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Elevated extinction risk of cacti under climate change

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Cactaceae (cacti), a New World plant family, is one of the most endangered groups of organisms on the planet. Conservation planning is uncertain as it is unclear whether climate and land-use change will positively or negatively impact global cactus diversity. On the one hand, a common perception is that future climates will be favourable to cacti as they have multiple adaptations and specialized physiologies and morphologies for increased heat and drought. On the other hand, the wide diversity of the more than 1,500 cactus species, many of which occur in more mesic and cooler ecosystems, questions the view that most cacti can tolerate warmer and drought conditions. Here we assess the hypothesis that cacti will benefit and expand in potential distribution in a warmer and more drought-prone world. We quantified exposure to climate change through range forecasts and associated diversity maps for 408 cactus species under three Representative Concentration Pathways (2.6, 4.5 and 8.5) for 2050 and 2070. Our analyses show that 60% of species will experience a reduction in favourable climate, with about a quarter of species exposed to environmental conditions outside of the current realized niche in over 25% of their current distribution. These results show low sensitivity to many uncertainties in forecasting, mostly deriving from dispersal ability and model complexity rather than climate scenarios. While current range size and the International Union for Conservation of Nature's Red List category were not statistically significant predictors of predicted future changes in suitable climate area, epiphytes had the greatest exposure to novel climates. Overall, the number of cactus species at risk is projected to increase sharply in the future, especially in current richness hotspots. Land-use change has previously been identified as the second-most-common driver of threat among cacti, affecting many of the ~31% of cacti that are currently threatened. Our results suggest that climate change will become a primary driver of cactus extinction risk with 60–90% of species assessed negatively impacted by climate change and/or other anthropogenic processes, depending on how these threat processes are distributed across cactus species.

Cactus species are distributed in North and South America across many different ecosystems, ranging from sea level to the high Andes. While the highest diversity is found in the arid and semiarid subtropical regions on both sides of the Equator[1–3], many cacti have specialized ecologies and life histories, and many thrive in wetter tropical forests and even in colder environments. According to the Global Cactus Assessment (GCA), 31% of cactus species are currently threatened with extinction[4]. The threat processes affecting cacti include agriculture and aquaculture, biological resource use and human development[4]. At the time the GCA was conducted (2008–2013), the literature on the effects of climate change on cacti was limited. At the time, just under 10% of threatened cacti were identified as being threatened by climate change[4]. This is, in part, due to the lack of a family-level assessment of climate change impacts[5]. Overall, a thorough accounting of the expected effects of climate change on cacti is needed to accurately assess conservation status as well as design and implement future-proof conservation strategies.

On the basis of the first principles of plant physiology, it has been expected that future climates with hotter and drier climates will favour taxa with Crassulacean acid metabolism (CAM), the photosynthetic pathway characteristic of most cacti and other succulent plants. The heightened water-use efficiency and benefits of increased atmospheric carbon dioxide are expected to favour CAM metabolism[6,7]. For example, assessment of heat tolerance in 14 cactus species found acclimation to high temperatures[8]. While the early life stages of cacti are often found to be the most vulnerable and important for population growth[9,10], with survival of old individuals having some ability to buffer populations[9], increased germination efficiency has been predicted for 75% of cactus species by the end of the twenty-first century[11]. Together, earlier physiological arguments from arid regions suggest that high-temperature tolerances and water-use efficiencies will result in a competitive advantage compared to non-CAM species due to their generally superior ability to withstand drought stress. Furthermore, cacti are adapted to xeric environments and occur mostly in drylands, where precipitation is counterbalanced by evapotranspiration[12]. Global climate change has been predicted to lead to accelerated dryland expansion[12], with estimates that drylands will cover over half of the total terrestrial surface by the end of the century, up from 45% currently. The potential for expansion of arid lands complicates the assessment of habitat loss being one of the top threats to cacti[4], as cacti are an integral part of these ecosystems in the Americas.

However, increasing evidence from physiological, demographic, population and niche studies tends to paint a more pessimistic future. Many cacti cannot tolerate high temperatures, and other species have specific habitat and climatic tolerances that are not directly related to temperature[13–15]. Functional trade-offs resulting from

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differences in stem volume–surface area ratios among columnar cacti predict variable responses to climate change[16]. Other studies have shown that some species actually show impaired photosynthetic performance under just 2 °C of induced warming[17]. Some species have shown reduced germination performance with higher temperature[11]. Furthermore, many recent studies on cactus species indicate past and future potential reductions in range or population sizes with climate change[5,9,18–26], although studies have also shown some species with predicted expansions of suitable climate area (SCA)[5,27]—that is, regions with climate within the current realized niche—where species are actually found.

A limitation with many of the studies showing either positive or negative impacts of climate change on cacti is sample size. Most studies have been limited to one or a few species, typically from the same region, limiting the ability to infer trends for the family as a whole. Recent climate niche studies for specific geographic regions and taxa suggest that some species may exhibit a decrease in overall climate suitability[5]. Furthermore, given the large number of endemics and the threat status of many species within this family[4], there are reasons to suspect that the impact of climate change may be confounded by the level of endemism and conservation status of the species[5,28,29].

In this Article, we present results from a large analysis of climate change vulnerability of cacti, assessing 408 species and encompassing the range of future greenhouse gas emission scenarios under three Representative Concentration Pathways (RCP 2.6, 4.5 and 8.5) for both 2050 and 2070. We assessed the hypothesis that cacti will be favoured by climate change, as borne out by (1) an expansion in SCA at the level of individual species and (2) an increase or maintenance of species richness at the level of Cactaceae as a whole. With these results, we were able to evaluate whether climate change is an important stressor for cacti as compared with direct anthropogenic drivers.

For each species, our range forecasts are based on species distribution models. We used occurrence records from the Botanical Information and Ecology Network (BIEN), the largest standardized plant biodiversity records database[30]. We use projected range changes under climate change as a proxy for future SCA. To assess uncertainty in forecasts and the robustness of our results, we parameterize our forecasts using many different modelling and climatic choices, resulting in 6,480 forecasts per species (over 2.5 million forecasts in total). We quantify the magnitude and sources of uncertainty stemming from modelling and climatic choices, both at the level of individual species and aggregate diversity, using analysis of variance (ANOVA). We also explore the impact of modelling and climatic decisions on SCA changes with regression analysis. We then investigate whether ecological covariates can explain changes in SCA. Finally, we look for geographic relationships between cactus species richness and human footprint.

Results

Model quality. Models were cross-validated with fivefold environmental blocking, resulting in a mean area under the curve (AUC) for a receiver operating characteristic (ROC) plot, a threshold-free metric of model performance, of 0.88 and a median AUC of 0.89. Full models were then built using all available data. After removal of 22 species for which at least one model AUC was below 0.5, 14,688 models (36 models for each of 408 species) were retained. Mean and median AUC for final models are 0.88 and 0.87, respectively, with a standard deviation of 0.09. Model AUCs show a strong negative skew, indicating favourable model performance (Supplementary Fig. 1). The AUC of full models is, on average, less than 0.01 lower than for corresponding cross-validated models. We therefore use the full models for predicting SCA, reducing computational requirements.

Changes in SCA. Our analyses show that the majority of cacti will experience a reduction in favourable climate, with about one fourth of species projected to be exposed to environmental conditions out-

Table 1 | Ordinary linear regression of SCA changes (n = 2,643,840) relative to the present on variables representing modelling decisions

Variable	Coefficient estimate	95% CI	P value
Time: 2061–2080	−0.01	(−0.01, −0.01)	<0.001
RCP: RCP 4.5	−0.02	(−0.02, −0.02)	<0.001
RCP: RCP 8.5	−0.02	(−0.03, −0.02)	<0.001
GCM: CCSM4	−0.02	(−0.02, −0.02)	<0.001
GCM: GFDL-ESM2M	−0.05	(−0.05, −0.05)	<0.001
GCM: HadGEM-AO	−0.03	(−0.03, −0.03)	<0.001
GCM: NorESM1-M	0	(0, 0.01)	0.018
Threshold: 5% omission rate	−0.08	(−0.09, −0.08)	<0.001
Variables: PCA (raw variables)	0.06	(0.06, 0.07)	<0.001
Variables: PCA (principal components)	0.06	(0.06, 0.06)	<0.001
Variables: random	0.11	(0.10, 0.11)	<0.001
Features: linear + quadratic	−0.11	(−0.12, −0.11)	<0.001
Features: linear + quadratic + hinge	−0.19	(−0.20, −0.19)	<0.001
Projection: 100 km	0.05	(0.04, 0.05)	<0.001
Projection: 500 km	0.13	(0.13, 0.13)	<0.001
Sampling: 500 km	−0.02	(−0.02, −0.02)	<0.001
Correlation filter	0.06	(0.06, 0.06)	<0.001

Model complexity and projection distance are estimated to have the highest impact on SCA changes. Baselines for variables are 2041–2060 (time), RCP 2.6 (RCP), BNU-ESM (GCM), maximum true skill statistic (threshold), 'one-size-fits-all' (variable selection), linear features only (model feature complexity), 0 km (projection distance), 100 km (sampling distance) and no correlation filter (correlation filter). GCMs used are CCSM4 (Community Climate System Model version 4), GFDL-ESM2M (Geophysical Fluid Dynamics Laboratory - Earth System Model version 2M), HadGEM-AO (Hadley Centre Global Environment Model version AO), NorESM1-M (Norwegian Earth System Model version 1-M) and BNU-ESM (Beijing Normal University Earth System Model). PCA stands for principal component analysis.

side of their realized niche in over a quarter of their current distribution, averaged across all model decisions and climatic parameters (Supplementary Table 1). The distribution of proportional SCA changes relative to the present is positively skewed with projection averages routinely showing contracting SCA (Supplementary Fig. 2). Averaging SCA changes for all climate change projections (including maps for both 2050 and 2070) per species, we find a predicted average SCA decrease of 6% relative to the present for the modelled 408 taxa. While this decline seems relatively minor, it is driven by the large projected increases of just a few species (for example, *Cylindropuntia munzii* and *Epiphyllum caudatum*). Median SCA change is more pessimistic, projecting a decline of 8% relative to the present. For both mean and median changes, 23% of species are projected to lose over one fourth of their current SCA. Only 12% (mean) or 2% (median) of species are expected to gain over one fourth of their current SCA. Overall, 60% of species are predicted to undergo a decrease in SCA, increasing to 63% when using medians. Across the 246 species predicted to experience a decrease in SCA, the possibility of an increase does not fall within a standard deviation of the mean change for 57 species. Conversely, of the 162 species predicted to experience an SCA increase, considering SCA changes one standard deviation below the mean (hence, less SCA lost), only one species is not at risk of a decline. This suggests a robust decline for 14% of species and a robust increase for less than 1% of species.
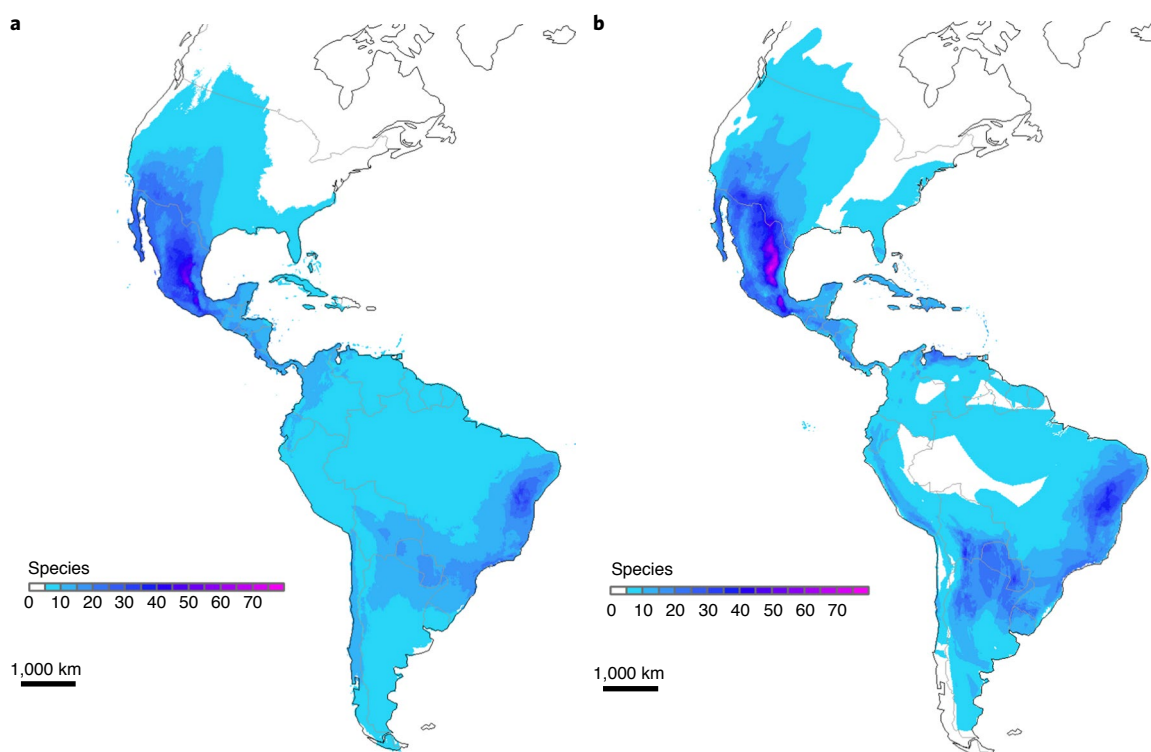
Fig. 1 | Comparison of predicted current cactus species richness. a, Average richness across all maps. **b**, Richness based on expert maps by the IUCN.

Linear regression of SCA changes on parameters representing modelling decisions revealed the effects of these decisions on SCA estimates. As coefficient estimates in a mixed-effects model with species as a random effect were nearly identical (Supplementary Table 2), only results from ordinary linear regression are reported here (Table 1). The thresholding method, used to convert continuous suitability maps to binary presence/absence maps; the variable selection approach; the filtering of correlated variables and feature complexity all had strong effects on SCA change estimates, ranging from 6% to 19% ($P < 0.001$ for all coefficients). Unsurprisingly, increasing the projection distance within which climate suitability is predicted (a proxy for dispersal ability) increases SCA estimates by 5% for 100 km and 13% for 500 km, relative to a baseline of 0 km ($P < 0.001$ for both coefficients). The SCA change effects of climatic parameters (global climate model (GCM) and RCP), as well as sampling distance for model fitting, are much more limited (Table 1).

Sources of uncertainty in SCA change were explored through ANOVA. Excluding residual variance, the three largest contributors (Supplementary Fig. 3) to species-level uncertainty are model feature complexity (46% of variance explained), projection distance (that is, dispersal ability; 21%) and the thresholding approach to create presence/absence maps from maps representing relative probability of occurrence (13%). Of lesser importance are the algorithm used to select environmental variables to be included in the distribution model (10%), whether these environmental variables were filtered before selection to exclude strongly correlated variables (5%) and choice of GCM (3%). The year for which projections are made (2050 versus 2070; <1%), choice of RCP (<1%) and sampling distance (1%) have little effect on uncertainty.

We explored the relationship between mean predicted SCA change by species and four species-level covariates using linear regression (Supplementary Table 3): (1) growth form (columnar/ tree, globular, epiphytic and shrubby); (2) International Union for Conservation of Nature's (IUCN) Red List category (Critically

Endangered, Endangered, Threatened, Near Threatened, Vulnerable, Least Concern and Data Deficient); (3) mean SCA size in the present; and (4) mean cactus species richness in the present (extracted from the IUCN expert range map at the locations of observations). Current SCA size and Red List category were not statistically significant predictors of predicted SCA change. Using columnar/tree-like cacti as the baseline group, only epiphytic species have a significantly stronger SCA decrease (estimated to be 34% lower, 95% confidence interval (CI) from −43% to −25%, $P < 0.001$). A ten-species increase in cactus richness within a species' current SCA is associated with an additional decrease in projected SCA change by 7% (95% CI from −8% to −5%, $P < 0.001$), suggesting that species in areas of higher richness will lose a larger fraction of their SCA.

Changes in number of species at risk. Next, we assessed whether our species distribution modelling accurately captures current diversity patterns. Our analyses show that the average richness map based on our models qualitatively agrees with a richness map based on expert species ranges produced by the GCA[4] (Fig. 1). Hotspots of cactus diversity visible on the expert map, such as the American Southwest, Mexico, eastern Brazil and northern Argentina, are reflected in our map. Concordance seems to be more limited in western Peru and northern Venezuela, where our richness map shows more limited diversity. Overall, richness values for our map and the expert map are very strongly correlated (Pearson's product-moment correlation test, $\rho = 0.84$, 95% CI from 0.84 to 0.84) at our mapped resolution of 10 km. Correlation only decreases slightly when aggregating richness maps to 50 km (Pearson's product-moment correlation test, $\rho = 0.83$, 95% CI from 0.82 to 0.83) and 100 km (Pearson's product-moment correlation test, $\rho = 0.82$, 95% CI from 0.81 to 0.83). Mapping pixel-wise standard deviation of modelled richness shows patterns very similar to the average richness map, with standard deviation generally increasing with mean richness (Fig. 2). The coefficient of variation was low across the map, except at the northern edge of our predictions in North America, California
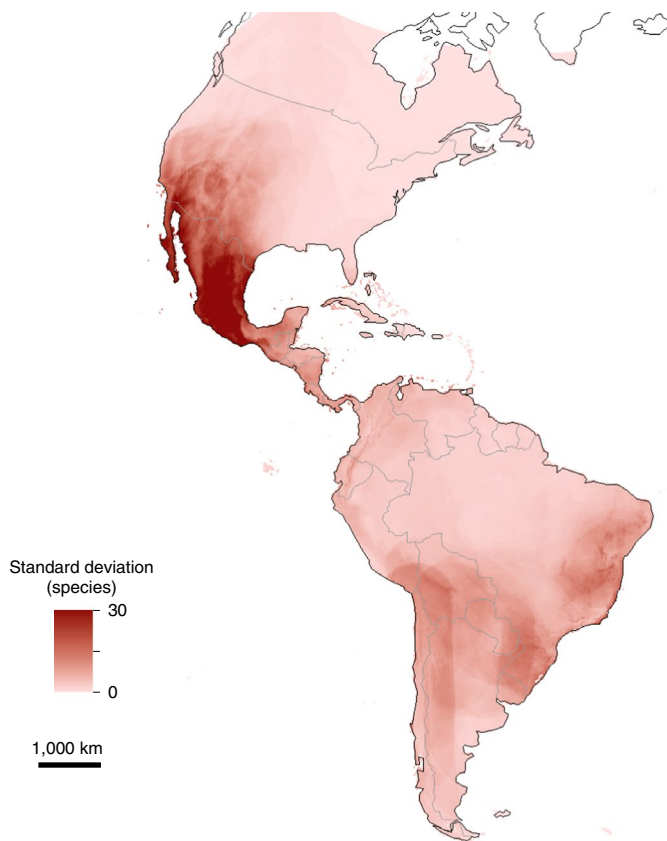
Fig. 2 | Standard deviation of predicted current species richness. Predicted current species richness displayed as standard deviation of the number of species.

and parts of Argentina, Peru, Bolivia, Uruguay and Chile (Supplementary Fig. 4). Most of these areas correspond to regions of low cactus diversity.

Widespread increases in the number of species at risk (SAR) due to changes in SCA are apparent from averaged maps for both 2050 and 2070 under RCP 4.5 and RCP 8.5 (Fig. 3 and Supplementary Fig. 5). Many hotspots of cactus diversity are projected to experience sharp increases in SAR relative to current richness, including central Mexico, the Brazilian Atlantic Forest and eastern portions of the Brazilian Caatinga. Projections for Florida and large swaths of central South America exceed a loss of 50% of cactus species. We also predict strong increases in SAR in most of Central and South America as well as the Caribbean. Projected decreases in SAR are mostly limited to regions with low richness in the present, including most of the United States, southern South America, western portions of the Brazilian Caatinga, northern parts of the Brazilian Cerrado and narrow strips along the Andes. Portions of northwestern Mexico, particularly along the coast of the Gulf of California, as well as the states of Sonora and Chihuahua, show decreases in SAR and currently have high cactus diversity. An index of human footprint for 2009 is positively correlated with current predicted species richness (Pearson's product-moment correlation test, $\rho = 0.13$, 95% CI from 0.13 to 0.14) and negatively correlated with projected change in absolute species richness for 2050 (Pearson's product-moment correlation test, $\rho = -0.08$, 95% CI from −0.09 to −0.08) and 2070 (Pearson's product-moment correlation test, $\rho = -0.09$, 95% CI from −0.10 to −0.09). This indicates that areas with higher human footprint both have higher cactus richness currently and are expected to have a higher SAR in the future, although the human footprint is unlikely to remain static into the future.

Our analyses indicate strong agreement of SAR projections, especially in current hotspots expected to increase in SAR in the future. Maps of the coefficient of variation for richness projections show low variation in diversity predictions (Supplementary Fig. 6). Our results show slightly elevated coefficients along western and northern North America, southern South America as well as western Peru, southern Bolivia and central Argentina. Sources of uncertainty in richness vary geographically (Fig. 4). A map at 100 km resolution of modelling decisions explaining the most uncertainty in each grid cell reveals that projection distance (dispersal ability) and model complexity are the most common factors inflating uncertainty (projection distance in 75% of grid cells, model complexity in 21% of grid cells). In areas of high diversity in the present, including the American Southwest, eastern Brazil and Mexico, projection distance is the most important source of uncertainty. Model complexity is mostly restricted to northern Brazil. Compared with forecasts of cactus richness, these two sources are also the most influential in regions projected to experience strong increases in SAR. The effect of dispersal distance on forecasts is clearly visible by comparing maps for the three dispersal scenarios (Supplementary Fig. 7). Diversity hotspots are smaller in extent and intensity under the no-dispersal scenario and become larger and more intense as projection distance increases. In areas with lower diversity, increasingly optimistic dispersal scenarios allow more species to track suitable climate northwards in North America, southwards in South America and up in elevation in the Andes. Uncertainty not explained by model complexity and projection distance is attributed to variable selection approach, correlation pre-filtering and sampling distance, making up the remaining 4% of grid cells, but lacks a geographic pattern. Time, RCP and GCM do not explain the most uncertainty in any grid cell.

Discussion

Our overall predictions that 60% of cacti in this study will undergo SCA contractions, with only 2–12% of species gaining significant SCA, provides evidence against the hypothesis that cacti will be favoured under climate change. Since models are fit using data from the realized, observed niche, projected ranges do not represent the fundamental niche but, rather, exposure to unfavourable climate across large parts of current species distributions for most cacti. The robustness of our results under many different modelling assumptions and possible climate futures, as well as model quality, underscores the need for rapid conservation action beyond limiting future climate change. In particular, the effect of varying the degree of warming is extremely limited, even under the optimistic RCP 2.6, more liberal than RCP 1.9 as targeted by the Paris Agreement. Similarly, results are very similar for 2050 and 2070, suggesting that environmental conditions will become strongly unfavourable before 2050. Our results show that climate change has the potential to become a more ubiquitous threat to cacti than direct anthropogenic factors. Indeed, using 23% of species losing over a quarter of their SCA as a proxy for being threatened by climate change would shift climate change from ninth to fourth place in the ranking of threats by Goettsch et al.[4]. Using any projected loss as a proxy shifts climate change to first place.

It is important to emphasize that our projections will need to be combined with demographic data to infer conservation status as assessed by the IUCN. However, such data—for example, generation length—are often sparse and difficult to obtain. Importantly, predicted SCA changes are unaffected by current SCA size and conservation status, with epiphytic species and taxa in areas of high richness being disproportionally affected. This is in contrast to a recent large-scale study for cacti in Baja California, Mexico[5], which found that threatened species perform better. While this suggests that trends may be regional, it could also be explained by the use of different indices for conservation status. In Baja California, winners under climate change are predicted to be concentrated in southern
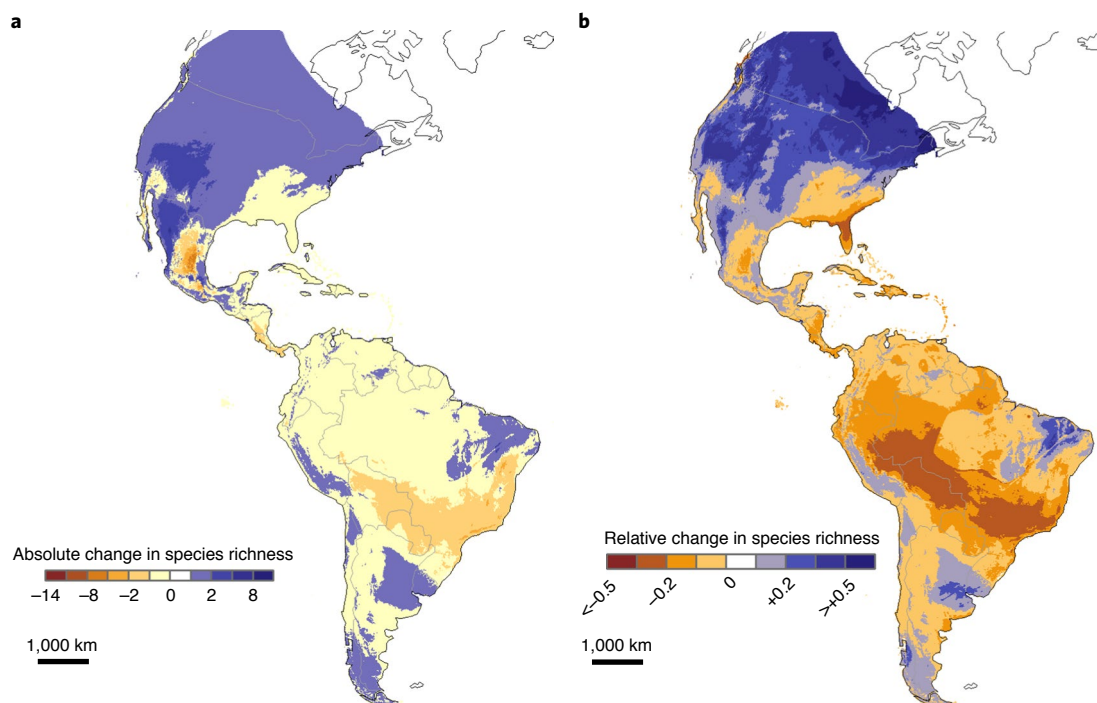
Fig. 3 | Predicted SAR relative to the present for 2061–2080. a,b, Map depicting predicted SAR on an absolute scale (**a**) and a relative scale (**b**). SAR values are based on an average across all model runs. Maps for 2041–2060 are provided in the Supplementary Information (Supplementary Fig. 5).

regions, a pattern we also find here. The predicted sensitivity of epiphytic cacti to climate change remains unexplained but may be linked to narrow climate tolerances and habitat specificity. While we found no impact of current SCA size on projections, many species with a small range are not modelled given the lack of data across such species' ranges. Several small-bodied South American taxa remain underrepresented (for example, *Gymnocalycium*) and should be more intensively sampled. A better understanding of the importance of edaphic factors, dispersal ability and extreme events in determining the distribution of cactus species will be needed to produce more accurate range forecasts and will probably make prospects even more prickly. The scenarios presented here should therefore be interpreted as a conservative estimate of potential distribution changes. Our results also suggest that the impacts of human land use are strongest in areas with existing high cactus diversity. This indicates that cactus hotspots of diversity will be further impacted by human land use. Our predictions that future increases in SAR are stronger in current diversity hotspots and coincide with areas with a high human footprint allow for some prioritization of resources in a family beset by conservation challenges. Continental projections as presented here need to be augmented with smaller-scale studies to better understand geographic patterns and design regional conservation strategies.

Our results suggest that uncertainty is not greatly influenced by future climatic uncertainty but, instead, is largely driven by modelling decisions associated with geographic range modelling. The lack of influence of choice of future climate scenario on cactus forecasts, as well as the importance of dispersal, have been previously noted[5]. Together, the overwhelming influence of model complexity and dispersal limitation on uncertainty in SCA changes and SAR provide a comprehensive accounting of sources of uncertainty in climate change forecasts for a major plant group. However, in studies assessing SCA changes for animals, choices of modelling algorithm, RCP and GCM have been found to be the top sources of uncertainty in forecasts[31,32]. Additional research is needed to conclude whether this contrast in sources of uncertainty is due to inherent differences
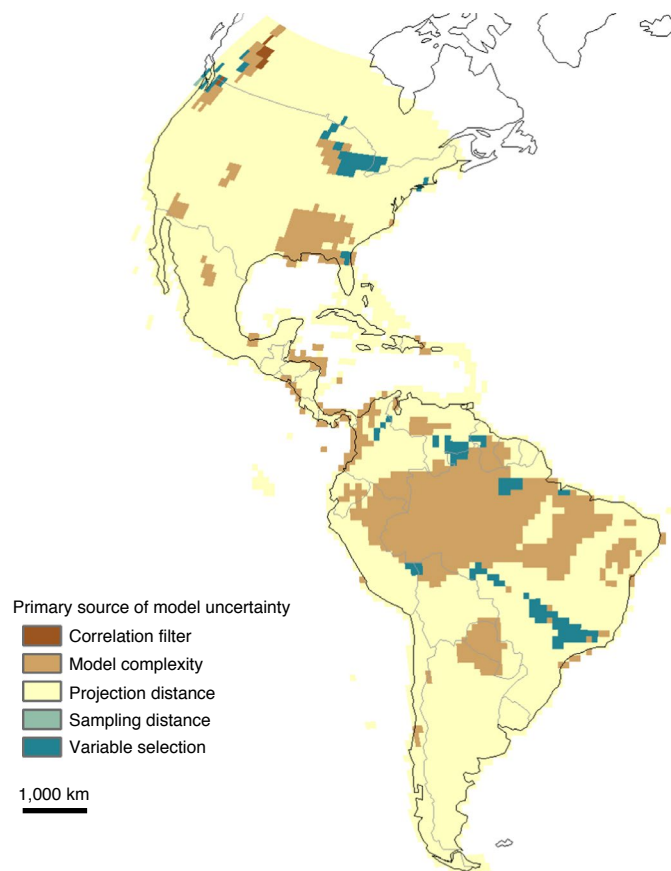

Fig. 4 | Map of modeling decisions explaining the most uncertainty in species richness. Model complexity and projection distance explain the most uncertainty in the majority of the Americas. Map (grid cell) is at 100 km resolution.

among taxa or to differing approaches in attributing uncertainty to sources, as the impact of model complexity and dispersal distance has yet to be tested for animals. The strong influence of dispersal distance on uncertainty, both at the level of individual SCA changes as well as SAR, is reflected by a decrease in the percentage of species projected to lose SCA from 71% without dispersal to 52% when an unrealistic 500 km of dispersal is permitted. This emphasizes the importance of dynamic, climate-change-informed geographic conservation planning, as cacti currently enjoy much less coverage by protected areas than other major taxonomic groups[33].

Cacti currently experience a diverse range of threats to their conservation. The predominant threats are direct human activities associated with land use: habitat degradation, destruction and/or impairment of biodiversity due to land conversion, collection as biological resources and development[4]. Agriculture is the most widespread threat to cacti, affecting species in large parts of northern Mexico, Mesoamerica and the southern portion of South America. Our results show that future climates of hotter and more arid conditions do not appear to favour cactus diversity. Most current hotspots of cactus diversity (including the Brazilian Atlantic Forest, eastern portions of the Brazilian Caatinga and portions of northern and central Mexico) are projected to experience sharp declines relative to current richness. Improving the conservation outlook for cacti will require an understanding of the interactions of human land use and climate change, particularly whether direct anthropogenic drivers and climate change affect different species or the same species will be impacted by both. Depending on how strongly these threats compound, prospects will become increasingly prickly for cacti by the middle of this century. Assuming the 408 species (~25–30% of the family) assessed here represent the family as a whole, and climate change (here estimated to negatively impact 60% of species) and other threat processes (impacting ~30% of species[4]) do not affect the same species, up to 90% of all cactus species could become threatened.

Methods

Data acquisition and processing. We downloaded 187,439 occurrence records belonging to 1,257 species of the family Cactaceae from the BIEN database (https://bien.nceas.ucsb.edu/bien/), version 4.2 (ref. [34]), on 24 October 2020. Records flagged as cultivated, non-native (using the Native Species Resolver; http://bien.nceas.ucsb.edu/bien/tools/nsr/) or outside of the Americas were excluded. Occurrence data were split by species, and only species with 10 or more occurrences for which unique climate conditions could be extracted at a resolution of 10 km were retained (441 species).

Nineteen current (1979–2013) and future (2041–2060 and 2061–2080) bioclimatic layers were downloaded from the Climatologies at high resolution for the Earth's land surface areas (CHELSA repository) (https://chelsa-climate.org/; CMIP5), version 1.2 (ref. [35]), at a 30-arc-second resolution. Future layers included RCP 2.6, 4.5 and 8.5. Five GCMs (CCSM4 (Community Climate System Model version 4), GFDL-ESM2M (Geophysical Fluid Dynamics Laboratory - Earth System Model version 2M), HadGEM-AO (Hadley Centre Global Environment Model version AO), NorESM1-M (Norwegian Earth System Model version 1-M) and BNU-ESM (Beijing Normal University Earth System Model)) were chosen based on a method to select the most diverse models[36]. Layers were aggregated using pixel averages to a resolution of 5 arc minutes (~10 km at the Equator) for computational reasons and to account for uncertainty in occurrence data and projected to the equal-area Coordinate Reference System WGS 84/NSIDC EASE-Grid 2.0 Global (EPSG:6933)[37].

Expert maps were obtained from the IUCN Red List of Threatened Species and the IUCN Species Survival Commission (SSC) Cactus and Succulent Plants Specialist Group. The expert richness map was created by superimposing individual expert range maps. IUCN Red List categories were obtained from the IUCN Red List database (https://www.iucnredlist.org/). Growth habit data were manually created based on species photographs. The Human Footprint map for 2009 (at a resolution of 1 km) was downloaded from Venter et al.[38] and then projected and resampled to the projection and resolution of the aggregated climate data.

Model fitting. For each species, a minimum convex polygon containing the occurrence data was first constructed in geographic space. Buffers of 100 km and 500 km were added to these polygons to use in model fitting. For each of these buffers, current bioclimatic data from 1,000 cells were randomly sampled without replacement as a background sample for model fitting, representing, on average, ~20% of the geographic domain. When fewer than 1,000 cells were available,

all cells were sampled. Models were fit with the maxnet package[39], which uses regularized regression as implemented in the glmnet package[40].

Variables were then selected using four approaches. First, 6 variables were randomly selected for each species from the 19 bioclimatic variables as a control. In the 'one-size-fits-all' approach, the same six variables were used for all species: annual mean temperature, mean diurnal temperature range, annual precipitation, precipitation seasonality, precipitation of the warmest quarter and precipitation of the coldest quarter. The last two variable selection techniques were based on principal component analysis (PCA). For these, PCA was performed on the centred and scaled 19 bioclimatic variables from the background sample. A correlation filter was or was not first applied by iteratively filtering out variables until no variables with correlations of over 0.7 remain[41]. In the first PCA approach, models were then fit using the six variables with the highest absolute loadings in the first principal component. If fewer than six variables were available (due to the correlation filter), all are used. In the second PCA approach, a parallel analysis[42] (1,000 iterations, 95th percentile) was performed to determine the number of principal components to retain, which were then used to fit models. In all cases, models were built allowing three levels of complexity: linear features only; linear and quadratic features only or linear, quadratic and hinge features. The maximum number of iterations for convergence was 10,000. Species for which not all models converged were not retained (11 species). All other parameters, such as regularization parameters, were set to default settings.

Models were evaluated with fivefold cross-validation, where the folds were selected using environmental blocking[43]. All data were then used to build the final model, and only the 408 species for which all model AUCs of the ROC were equal to or greater than 0.5 were retained (22 species removed).

SCA maps. After model fitting, final models were used to construct geographic maps by using the model to predict environmental suitability in the form of relative probability of occurrence[44] in each grid cell. The effect of dispersal was simulated by restricting projection distances to 0 km (no dispersal), 100 km and 500 km beyond the minimum convex polygon. While this precludes the possibility of rare long-distance dispersal events, such events would be insufficient to establish new populations within 30 or 50 years, especially for species with long generation times such as the iconic *Carnegiea gigantea* (saguaro). No clamping was implemented to more realistically test the effect of different dispersal distances on SCA changes.

Suitability maps were then thresholded to binary (presence/absence) maps. Two different thresholds were used: the threshold that maximizes the true skill statistic[45] (the sum of sensitivity and specificity minus one) and the threshold that sets the omission (false negative) rate at 5%. Binary maps were then used to calculate SCA sizes, which were analysed further by regressing SCA changes on model parameters using both ordinary linear regression and a mixed-effects model with species as a random effect. SCA changes were also regressed using ordinary linear regression on several ecological covariates, including growth habit, mean current SCA size, cactus species richness derived from IUCN expert maps and IUCN Red List category. An uncertainty analysis was performed using ANOVA by calculating the proportion of variance in SCA changes explained, excluding residual variance, by each model parameter.

Richness maps. Richness maps were created by superimposing suitability maps, which reduces overestimation of richness as observed in stacking of thresholded maps[46]. As all SCA maps were aligned, no resampling was performed. *Selenicereus* (*Hylocereus*) *undatus* and *Opuntia ficus-indica* were excluded from diversity maps as their natural range is uncertain. Maps were aggregated to 100 km resolution with cell averages for the uncertainty analysis to conserve computational resources. An uncertainty analysis was performed for each grid cell using ANOVA by calculating the proportion of variance in species richness explained, excluding residual variance, by each model parameter. All analyses were performed with R version 3.6.0 (ref. [47]).

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

Data availability
Occurrence data used for analyses are available only upon request to protect the many threatened species modelled. Requests should be made through the BIEN portal at https://biendata.org/. Bioclimate data were retrieved from the CHELSA repository, version 1.2 (https://chelsa-climate.org/; CMIP5). Expert maps were obtained from the IUCN Red List of Threatened Species and the IUCN SSC Cactus and Succulent Plants Specialist Group. IUCN Red List categories were obtained from the IUCN Red List database (https://www.iucnredlist.org/). The Human Footprint map for 2009 (at a resolution of 1 km) was downloaded from Venter et al.[38].

Code availability
Code is available at https://github.com/mdpillet/PricklyProspects/.

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Author contributions

M.P. created, developed and led the project. B.G. contributed expert maps. All authors contributed to the analyses. M.P. drafted the manuscript, and all authors provided comments on the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

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Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection	No software was used to collect data used in this project. Data was retrieved from existing sources.
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Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	Analysis of climate change impacts on cacti.
Research sample	All geographic occurrence records (n = 187,439) for Cactaceae, retrieved from BIEN 4.2. Scale is the Americas. Data span the 20th and 21st centuries. Organisms were not manipulated. Sample meant to represent the entire family.
Sampling strategy	All available data.
Data collection	Retrieved via database BIEN 4.2. BIEN aggregates data from many different biodiversity databases, which contain records recorded by numerous individuals. Instrumentation is not explicitly recorded in these databases, but is mostly digital using GPS. Data sources are recorded within the occurrence data, which are available upon request.
Timing and spatial scale	All available temporal data within BIEN 4.2, limited to the Americas. Data span the 20th and 21st centuries. Data are point occurrence records. Dates are recorded within the occurrence data, which are available upon request.
Data exclusions	Species with less than 10 occurrence records excluded, which is a common threshold for excluding species from analysis during species distribution modeling. Threshold pre-established. Species with uncertain native range excluded. Exclusion pre-established.
Reproducibility	Five-fold cross-validation of models using environmental blocking. No impact on results.
Randomization	Five-fold cross-validation of models using environmental blocking. This type of cross-validation is useful in environments with spatial structure to provide robust error estimation, as traditional cross-validation can underestimate prediction error. No impact on results. Final models use all available data so randomization is not applicable.
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