severity of droughts are anticipated to substantially impact natural ecosystems. Here, we predicted the extent to which 1221 terrestrial vertebrates in the contiguous United States will be increasingly exposed to annual (12-month) and prolonged (36-month) drought, under three global climate models and two representative concentration pathways. On average, a 377% increase in annual drought exposure and a 579% increase in prolonged drought exposure are anticipated for the study area by 2050–2080, compared to 1950–2005. Species in the southwestern USA could see the largest increases in drought exposure, while this area also has the highest vertebrate diversity and an abundance of drought-threatened species. Our results aid in identifying vertebrates and ecoregions anticipated to see large increases in drought exposure, which can inform conservation strategies aimed at mitigating vertebrate extinction risks.

Rapid global warming, triggered by human-induced climate change, is altering patterns of extreme weather events such as heatwaves, floods, wildfires, and droughts, with potentially grave impacts on wildlife communities¹. As climate change modifies precipitation and evapotranspiration dynamics, it impacts the severity, duration, and frequency of droughts, and is expected to lead to increased drought occurrence in many world regions^{1,2}. Drought, abnormal soil moisture deficits due to low precipitation and excess evapotranspiration¹, is a major environmental stressor with multifaceted effects on wildlife communities and habitat, including the modification of microbial soil composition³, forest die-offs⁴, the proliferation of invasive species⁵, and the destabilization of species interactions through changes in competition⁶ and trophic dynamics⁷. Extreme drought, defined as the 1% most severe drought conditions that occurred between 1950 and 2000, is expected to annually affect 30% more land area by the end of the 21st century⁸.

Concurrently, a global wildlife extinction event is unfolding⁹, primarily driven by anthropogenic habitat loss and fragmentation¹⁰, and climate change^{11,12}. Climate change and biodiversity loss are suggested to exacerbate each other. Rapid climate change may exceed species' capacities to adapt to

variable environments, thus furthering biodiversity loss^{12,13} and the destabilization of ecological communities caused by biodiversity loss may diminish ecosystems' capacity to sequester carbon, thus accelerating climate change^{14–16}. The 2023 Red List update of the International Union for Conservation of Nature (IUCN) holds that 41% of assessed amphibian species, 26% of assessed mammal species, 21% of assessed reptile species, and 12% of assessed bird species are threatened with extinction, and the number of species approaching extinction continues to accelerate^{17,18}.

Drought affects wildlife directly, through physiological impacts that affect survival^{19–21} and fecundity²², but also indirectly through the alteration of habitat²³, resources²⁴, and interspecific interactions⁷. Additionally, drought effects on wildlife populations depend on drought duration and intensity^{21,25}. Minimizing biodiversity loss induced by climate change requires not only mitigating climatic change itself but also large-scale assessments of species' vulnerability to climate change effects such as extreme weather events, to prioritize conservation actions^{26,27}.

Identifying biodiverse areas where increases in drought exposure are most likely is an urgent step in developing effective conservation management actions specific to species' needs. Droughts are causing population

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declines and local extinctions across vertebrate classes^{22,28–30}, but there are few large-scale assessments of drought exposure for wildlife³¹. To understand species' vulnerability to changing drought patterns, studies of changing drought exposure for wildlife are needed to complement our understanding of individual species' sensitivity and adaptive capacity to drought^{31,32}.

Here, we first contextualized future drought projections by summarizing observed changes in drought exposure between the middle of the previous century (1953–1982) and the early 21st century (1991–2020) in the contiguous United States. We then projected drought exposure for terrestrial vertebrates between 2050–2080, under six combinations of global climate models and Representative Concentration Pathways, whereby drought was quantified on an annual (12-month) and a prolonged (36-month) timescale. We mapped the vertebrate richness within ecological regions and the projected changes in drought exposure for these regions, as well as projected changes in drought exposure coincident with the presence of vertebrate species the IUCN currently considers threatened by drought.

Results

Observed changes in drought exposure

Between 1952–1983 and 1991–2020, 52 out of 84 ecoregions in the CONUS were subject to decreases in drought, but those in the western third of the CONUS experienced increases of up to 200%, resulting in a marginal increase across ecoregions (Mean = 8%, 25–75 CI = –61–56%; Fig. 1). Two ecoregions, in the southwestern USA, were subject to annual drought increases of over 200%. Observed changes in prolonged drought exposure were markedly larger across ecoregions (Mean = 753%, 25–75 CI = –87–723%, Fig. 1). Even though 54 out of 84 ecoregions were subject to decreased drought exposure, primarily in the eastern CONUS, most western ecoregions were subject to increases of over 400%.

Projected changes in annual drought exposure

Averaging projected changes in annual drought exposure for all ecoregions (for RCP 4.5: Mean = 290%, 25–75 CI = 172–389%, for RCP 8.5: Mean = 467%, 25–75 CI = 264–646%) across the six future scenarios between 1950–2005 and 2050–2080 suggests that particularly in the southwestern United States, ecoregions will see large increases in drought exposure, with 29 out of 84 ecoregions being subject to increases over 200%, and 19 ecoregions being subject to increases over 400% under RCP 4.5. Under RCP 8.5, there would be consistently larger increases (Fig. 2). Ecoregions with the greatest predicted increases are located in the southwestern USA and have some of the highest area-weighted vertebrate richness. Overall, average projected changes between 1950–2005 and 2050–2080 are substantially larger than the observed changes in annual drought exposure between 1952–1983 and 1991–2020. Further, there is notable increase in the total area subject to increases in annual drought (Fig. 1; Fig. 2).

Projected changes in prolonged drought exposure

Predicted changes in prolonged drought exposure for all ecoregions, averaged across six future scenarios, are larger (for RCP 4.5: Mean = 469%, 25–75 CI = 282–604, for RCP 8.5: Mean = 692%, 25–75 CI = 446–923%) than changes in annual drought exposure, with 24 out of 84 ecoregions predicted to have increases in drought exposure exceeding 400%, and 21 ecoregions to have increases exceeding 600% under RCP 4.5. Under RCP 8.5 there would be consistently larger increases (Fig. 2; Supplementary Fig. 1). The geographic distribution of increases in prolonged drought is similar to that of annual drought, although the group of ecoregions projected to experience the greatest increases in prolonged drought exposure extends to the most northern parts of the interior West. The average change in observed prolonged drought between 1952–1983 and 1991–2020 exceeded that of changes in projected prolonged drought between 1950–2005 and 2050–2080. However, the projected data indicated all but one ecoregion will be subjected to increases in prolonged drought exposure exceeding 100%, under either RCP 4.5 or RCP 8.5, while this was only the case for 35 out of 84 ecoregions for recently observed changes in prolonged drought exposure. This illustrates a marked rise in the total area subjected to projected increases in prolonged drought.

Drought exposure changes by vertebrate richness, class, and drought as IUCN-assigned threat

The six future scenarios generally conformed to expected patterns in changes in drought exposure relative to the GCMs they represented, with drought exposure increases being, on average, greatest for the dry GCM, followed by the middle and wet GCMs, respectively (Supplementary Fig. 1). Similarly, drought exposure changes on both timescales were larger under future scenarios including RCP 8.5 than future scenarios including RCP 4.5. The southwestern quarter of the CONUS (Fig. 2, Fig. 3) is predicted to have the largest increases in annual and prolonged drought exposure across future scenarios, while it is also the region with the highest number of the 84 vertebrate species considered drought-threatened by IUCN in our dataset ($n = 25$; Fig. 3), and the highest overall vertebrate species richness (Fig. 3). Other ecoregions with high vertebrate richness, for example along the Pacific coast and the Northeastern USA, are predicted to experience smaller but notable (under 200%) increases in annual drought exposure. Most ecoregions in the interior West may be subjected to relatively large increases in annual and prolonged drought exposure, and these ecoregions have relatively low vertebrate richness. In terms of terrestrial vertebrate richness, the southwestern quarter of the CONUS has the highest number of resident bird, mammal, and reptile species, while only the southeastern quarter of the CONUS has a high number of amphibians (Fig. 3).

Among the four classes of terrestrial vertebrates across the contiguous United States, the class of amphibians is predicted to have, on average, the smallest increases in annual and prolonged drought exposure (mean across future scenarios and the two SPEI timescales = 371%, 25–75

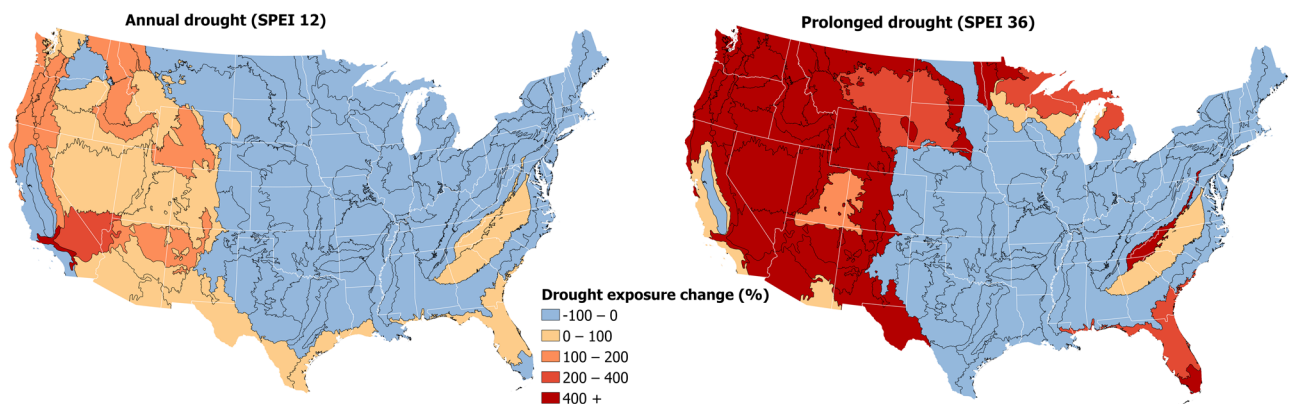


Fig. 1 | Observed changes in drought exposure. Observed change (%) in annual (12-month) and prolonged (36-month) droughts between 1952–1983 and 1991–2021, across Level 3 Ecoregions in the contiguous United States.

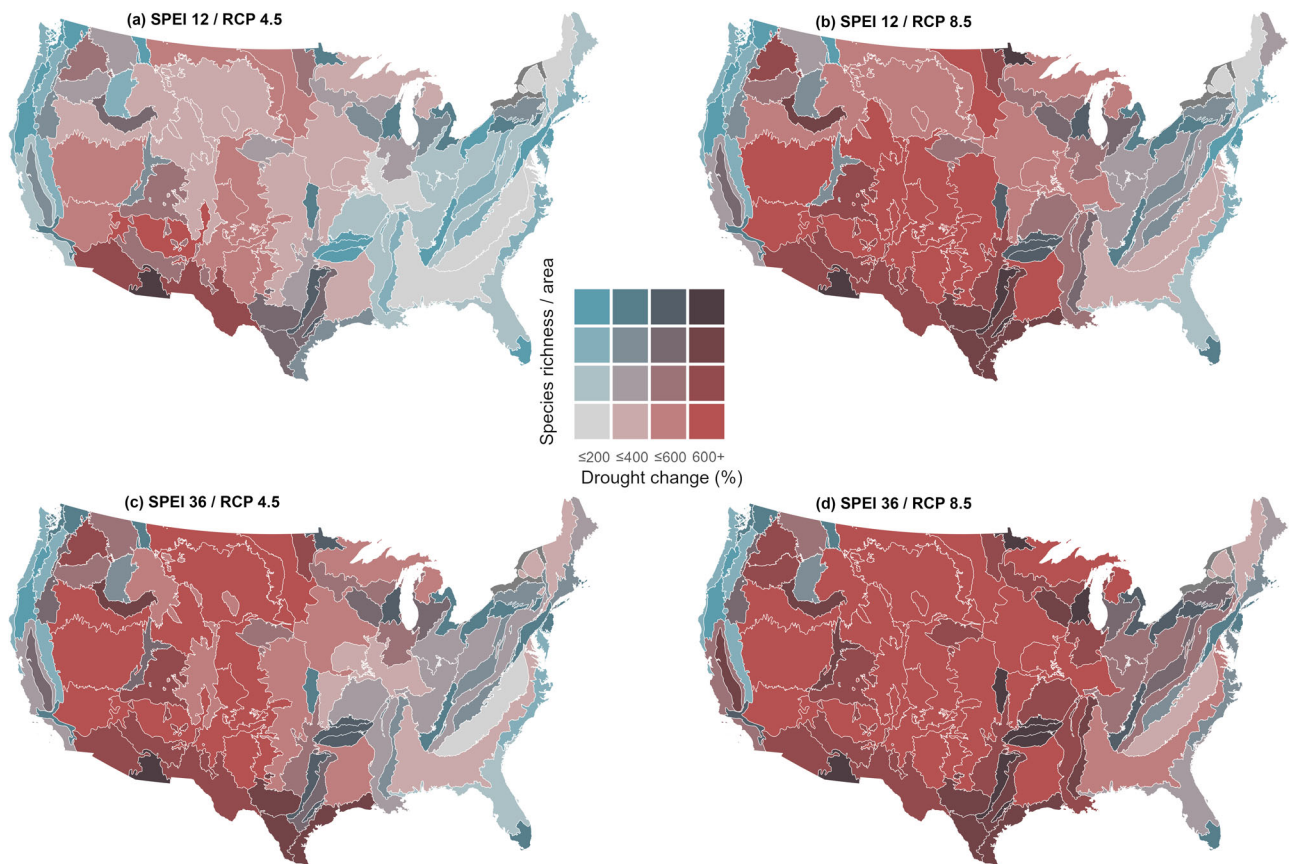


Fig. 2 | Predicted changes in drought exposure. Average predicted change (%) in annual droughts under (a) RCP 4.5 and (b) RCP 8.5 and prolonged droughts under (c) RCP 4.5 and (d) RCP 8.5 between 1951–2005 and 2050–2080, along with area-weighted terrestrial vertebrate species richness, for the contiguous United States.

Numbers below the x-axis color legend indicate four breaks of percent change in drought between the historical period and average future scenario, species richness is categorized into four equal quantiles along the y-axis legend.

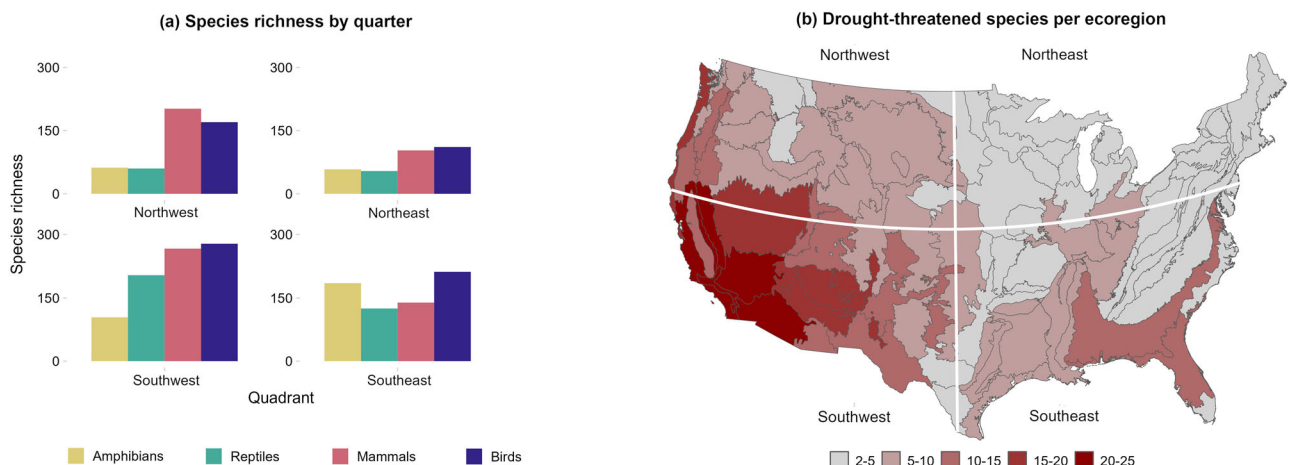


Fig. 3 | Vertebrate and drought-threatened vertebrate species richness. **a** The total number of species per terrestrial vertebrate class that occur within the quadrants shown in (b) and **b** The contiguous United States, divided into quadrants, showing the number of vertebrate species classified by the IUCN as threatened by drought, per ecoregion.

CI = 127–513%), followed by birds (mean = 546%, 25–75 CI = 271–765%) and mammals (mean = 574%, 25–75 CI = 280–812%), while reptiles (mean = 671%, 25–75 CI = 321–973%) would be exposed to the largest increases in annual and prolonged droughts (Fig. 4, Supplementary Data 1).

Discussion

We projected changes in drought exposure for terrestrial vertebrates across the contiguous United States (CONUS) between 1950–2005 and

2050–2080. Across six future scenarios used to predict changes, landscapes of the CONUS and its terrestrial vertebrates are predicted to be exposed to increasing frequencies of annual drought and even greater increases in prolonged (36-month) drought. For recent observed drought data (1950–2020), there has been a slight average increase in annual, and large average increase in prolonged drought frequency across the CONUS, though half of the CONUS land surface experienced stable or relatively slight decreasing trends in annual and prolonged droughts, primarily in the

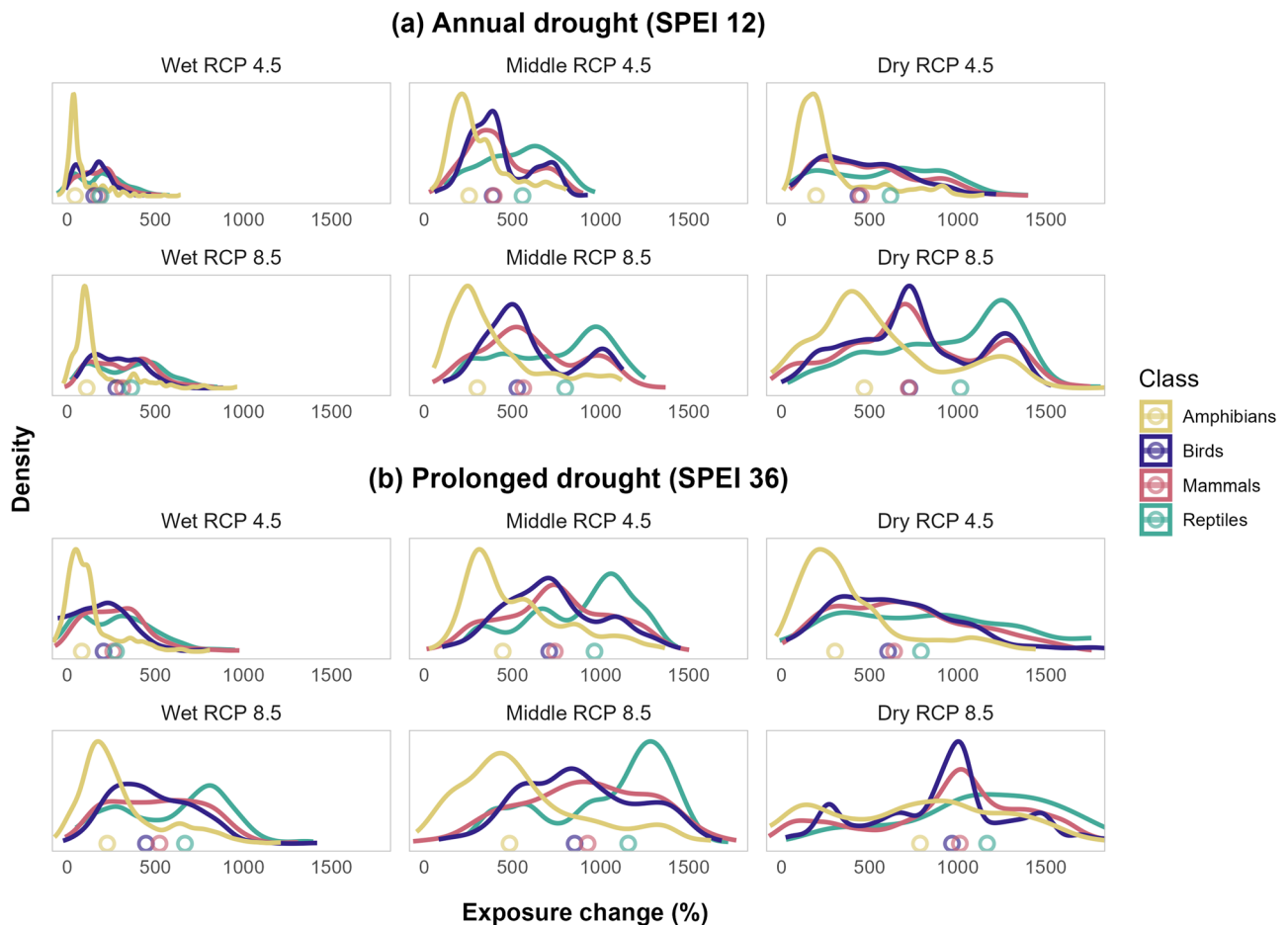


Fig. 4 | Predicted changes in exposure by vertebrate class. Density plots for predicted change (%) between 1951–2005 and 2050–2080 in (a) annual (12-month) drought exposure and (b) prolonged (36-month) drought exposure, for four classes of vertebrates, for six future scenarios (three Global Climate Models and two

Representative Concentration Pathways) across the contiguous United States. Circles below each density plot represent the mean predicted change per vertebrate class.

eastern USA (Fig. 1). Our projections indicate that as climate change effects accelerate, most ecoregions in the CONUS will be subjected to increases in drought exposure by 2050–2080 that are higher than the increases observed recently. Among the vertebrate taxa assessed, reptiles are expected to be subjected to the largest increases in annual and prolonged drought exposure, followed by birds and mammals, while smaller increases are predicted for amphibians (Fig. 4). For the average amphibian species, this may nevertheless imply more than threefold increases in annual and more than fourfold increases in prolonged drought exposure.

Notably, ecoregions with the highest predicted increases in drought exposure are regions in the southwestern USA that also have high area-weighted vertebrate richness (Fig. 2) and a high number of species considered drought-threatened by the IUCN (Fig. 3). As an example, the Sonoran Basin and Range ecoregion, located in southern California and Arizona, is projected to undergo an eightfold increase in annual drought exposure and an elevenfold increase in prolonged drought exposure. The ecoregion is highly diverse and harbors 25 out of the 84 species in our analysis listed as drought-threatened by the IUCN. However, regions with modest increases in drought exposure may also see losses in vertebrate diversity. For instance, the Southern Coastal Plain ecoregion in the southeastern USA is projected to have below-average increases in annual (144%) and prolonged droughts (224%), but such changes could prove detrimental to endangered species such as the Dusky gopher frog (*Lithobates sevosus*) and Reticulated flatwoods salamander (*Ambystoma bishop*), which have reduced reproductive success under drought conditions^{33,34}. The geographic distribution of vertebrate diversity relates to differences in projected drought

exposure among vertebrate classes: southeastern parts of the USA have high amphibian diversity³⁵, and relatively low projected increases in drought exposure, while southwestern parts of the USA have high mammal, bird, and reptile diversity³⁵ and the highest projected increases in drought exposure.

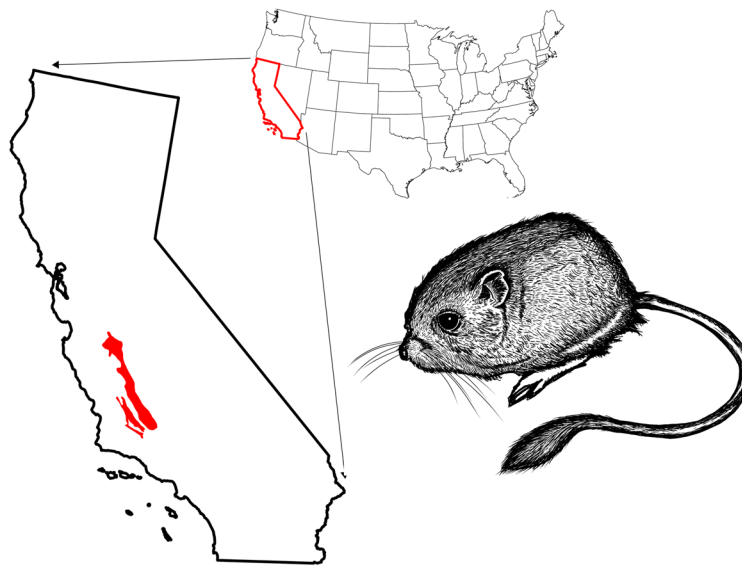
Care should be taken in directly comparing drought data calculated using different methodologies³⁶, as was the case for this study, in which we use different PET calculation methods for the observed and projected data. Because the focus of our analysis was on comparisons between the modeled past and modeled future drought exposure, and because previous research has shown the different PET calculation methods to yield similar SPEI values^{36,37}, we believe this has a negligible effect on the interpretation of our results. The three climate models we used represent the “wettest”, “driest”, and “middle” future scenarios for the entire CONUS³⁸. However, there is variability within these climate models so that, for example, the “wettest” climate model does not necessarily reflect the wettest potential future for each region or species’ range. The analysis was limited to resident species, as we prioritized consistency in drought exposure among species over an exhaustive assessment of all vertebrate species. This implied the omission of many species, primarily migratory birds. Lastly, drought effects are not bound to the ecoregion in which they occur, as vertebrate habitats within certain regions may depend on streamflow from other regions³⁹.

IUCN threat categories are assigned based on expert assessment, and while trait-based assessments are encouraged, these assessments may underestimate risks posed to species by long-term threats such as climate change and its effects^{40,41}. For example, of all species considered threatened

Box 1 | Case study of the Giant kangaroo rat

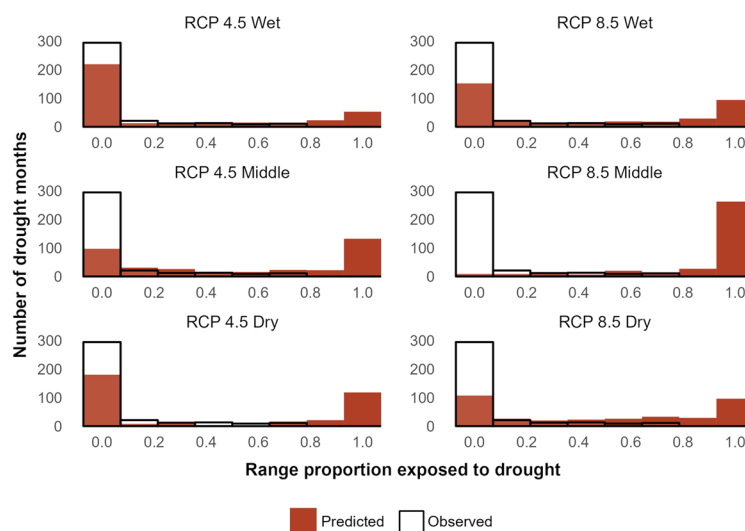
To illustrate the utility of this analysis for single-species conservation management, we projected changes in drought exposure for the Giant kangaroo rat (*Dipodomys ingens*; hereafter 'GKR'), an endangered rodent endemic to California, USA⁶² that is considered drought-threatened by the IUCN. GKR's can adapt to annual drought due to their food-caching habits, but elevenfold declines in GKR numbers have been observed in

response to a prolonged drought²¹. Furthermore, GKR's have lifespans of 2–3 years⁶², exacerbating the potential effects of multi-year droughts. We compared the observed proportions of its range exposed to prolonged (36-month) drought between 1991 and 2020 to the range proportions exposed to prolonged drought between 2050 and 2080 under the six future scenarios.



During 1991–2020, Giant kangaroo rat (GKR) range was free from prolonged drought 85% of the time. When prolonged drought did occur, it on average affected about 40% of GKR range. Each of the six modeled scenarios predicts that between 2050–2080, the number of months

during which proportions of, or the entirety of, GKR range is exposed to prolonged drought will strongly increase. Under the scenario including the Middle GCM and RCP 8.5, all GKR range would be almost continuously exposed to prolonged drought.



Histograms of the proportions of Giant kangaroo rat (*Dipodomys ingens*) range exposed to prolonged drought under six future scenarios for 2050–2080, compared to the observed proportions of kangaroo rat range exposed to prolonged drought between 1991 and 2020.

GKR's are ecosystem engineers that structure plant and small mammal communities⁶³, and our results indicate changes in drought trends are likely to prove problematic for this endangered species' survival.

in 2016, climate change was considered a threat for 11%⁴². Our analysis reveals that only 7% of all vertebrate species, but 38% of threatened (i.e., vulnerable, endangered, or critically endangered) vertebrate species in the CONUS currently have drought listed as a threat. One such species is the Giant kangaroo rat, which is listed as endangered by the IUCN. Our case study of this species (Box 1) projects exponential increases in the frequency with which large portions or the entirety of this species' range will be exposed to prolonged drought, to which this species is known to be vulnerable²¹. The increases in annual and prolonged drought exposure for vertebrates across the CONUS warrant in-depth assessments of the drought vulnerability of not only threatened vertebrates or those currently considered vulnerable to drought but also of other vertebrates that are nevertheless expected to experience dramatic increases in drought exposure^{27,43}.

Projected increases in drought exposure across most vertebrate ranges will affect wildlife directly and indirectly. Increased drought exposure can directly lead to wildlife mortality through dehydration and heat stress^{44,45}, which in some cases could be mitigated through the provisioning of artificial water sources⁴⁶. More commonly, increased drought exposure would alter habitats and resource availability for vertebrates, with wide-ranging consequences such as reduced fecundity or altered trophic interactions⁷. Addressing the indirect effects of drought may be more complex as this requires habitat restoration and preservation, but adaptive water management through, for example, dam removal or wetland restoration may offer mitigation⁴⁷. Our findings highlight drought as an increasingly important climate change effect with wide-ranging consequences for wildlife, underscoring the need for short- and long-term drought mitigation and adaptation strategies.

Methods

Species range data

Our study area included the contiguous United States of America (CONUS), consisting of the USA excluding Alaska, Hawaii, and offshore territories. We extracted the ranges of terrestrial vertebrates in the classes of amphibians, birds, mammals, and reptiles that intersected with the study area from the IUCN database¹⁸. We only retained year-round resident vertebrates (IUCN-code: Extant-resident), thereby omitting mostly migratory bird species. We further omitted species without permanent range within the CONUS that were nevertheless retained after the intersection with the study area, as IUCN uses national borders to delineate some species ranges (e.g., species ranges in Mexico that end at, but include part of the United States border). We also omitted species classified as terrestrial that nevertheless have a stronger association with marine habitats (sea lions, seals, sea turtles, petrels, shearwaters, etc.). After filtering based on the criteria above, we retained 1221 vertebrate species (349 bird, 339 mammal, 280 amphibian, and 253 reptile species). The IUCN uses threat classifications to list the factors thought to underlie the extinction risk of species that results in a particular conservation status⁴⁸. It includes threats such as "Habitat loss or degradation", "Invasive Alien Species", "Pollution", and "Drought" (IUCN Threat Classification 11.2). Drought is a threat category listed under "Climate change and severe weather"⁴⁹, and, in our dataset 84 out of 1221 species had this IUCN-assigned conservation threat.

Climate data

Our study area (CONUS) covers a wide range of ecoregions and climates, from tropical wet forests in southern Florida to deserts in Nevada and semi-arid highlands in Arizona⁵⁰, and for this region there are high-resolution data available for precipitation, potential evapotranspiration (PET), and projections of these data under three global climate models (GCM)⁵¹.

To analyze past and future drought occurrence, we used the Multi-variate Adaptive Constructed Analogs (MACAv2-METDATA) dataset^{51,52} as it provides monthly time series of precipitation and potential evapotranspiration on a 0.25 arc-degree resolution (~4 × 4 km cells). For a modeled historical (1950–2005) and future (2050–2080) period, we extracted data for three GCMs representing, on average, the wettest ("wet"; CNRM-CM5), middle ("middle"; NorESM1-M) and driest ("dry"; IPSL-

CM5A-MR) future conditions for the CONUS³⁸. Projected changes were calculated as the difference between modeled historical and future drought frequency for the same GCM to ensure the changes were internally consistent with model assumptions and uncertainties^{52,53}. We used 1950–2005 as the historical reference period, as 2005 is the most recent year for which modeled historical data are available⁵². For the modeled future period, we used downscaled future projections for each GCM under two representative concentration pathways (RCPs): 4.5 and 8.5. RCP 4.5 represents an intermediate pathway in which greenhouse gas emissions peak around 2040 and then gradually decline, with an expected global temperature rise between 2 and 3 °C by 2100. RCP 8.5 is a pathway with continuously increasing greenhouse gas emissions that could result in global temperature rise exceeding 5 °C by 2100^{54,55}. The result was a set of three modeled historical climates and six modeled future climate scenarios (hereafter; future scenarios)—three GCMs under each of the two RCPs.

To contextualize changes in drought between the modeled historical and projected periods, we used monthly time series of observed precipitation and PET on a 0.25 arc-degree resolution to calculate recently observed changes in drought occurrence from the PRISM dataset⁵⁶. We calculated drought indices for all months between 1953 and 1982 and all months in a more recent period, 1991–2020, thus the duration of the observed historical dataset differs from that of the modeled historical dataset (1950–2005).

SPEI drought data

We used the standardized precipitation evapotranspiration index (SPEI) to calculate past and future drought occurrences. Unlike most drought monitoring indices, SPEI is based not only on precipitation but also on potential evapotranspiration (PET), and the calculation of PET includes temperature data³⁶. SPEI is therefore considered more appropriate to model drought under climate change projections, which imply changing global surface temperatures, than drought indices based on precipitation data alone^{57,58}. For each month in our analysis, we calculated the water balance (precipitation minus PET) for each future and historical climate and calculated SPEI with 1950–2005 specified as the reference period. We used the "SPEI" package⁵⁹ in program R 4.2.2, which was the software used for all data analysis and visualization⁶⁰. We calculated SPEI using PET data estimated with the Penman-Monteith method for the modeled data. Penman-Monteith PET values are based on additional variables such as wind speed, which were unavailable for the observed data, so for observed data, we used PET data estimated with the comparable Hargreaves method, which uses only air temperature and solar radiation variables³⁶.

For each grid cell in the climate data, SPEI values represent the deviation of the climatic water balance from a historical average. SPEI value distribution has a mean of 0 and a standard deviation of 1, with negative SPEI values indicating drier conditions, and positive values indicating wetter conditions than normal⁵⁷. By using rolling time windows, monthly SPEI values are representative of the cumulative water balance over a given number of months preceding the target month⁵⁷. We calculated SPEI values on a 12-month timescale representing annual drought and a 36-month timescale representing prolonged drought, as the effects of drought on wildlife can vary based on drought duration²¹.

Calculation and summary of changes in drought exposure

To calculate drought exposure for the modeled SPEI data, we split data into a historical reference period (1950–2005) and a future period (2050–2080) for each of the six future scenarios, and for each of the two SPEI timescales (annual drought and prolonged drought). For these 24 datasets representing one period of data for a particular historical or future climate and one of two SPEI timescales, we reclassified each monthly SPEI raster into a binary raster where each cell was classified as exposed or not exposed to drought. We classified SPEI values ≤ −1.5 as drought and values > −1.5 as non-drought, thus, drought includes instances of severe (−1.50 ≥ SPEI ≥ −1.99) and extreme (SPEI ≤ −2) drought conditions according to the commonly used SPEI categorization^{53,61}. We defined changes in drought exposure as the change in frequency with which a given area is projected to be exposed to 12-

month (annual) or 36-month (prolonged) droughts ($\text{SPEI} \leq 1.5$) in the projected period, compared to the historical reference period. To calculate changes in drought exposure between the reference historical period and each potential future, we first stacked rasters for each period and calculated the proportion of drought months by summing the number of cells with SPEI values ≤ -1.5 , then divided this sum by the total number of months for that historical (1950–2005) or future period (2050–2080):

$$P_{\text{Drought}} = \frac{N_{\text{droughtmonths}}}{N_{\text{months}}}$$

We calculated the percentage change in proportions of drought months between each future scenario and the corresponding historical reference period, resulting in rasters of changes in the frequency of annual and prolonged drought under six potential future scenarios.

$$\Delta P_{\text{Drought}} = \frac{P_{\text{drought(future)}} - P_{\text{drought(reference)}}}{P_{\text{drought(reference)}}} \times 100$$

We created twelve rasters representing changes in drought exposure between 1950–2005 and 2050–2080, for each of the six future scenarios, on the annual and the prolonged SPEI timescale. We used the same methodology to calculate changes in drought exposure between the observed SPEI data in 1953–1982 and 1991–2020.

We calculated the change in annual and prolonged drought exposure for each vertebrate species range and for each Level III Ecoregion in the CONUS⁵⁰, for each of the six future scenarios. We summarized drought exposure changes and area-weighted vertebrate species richness per ecoregion (species richness divided by area of the ecoregion) by averaging changes in drought exposure across the six potential futures. To indicate absolute changes in drought exposure, in addition to proportional changes, we calculated the percent of drought months in each future scenario in comparison to the historical reference period (1950–2005), geographically summarized by splitting the CONUS into four quadrants, using its geometric center.

Case study

We assessed changes in drought exposure for a vertebrate species considered drought-threatened by the IUCN: the Giant kangaroo rat (*Dipodomys ingens*), an endangered rodent endemic to California, USA⁶². We compared the observed proportions of its range exposed to prolonged (36-month) drought between 1991 and 2020 to the range proportions exposed to prolonged drought between 2050 and 2080 under the six future scenarios.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

IUCN range data cannot be freely redistributed, and the size of the climate data files makes them unsuitable for uploading to the repository. Therefore, the Dryad repository provides detailed instructions on how to access the climate and species data used in our analyses. The repository also contains all other data and code required to replicate our analysis and can be accessed through <https://doi.org/10.5061/dryad.9kd51c5sf>.

Code availability

Code related to the data analysis is available from the Dryad repository at <https://doi.org/10.5061/dryad.9kd51c5sf>.

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Competing interests

The authors declare no competing interests.

Additional information

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