

Heat and desiccation tolerances predict bee abundance under climate change

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Climate change could pose an urgent threat to pollinators, with critical ecological and economic consequences. However, for most insect pollinator species, we lack the long-term data and mechanistic evidence that are necessary to identify climate-driven declines and predict future trends. Here we document 16 years of abundance patterns for a hyper-diverse bee assemblage¹ in a warming and drying region², link bee declines with experimentally determined heat and desiccation tolerances, and use climate sensitivity models to project bee communities into the future. Aridity strongly predicted bee abundance for 71% of 665 bee populations (species × ecosystem combinations). Bee taxa that best tolerated heat and desiccation increased the most over time. Models forecasted declines for 46% of species and predicted more homogeneous communities dominated by drought-tolerant taxa, even while total bee abundance may remain unchanged. Such community reordering could reduce pollination services, because diverse bee assemblages typically maximize pollination for plant communities³. Larger-bodied bees also dominated under intermediate to high aridity, identifying body size as a valuable trait for understanding how climate-driven shifts in bee communities influence pollination⁴. We provide evidence that climate change directly threatens bee diversity, indicating that bee conservation efforts should account for the stress of aridity on bee physiology.

Reports of alarming declines in terrestrial arthropod biodiversity highlight the need to pinpoint which insect taxa and ecosystem services are most threatened and why⁵. Bee declines are particularly concerning, because bees are the most important pollinators of many wild and agricultural plants^{6,7}, accounting for billions of dollars in crop production annually⁸. Bumblebee declines and honeybee colony losses are well-documented^{9–11}, and some evidence indicates decreasing bee diversity in Europe and North America^{12,13}. However, for most of the world's approximately 20,000 bee species, more than 98% of which are neither bumblebees nor honeybees¹⁴, we lack the data to assess trends in abundance or causes of biodiversity declines.

Growing evidence implicates climate change as an important driver of bee declines^{10,15–21}, but it remains less studied relative to other stressors^{6,22} such as habitat loss, disease and pesticides. Climate change could directly reduce bee fitness when ambient conditions exceed physiological tolerances, but these tolerances have not been measured for most bee species²³ (but see refs. 18, 24, 25). Climate studies have largely focused on geographical or phenological shifts, particularly potential phenological mismatches between bees and plants, often finding that mismatches are unlikely^{6,26}. However, climate change could affect bees directly as well as indirectly via floral resources²³. Recent studies indicate that climate is correlated with bumblebee distributions^{10,17} and native bee abundances^{19,20}, and relate bumblebee population trends to historic thermal habitat and heat shock tolerance¹⁸. These studies suggest the probable importance of direct

climate threats to bees, and highlight the urgent need for mechanistic research on diverse species. In particular, predicting vulnerability to no-analogue future climates requires understanding the physiology underlying animals' climate sensitivities. Insects have high water loss relative to their metabolic rates, making it critical to measure both thermal and desiccation tolerances, which very few studies have done²⁷ (but see ref. 28).

In addition, body size may be a critical trait for understanding climate vulnerability and its ecological consequences across diverse organisms. Surface area:volume ratio scales with body size, affecting heat retention and water loss in ectotherms²⁹. In bees, body size correlates with nutritional requirements³⁰, competitive ability³¹, flight distance³² for floral resource acquisition, and disease transmission³³. Size could thus mediate climate effects on bees directly by governing physiological responses, or indirectly by determining interactions with plants, competitors or natural enemies, especially when floral resources decline. Studies show contrasting patterns of change in bee body size along spatiotemporal gradients in temperature^{19,34–37}, as well as differing body size–thermal tolerance relationships in bumblebees^{18,38}, establishing the value of examining this trait and highlighting the need to clarify its role across the bee phylogeny and across ecosystems. Body size also links bees' climate vulnerabilities to their ecological consequences for pollination via size matching with flowers^{4,39}. Forecasts of changes in body size could thus enable community-level predictions of climate change threats to critical pollination services.

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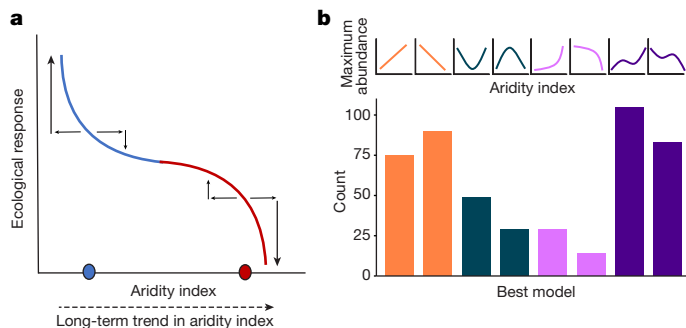


Fig. 1 | CSF theory and summary of results. **a**, A nonlinear relationship between aridity and an ecological variable signals the importance of climate variability, in addition to climate mean, in determining the ecological response, which depends on the shape of the nonlinearity. A concave up quadratic function (blue) signals a net benefit of increasing variance around the mean (black arrows), whereas a concave down relationship (red) signals a net cost of increasing variance. Under a cubic relationship (full curve), variance may be either costly or beneficial, depending on the climate mean, indicating a mean $\times$ variance interaction. **b**, Summary of the CSFs relating aridity to maximum yearly abundance for 474 climate-sensitive bee populations out of 665 populations in total. The climate-sensitive populations represented 243 bee species across 3 ecosystems. The count indicates the number of populations for which a given model type was best. Orange bars represent sensitivity to shifts in mean aridity alone, whereas teal bars indicate sensitivity only to variance in aridity. Purple bars denote sensitivity to changes in the mean and variance of aridity, with light purple indicating additive effects of mean and variance, and dark purple indicating interactive effects.

Understanding bees' climate vulnerability requires considering their sensitivity to changes in both climate mean and climate variability, which has increased over time in many regions but has been little-studied^{40,41}. Climate sensitivity functions (CSFs) describe how an organism's abundance tracks the distribution of a climate variable (mean and variance)². Specifically, a nonlinear CSF signals that climate variability alone will affect abundance, even if the climate mean does not change; this is referred to as Jensen's inequality (Fig. 1a). Laboratory trials suggest that greater variance in temperature can reduce insect population growth⁴⁰, but CSFs are unexplored for bees, impeding predictions of future bee biodiversity under increasingly variable climate conditions. In the southwestern USA, a global hotspot of bee diversity⁴², the climate has become drier and more variable from year to year² (Extended Data Fig. 1a,b), providing an ideal test bed to assess the climate vulnerabilities of bees.

We combined 16 years of bee survey data (from 2002–2019, with the exception of 2016–2017, comprising 339 species) from the Sevilleta Long-Term Ecological Research Program (SEV-LTER) carried out in New Mexico, USA, with physiological tolerance and body size measurements to address the following questions spanning population to ecosystem scales. (1) Population scale: How sensitive is bee abundance to climate, and how will abundance change under future climate scenarios? Do thermal and desiccation tolerances explain which bees are winners and which are losers under climate change? We hypothesized that bee abundance tracks aridity with species-specific patterns of physiologically tolerant winner species and vulnerable loser species. (2) Community scale: How have bee biodiversity and body size tracked climate over time, and what changes are expected under future climate scenarios? We hypothesized that hot, dry years favour larger-bodied bees with high heat and desiccation tolerances, shifting communities toward dominance by larger bees and reducing bee diversity. (3) Ecosystem transitions: Will climate-induced ecosystem transitions alter bee vulnerabilities to future climates⁴³? We addressed this question using bee monitoring data from three common ecosystem types of the southwestern USA (Extended Data Fig. 2). We hypothesized that predicted

transitions in which desert grasslands overtake plains grasslands and shrublands engulf grasslands⁴³ will reshape future bee communities to be less diverse but more resistant to aridity.

Bee abundance strongly tracked aridity

Bee abundance strongly tracked aridity at the population level, demonstrating an important linkage between climate and bee population health (Fig. 1b). As an aridity metric, we used the inverse of the standardized precipitation evapotranspiration index (SPEI), which integrates temperature and precipitation. Positive aridity values indicate hotter and drier conditions relative to the mean, and negative values represent cooler and wetter conditions (Methods). Seventy-one per cent of bee populations were sensitive to change in the aridity index (474 out of 665 species $\times$ ecosystem combinations; Supplementary Fig. 1 and Supplementary Table 1); these populations represented 243 species. Results derive from mixed effects models of maximum yearly bee abundance as a function of the aridity index, built for each of the 665 populations (Methods). Among the populations that tracked aridity, 35% had linear relationships with aridity signalling sensitivity to changes in mean aridity alone (Fig. 1b), 16% had quadratic relationships indicating sensitivity to the variance but not the mean of aridity (nonsignificant linear parameter; Fig. 1b), and 9% were sensitive to mean and variance additively (significant linear and quadratic parameters; Fig. 1b). However, 40% of populations had cubic relationships with aridity, signalling sensitivity to the interactive effects of more arid and variable climate conditions (Fig. 1b). Most aridity-insensitive populations (29% of all populations) were rare species for which there was low statistical power to detect trends (Supplementary Table 2).

Additional model comparisons indicated that approximately half of bee species may experience lagged effects of climate change. The aridity of the present year best predicted abundance for 48% of populations, whereas that of the previous year best predicted abundance for 52% of populations. Spring season aridity predicted abundance better for a slightly larger number of populations (56%) than summer monsoon season aridity (44%). These results suggest the importance of considering time lags, seasonal specialists and bee phenology to understand population-level sensitivities to climate change. Our findings are consistent with evidence that desert bees use environmental cues to emerge in favourable years and remain in diapause in unfavourable ones, and 'bet-hedge' such that in any given year, some individuals remain in diapause to spread risk across years^{44–46}.

Physiology predicted winners and losers

The bee genera that were most tolerant of heat and desiccation in field-based physiological trials (Methods) were those that increased most strongly under historical climate change (Fig. 2a,b and Supplementary Table 3). A metric that combined thermal and desiccation tolerance predicted both sensitivity to mean aridity (linear parameter from CSFs; likelihood $R^2 = 0.37$) and the magnitude of change in bee taxon abundance over time (likelihood $R^2 = 0.80$), indicating the importance of considering insect water relations in conjunction with temperature regulation (Fig. 2a,b and Supplementary Table 3). Among individual metrics of bee physiology, tolerance to vapour pressure deficit (VPD at the time bees lost responsiveness in thermal trials) best predicted change in abundance over time, again suggesting that temperature and water regulation together govern bee performance (Supplementary Table 3). In our models, physiological tolerance metrics did not predict sensitivity to variance in aridity (best quadratic model: $P = 0.42$). We therefore suggest that heat and drought tolerance more strongly underlie bee responses to climate mean rather than climate variance. Thermal tolerance differed by 37% between the least and most tolerant bee genera, and vapour pressure deficit tolerance differed by 138%. Relating thermal tolerances to future aridity, on average across

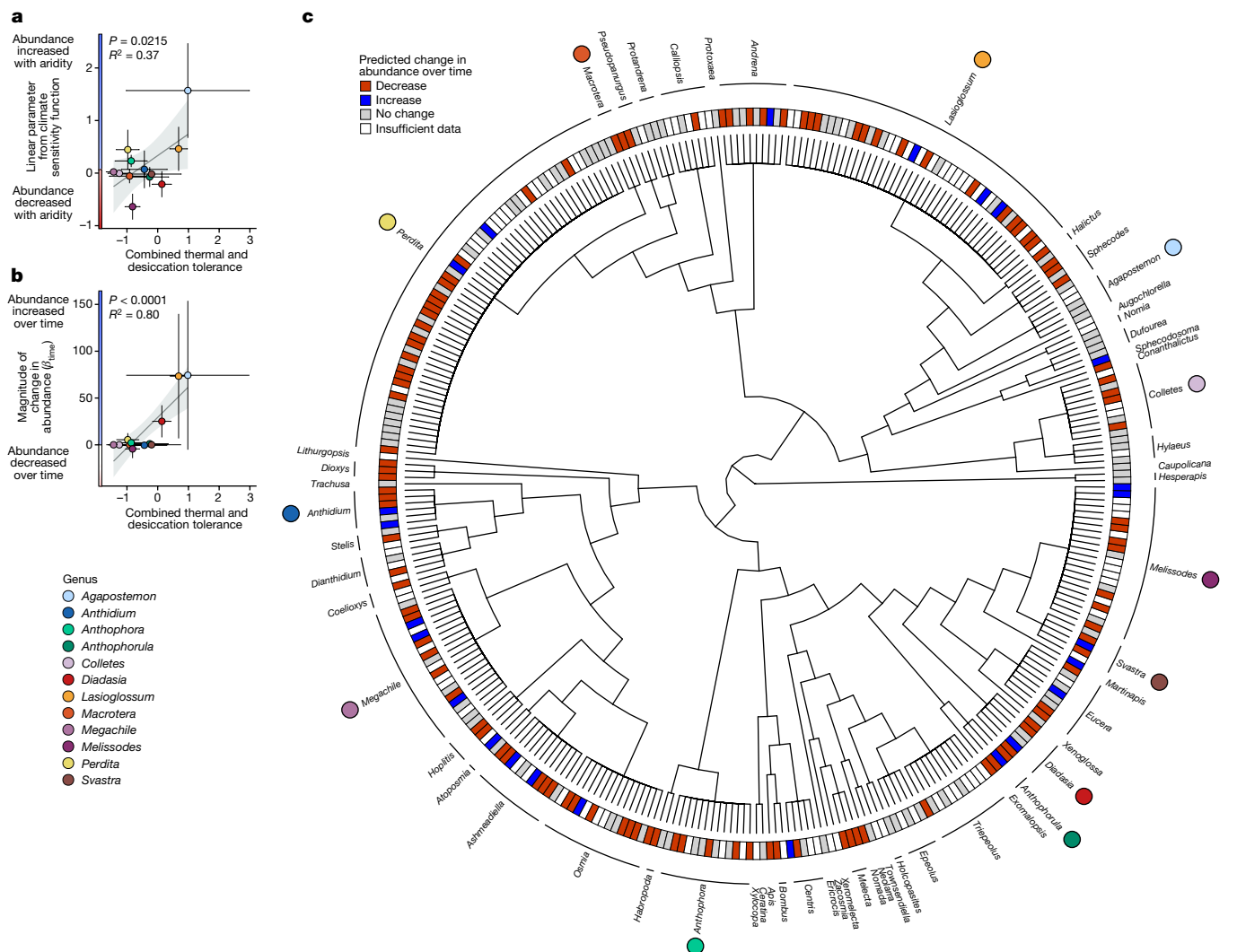


Fig. 2 | Physiology predicts sensitivity to aridity and change in abundance over time. **a**, Combined thermal and desiccation tolerance predicted how bee abundance varied with aridity (linear parameter estimate from climate sensitivity analysis), for 12 focal bee genera. Higher physiological tolerance values indicate greater resilience to aridity. **b**, Combined thermal and desiccation tolerance predicted the magnitude of change in bee abundance over time (2002–2019), for 12 bee genera. β_{time} estimates are from models of total abundance as a function of year. **a, b**, Points represent means across individuals within a genus and error bars indicate s.e.m. (mean $n = 11$ for

thermal tolerance and 16 for desiccation tolerance; see Methods for sample sizes per species and statistical methods). Error bands represent 95% confidence intervals, and statistical results are from mixed effects models with phylogeny incorporated as a random effect (Methods). **c**, Phylogeny of the 339 bee species collected at the Sevilleta National Wildlife Refuge from 2002–2019, labelled by genus, with direction of predicted change in abundance from 2002–2100 (decrease, increase, no change, or insufficient data) based on averaged projections from six GCMs of global climate. Coloured dots indicate focal genera. See Extended Data Fig. 4 for the phylogeny with species names as tip labels.

general circulation models (GCMs) of global climate under a moderate climate change scenario through 2100, we project that in 17% of the next approximately 80 years, monsoon season conditions will exceed the thermal maxima of the least tolerant bee taxa (range across GCMs: 5–26%; Extended Data Fig. 3a). These results derive from our direct measurements of critical thermal maxima (CTMax) and desiccation tolerances (time to loss of responsiveness under dry conditions) of bee individuals netted in the field, using experimental methods²⁷. Bee evolutionary history, as represented by the current bee phylogeny, did not predict the combined physiological tolerance metric (Blomberg's $K = 0.91$, $P = 0.054$), the change in bee species abundance ($K = 0.054$, $P = 0.936$; Fig. 2c), or sensitivity to mean aridity ($K = 0.59$, $P = 0.424$). Thus, across the focal bee community, climate tolerance traits were not phylogenetically conserved.

Most desert bees overwinter as prepupae (last-instar larvae) that can remain in extended diapause until favourable conditions occur⁴⁵. Drought resistance of larvae could thus strongly influence bee species'

responses to climate change. Measuring larval physiological tolerance for multiple species would be extremely difficult but could explain some of the variance in Fig. 2a,b, as adult and larval tolerances may not correspond⁴⁷. Demographic models that incorporate life history transitions could elucidate mechanisms of reduction in fitness under climate change (for example, how do thermal or hydric stress in adults versus larvae, and changes in floral resource quantity or quality, influence stage-specific survival and reproduction?). However, collecting sufficient data would be extremely challenging given our species-rich bee assemblage dominated by ground-nesting species with difficult-to-study larval stages⁴⁵.

For the 243 bee species that are sensitive to aridity, our models projected that 10% will 'win' (increase in abundance) under future climate conditions⁴⁸, 46% will 'lose' (decrease in abundance), and 44% will experience no net change in abundance by 2100 (Fig. 2c and Supplementary Table 4). To obtain these results, we used projected future aridity values from ClimateNA⁴⁹, with data originating from six different

GCMs, in the CSF equations from above to predict the abundance of each bee population during 2020–2100 for three Intergovernmental Panel on Climate Change (IPCC) scenarios representing low, moderate and extreme climate change (moderate scenario results averaged across GCMs are presented here; see Supplementary Table 4 for other results). To capture uncertainty, separate model runs for each of the six GCMs indicated that decreases could occur for 41–58% of species, increases could occur for 0–19% of species, and no change could occur for 40–48% of species (Supplementary Tables 4 and 5). In contrast to physiological traits, bee life history traits (sociality, overwintering life stage and diet breadth) did not predict ‘winner’ versus ‘loser’ status (Supplementary Table 6).

These results suggest the concerning likelihood of climate-driven declines in bee diversity in the southwestern USA. However, they also indicate the resilience of many dryland bees to climate change, given that population increases or stability were predicted for 54% of species. Some of these desert species appear well-adapted to aridity, increasing as mean aridity increased. But for 94 species (39%), future increases in the year-to-year variability in aridity may buffer against declines caused by increasing mean aridity. We thus highlight that understanding bees’ climate responses requires attention to the nonlinearities that signal sensitivity to climate variance in addition to changes in the mean. Adaptations underlying bees’ resilience to climate may be physiological, in accordance with our results, or could relate to morphological or behavioural traits that have not yet been commonly measured across diverse bee taxa. Our results align with studies of arid-adapted bee species in Australia and Brazil, where some bee species are predicted to undergo range expansions with increased aridification^{21,50}, and also align with occupancy models that predict expansion of potential habitat for some bumblebees in North America and Europe¹⁰.

Both diet specialists and generalists were among predicted winner and loser bee species (Supplementary Table 6), indicating that specialists and their host plants may not be most vulnerable to losses in drylands, as can occur in some locations⁵¹. For instance, *Diadasia rinconis*, a Cactaceae specialist, is predicted to remain stable over time, whereas *Lasiglossum* (subgenus *Dialictus*) *semicaeruleum*, a broad generalist, is projected to increase in abundance up to intermediate aridity (as in previous findings for this subgenus⁵²), but then to decline under the most arid conditions. These results highlight the importance of considering bees’ direct responses to climate to predict future pollination outcomes for plants.

Larger bees dominated under aridity

At the community scale, larger-bodied bees were more abundant than smaller bees during years with intermediate to high monsoon season aridity (Fig. 3 and Supplementary Table 7). Historically, body mass (community-weighted mean) increased linearly with aridity across the three focal ecosystems (Fig. 3a). However, the ecosystems diverged in predicted future trends: models generally projected increases in community-level bee body mass in the plains grassland, but suggested future nonlinear dynamics in the two desert ecosystems, with average body mass peaking at moderate aridity and decreasing at the highest predicted aridity levels, which exceeded conditions recorded in the historic data (moderate scenario, Fig. 3b–g; results from other climate scenarios are presented in Extended Data Fig. 5). Intraspecific body mass did not change over time within 16 of the most common bee species preserved yearly as museum specimens (Extended Data Fig. 6), suggesting little phenotypic plasticity or evolutionary change within species. Instead, historic change in community-level body mass occurred through shifts in the relative abundances of large versus small bee species.

We hypothesize that non-physiological mechanisms underlie increases in community-level body mass, because mass did not predict bee species’ physiological tolerances to heat or desiccation ($P = 0.86$,

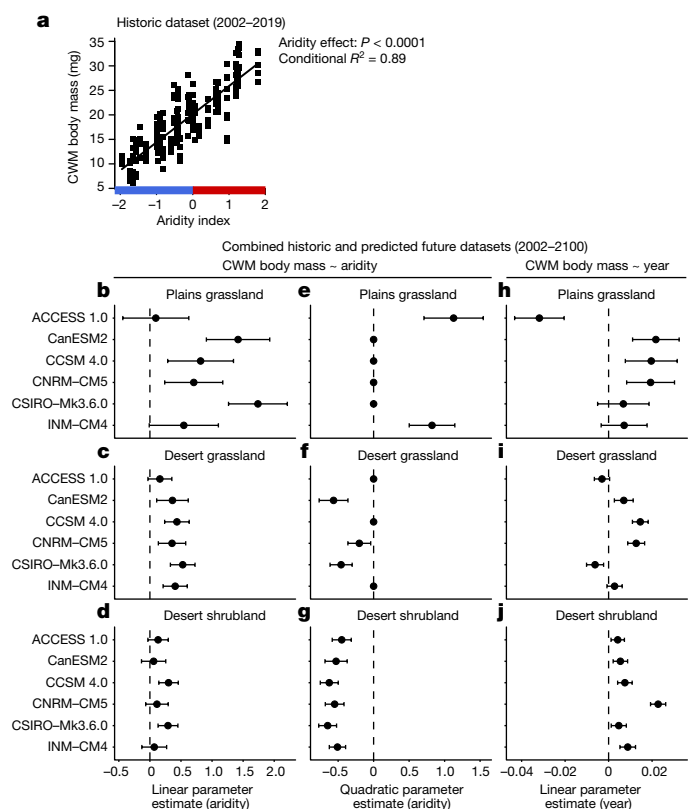


Fig. 3 | Change in community-weighted mean bee body mass with aridity and over time. **a–g**, Community-weighted mean (CWM) body mass closely tracked the monsoon season aridity index in the long-term historic dataset across ecosystems (visreg plot showing fitted values from mixed effects model) (**a**) and in the combined historic and predicted future data up to 2100 under the moderate climate change scenario, in each of three common ecosystem types of the southwestern USA (**b–g**). **h–j**, Models generally projected future increases or no change in CWM body mass depending on the ecosystem and GCM. **b–j**, Mean and s.e.m. of the linear or quadratic effect of aridity or year on CWM body mass using results from each of six GCMs (listed on the y-axis). Positive and negative aridity values indicate hotter/drier and cooler/wetter conditions, respectively, relative to the historic mean (2002–2019). Statistics in all panels are from mixed effects models (Methods).

$R^2 = 0.10$ for the best model; Supplementary Table 8). The greater foraging distances typical of larger bees³² may be advantageous when floral resources are most scarce, such as under arid conditions in the southwestern USA (Extended Data Fig. 7). Loss of floral resources under agricultural expansion favoured larger female bees capable of flying greater distances to reach food⁵³, and a similar mechanism could be at play in drylands. Drought-induced floral scarcity may also amplify interspecific competition, which could favour larger-bodied bees that can outcompete smaller species³¹. Small bees may also be at a disadvantage because they have high nutritional requirements relative to their size owing to the allometric scaling of metabolic rate with body mass⁵⁴. However, during extremely dry future years in the two desert ecosystems, resource scarcity might disproportionately harm larger-bodied bees owing to their greater absolute resource needs, countering any advantages conferred by longer flight distances, better competitive abilities or lower metabolism, and generating the predicted hump-shaped nonlinear dynamics with aridity (Fig. 3f,g).

Our results pinpoint body size as an important and tractable trait that links increasing aridity with consequences for pollination services and bee susceptibility to non-climate stressors. Bee–flower size matching increases fruit set and promotes plant–pollinator interaction network stability⁴, indicating that climate-induced community-level shifts in

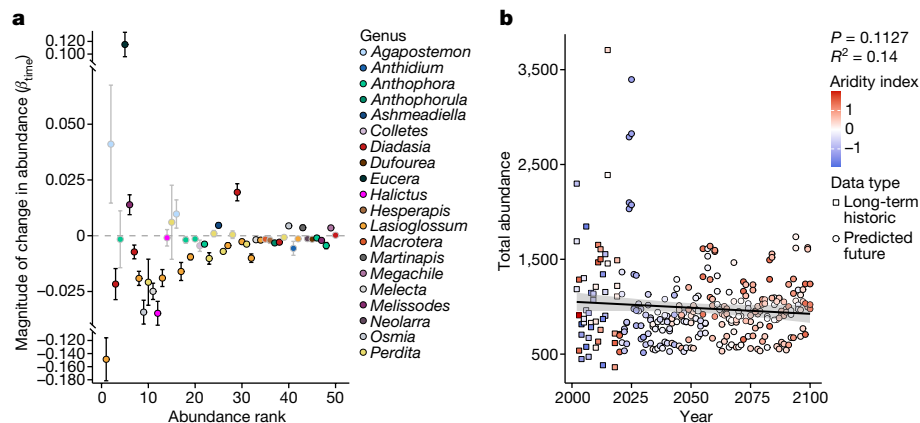


Fig. 4 | Winners and losers in bee communities under climate change.

a, Magnitude of predicted change in bee species abundance over time for each of the 50 most abundant bee species (2002–2100 averaged projections from six GCMs; moderate climate change scenario; points indicate mean slope and error bars represent s.e.m.) as a function of each species' abundance rank in the historic dataset (2002–2019). Each point represents a bee species, colour-coded by genus. Error bar and point circumference colour indicates whether change over time was significant (black) or not significant (grey). **b**, Total bee abundance

is projected to remain stable over time (moderate climate change scenario; year effect from linear regression: $F_{1,285} = 2.53$, $P = 0.11$). Each point represents the sum for each ecosystem $\times$ year combination of all species-level mean predicted abundance values that were calculated by averaging across predictions from six GCMs. Points are coloured by monsoon aridity averaged across the six GCMs. Positive aridity values indicate hotter/drier conditions, and negative values indicate cooler/wetter conditions relative to the historic mean (2002–2019). The error band represents the 95% confidence interval.

bee body size could destabilize pollination networks. Larger-bodied bees may also transmit pathogens more readily than small bees, suggesting that increases in large bee species could reduce overall bee community health³³.

Ecosystem transitions may enhance declines

Future ecosystem transitions⁴³ could alternatively aggravate or dampen the vulnerabilities of bees to climate change. Specifically, in the southwestern USA, desert grassland is predicted to overtake plains grassland, and desert shrubland is predicted to overtake grassland⁴³. In our study, 143 bee species occurred in more than 1 ecosystem. For 87% of these species, sensitivity to aridity differed among ecosystems (Supplementary Table 1). In the drier desert ecosystems (Extended Data Fig. 2), a greater percentage of species decreased in abundance as aridity increased (47% and 58% of species in the desert grassland and shrubland versus 32% in the plains grassland).

These results suggest that the vulnerabilities of bees to heat and drought will intensify as ecosystem transitions progress. This pattern may arise from a limited availability of microclimates that enable behavioural thermoregulation in the more arid ecosystems⁵⁵, or from ecosystem differences in floral abundance, diversity or phenology⁵⁶. Similar ecosystem-specific patterns were recently detected for small mammals across the southwestern USA⁵⁷, indicating that differing vulnerabilities to climate among ecosystems may be common for dry-land animals. Given that our three focal ecosystems differed in both bee community composition and seasonal turnover patterns¹, state transitions among them could alter bee communities through multiple mechanisms. Future work could document each bee's floral resources to evaluate the relative importance of indirect climate effects via changes in floral composition, abundance or phenology⁵⁶, which was beyond the scope of this study. Decreases in floral abundance and changes in plant community composition or phenology under increasing aridity could exacerbate bee declines in ways that our current models do not capture, making our estimates of declines conservative.

Models also predicted potential ecosystem divergence in future community body mass trends. Average bee body mass was generally projected to increase in all ecosystems (Fig. 3h–j). However, future body mass increases are expected to be largest in the plains grassland, whereas increases may be followed by declines past a threshold of

aridity intensification in the two desert ecosystems (Fig. 3 and Supplementary Tables 5 and 7; results from other climate scenarios are presented in Extended Data Fig. 5). These findings indicate that ecosystem transitions will contribute to determining the consequences of climate change for the community-level pollinator effectiveness of bees, as mediated by body size³⁹. In addition, the projected potential for community-level increases in body mass reinforces evidence against the hypothesis that body mass declines are a universal biological response to climate warming⁵⁸. The key to accurate prediction is contextualizing species traits and physiology within the appropriate exogenous climate context.

Our models projected lower interannual variability in future mean body mass relative to the historic period, particularly for the desert ecosystems. As projected future aridity has variance comparable to the historic record (Extended Data Fig. 1), this reduced variability in body mass probably resulted from our models not capturing non-climate factors that can drive fluctuations in bee communities, such as bet-hedging strategies, nest availability, parasitism, disease, predation and floral dynamics that are not explained by climate⁴⁵. These factors may dampen the ability to detect a direct influence of climate-induced changes from long-term observational data.

Abundant but less diverse communities

Our models project a rise in the dominance of a small number of bee species (10%) that benefit from increasing aridity, offsetting the declines predicted for 46% of species (Fig. 4a). As a result, total bee abundance across ecosystems is projected to remain stable over time on average across GCMs (Fig. 4b, $P = 0.11$; results from other climate scenarios are presented in Extended Data Fig. 5). Separate model runs for each GCM aligned with this result in the majority (50%) of cases, although particular GCMs predicted small increases (17% of GCMs) or decreases (33%) in total bee abundance (Supplementary Table 5). Individual species projected to increase most in abundance were members of the genera *Agapostemon*, *Eucera* and *Melissodes*, whereas species of *Lasioglossum*, *Osmia*, *Melecta*, *Halictus* and *Perdita* were projected to decline, and opposing trends were predicted for different species of *Diadasia* (Fig. 4a). We thus anticipate an abundant but less diverse and more homogeneous future bee community for the region. Our results bolster the pattern of biotic homogenization as a general community

response to diverse anthropogenic perturbations⁵⁹. Although bee species' responses to climate change may vary globally, we reveal that climate change and physiological mechanisms are likely to be of broad importance, and create an analytical framework that can be widely applied.

Conclusions

Here we reveal that direct physiological responses to heat and drought can underlie bees' vulnerability to climate change. Experimental field trials uncovered a mechanistic link between bees' physiological tolerances and their population dynamics, expanding on previous studies that documented correlations between bee abundance and climate variables^{10,20}. Our results align with findings from freshwater invertebrates for which desiccation resistance predicted community response to experimental drought, suggesting potential generality across invertebrate taxa²⁸. Results also demonstrate that understanding bees' responses to climate requires attention to nonlinearities that signal sensitivity to climate variance, in addition to changes in mean climate². Concerningly, our models predict abundance declines for 46% of 243 bee species studied in the southwestern USA, projecting less diverse, more homogeneous future bee communities dominated by species with high aridity tolerances and large body mass. This community reordering could have critical ecosystem-level consequences because bee functional diversity promotes pollination services³.

Evidence of a strong link between climate and bee population dynamics highlights that efforts to restore native habitat, reduce pesticide use or manage disease prevalence in bees²² will be most successful if they account for the physiological stress simultaneously imposed by climate change. To mitigate this stress, habitat restoration could intentionally integrate microclimates that provide refuge from heat⁵⁵. Bees experiencing high heat may have greater nutritional requirements⁵⁴, creating a need for drought-tolerant floral plantings that create phenological diversity in food resources⁶. Under heat and drought stress, bees may be particularly vulnerable to disease, and evidence suggests that pathogens can lessen bees' heat tolerance⁶⁰, enhancing the importance of reducing disease burdens⁶. Strategies such as assisted migration, although controversial, could prevent species losses due to thermoregulatory stress and conserve diverse pollinator communities in the face of climate change.

In sum, we demonstrate that identifying and mitigating bee declines requires knowledge of the direct, trait-mediated effects of climate on pollinator fitness and population persistence. This understanding is key to preserving the pollination services that are needed to maintain global crop production and ecosystem functionality for future generations.

Online content

Any methods, additional references, Nature Portfolio reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at <https://doi.org/10.1038/s41586-024-07241-2>.

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Methods

Study system

The Sevilleta National Wildlife Refuge (SNWR; Socorro, NM) spans 93,000 ha and includes five ecosystem types that together represent ~80 million ha of the southwestern USA. We focus on three common ecosystems in the Refuge that feature distinct plant communities (Extended Data Fig. 2): Chihuahuan Desert shrubland (dominated by creosote bush, *Larrea tridentata*), Chihuahuan Desert grassland (dominated by black grama grass, *Bouteloua eriopoda*), and plains grassland (dominated by blue grama grass, *Bouteloua gracilis*). Transitions among these ecosystem types are predicted to occur under climate change, with desert shrubland encroaching upon desert grassland, which is predicted to replace plains grassland^{61–63}. The two desert sites are separated by ~3 km and are ~10 km from the plains grassland site (Extended Data Fig. 2). Mean climate conditions are depicted in Extended Data Fig. 8; ~60% of precipitation falls during the summer monsoon season from June–September. The two desert sites are more arid on average than the plains grassland site (Extended Data Fig. 2); mean monthly cumulative precipitation for the period of the study was 19.9 mm for the desert sites and 20.9 mm for the plains grassland site; mean monthly temperatures were 14.5 °C and 15.3 °C, respectively.

Bee collection

The SEV-LTER has continuously collected bee abundance data at the SNWR since 2002. Here we report results using data from 2002–2019, excluding 2016 and 2017 owing to a temporary reduction in sampling effort during those two years. Bees are sampled from March–October (two weeks per month) in the three focal ecosystem types using passive funnel traps^{1,64} (Extended Data Fig. 2). One trap is located at each end of five 200 m transects per ecosystem type. Traps are opened each March as close as possible to the first day of spring, and left open for 14 days, after which the bee specimens are collected. The traps are then closed for 14 days. This two-week cycle is repeated until the end of October. Funnel traps provide a measure of bee activity, not a measure of presence, and may be biased by bee taxon, sociality, sex, pollen specialization, floral resource availability and microsite conditions^{65,66}. However, they mitigate human bias associated with net collection, enable long-term sampling simultaneously at multiple sites, and allow for the detection of temporal trends.

Bee identification

Bees were identified to species by K.W.W. and T.G. using dichotomous or interactive keys and reference specimens from the USDA-ARS Pollinating Insects Research Unit's US National Pollinating Insects Collection and the University of New Mexico's Museum of Southwestern Biology, where voucher specimens were deposited. Information related to these specimens is available via the Symbiota Collections of Arthropods Network (<https://scan-bugs.org>; dataset identifier: UNM-MBA).

Sensitivity of bee abundance to climate

All statistical analyses were performed in R⁶⁷. We built CSFs to examine how bee abundance varied with level of aridity at the population (species × ecosystem) level. We modelled ecosystem-specific climate sensitivity because ecosystems differed in climate conditions and plant community composition, the latter of which could influence bees' climate responses by altering microclimate conditions and resource availability. As an aridity metric, we used the SPEI, the standardized difference between precipitation and potential evapotranspiration (PET). SPEI reduces model complexity by integrating temperature and precipitation, providing a proxy for the effects of both heat and humidity, and has decreased over the past century in our study area (that is, aridity has increased)², whereas precipitation alone does not show a temporal trend⁶⁸.

We calculated PET using the Thornthwaite method⁶⁹, as variables needed for more complex PET calculations were not available in the projected future climate dataset (see the next section). The Thornthwaite metric is a temperature-only approximation that does not account for the potential effects of surface radiation, windspeed, or humidity. As a result, its use may bias SPEI values in a hotter, drier direction, and could overestimate the magnitude of increasing aridity and bees' responses to it. To consider this potential bias, we used 15 years of half-hourly data from two on-site eddy covariance flux towers (Ameriflux Program) to calculate PET with the Penman–Monteith equation, which incorporates additional climate variables, for the years 2008–2022 (Supplementary Information). We then calculated PET using the Thornthwaite method for the same data, and compared SPEI values derived from the two PET estimation methods (Supplementary Information). For the monsoon season, the Thornthwaite method yielded higher estimates of aridity in some years (40% of years in the plains grassland, 53% of years in the desert ecosystems), but lower estimates in other years (60% of years in the plains, 47% of years in the desert; Extended Data Fig. 3b). We thus did not observe a consistent Thornthwaite overestimation of a drying trend in the historic data. In addition, for both PET estimation methods, year-to-year variation in SPEI was 4–5 times greater in magnitude than within-year differences between methods (Extended Data Fig. 3b). Based on these results, we suggest that the Thornthwaite method captures sufficiently realistic year-to-year fluctuations in aridity to enable consideration of future bee abundance trends.

SPEI values were calculated using climate data from two on-site meteorological stations (Chihuahuan Desert station: 34.335° N, –106.729° W; Plains station: 34.335° N, –106.632° W) for 6-month spans representing the climate leading up to the spring and monsoon seasons of each year (spring: December–May; monsoon: April–September) for the years 2002–2020⁶⁹. The Chihuahuan Desert station is located between the two desert sites, ~679 m from the desert grassland and ~718 m from the desert shrubland. The Plains station is located ~261 m from the plains grassland site. A longer time series would capture additional variability in SPEI. However, the period of our study at the SNWR had temporal increases similar to the 100-year regional record for both mean aridity and year-to-year variability². A six-month SPEI integration allowed us to consider seasonality while acknowledging that our bee abundance estimates reflect processes that occur at different timepoints during the year (for example, survival, reproductive output, emergence from diapause). To confirm the utility of SPEI as a proxy for heat and dryness, we regressed SPEI against temperature, precipitation, humidity, and vapour pressure deficit for the spring and monsoon seasons, for each weather station (Extended Data Fig. 9).

Separately for each bee species × ecosystem combination, using 2002–2019 bee abundance data, we built mixed effects models⁷⁰ examining maximum yearly bee abundance (maximum abundance recorded on a given sampling transect in a given year) as a function of SPEI (main results presented using inverse SPEI for ease of interpretation). Maximum yearly abundance values were square-root transformed to improve normality of residuals and homogeneity of variances. Our models included the random effect of transect. We chose maximum yearly bee abundance to examine seasonal dynamics in climate response, based on the hypothesis that spring versus monsoon aridity levels would more strongly correspond with abundance maximum rather than total, which incorporates cross-season dynamics. Results were robust to using total rather than maximum yearly abundance as the response variable because these two metrics were very highly correlated (99% of populations had $r \geq 0.90$; 96% had $r \geq 0.95$).

We used a corrected Akaike information criterion (AICc)-based model selection process⁷¹ to determine whether abundance was best predicted by models containing linear, quadratic, or cubic effects of SPEI, allowing consideration of how climate mean versus variability influenced bee abundance. We similarly compared models containing the effects of present versus prior year's aridity, to examine potential time lags in

climate responses, and spring versus monsoon season aridity, to pinpoint the time of year most important for predicting bee population dynamics. Finally, we compared models containing different covariance structures to account for temporal autocorrelation (no covariance structure versus first or second order autoregressive). Models containing autoregressive terms (specified using the ‘correlation’ argument) tested if observations covaried with those from the same transect in the previous year (first order autoregressive) or previous two years (second order). All models were assessed relative to a null model containing only random effects. We considered a population to be ‘climate-sensitive’ if at least one model containing SPEI had a lower AICc value than the null model; for each of these populations, we identified a single best model that had the lowest AICc value⁷¹. We used power analysis⁷² to assess probability of detecting trends for populations in which aridity did not predict abundance.

Bee abundance change under future climate scenarios

To predict future bee abundances, we obtained projected mean monthly temperature and total monthly precipitation data for 2021–2100 from the ClimateNA v. 5.21 software package⁴⁹ for three IPCC climate scenarios: RCP 2.6, RCP 4.5, and RCP 8.5. These represent low, moderate, and extreme climate change, respectively. Data originated from six different GCMs produced as part of the IPCC’s CMIP5 project that have high validation statistics⁷³ and were available via ClimateNA: ACCESS 1.0, CanESM2, CCSM 4.0, CNRM-CM5, CSIRO-Mk3.6.0, and INM-CM4. RCP 2.6 data were only available for the CanESM2 GCM, while RCP 4.5 and 8.5 data were available for all GCMs. Studies indicate that CMIP5 models yield relatively similarly projections to more recent CMIP6 models for North American monsoon patterns⁷⁴ and precipitation/temperature⁷⁵. ClimateNA uses downscaling to calculate climate values for a specific location based on longitude, latitude, and elevation, with the PRISM interpolation method. We interpolated temperature and precipitation values for the centre point between our three study sites (34.335320° N, –106.682701° W), as evidence suggests that PRISM interpolation methods do not have the resolution to accurately predict climate variation within the SNWR (J.A.R., unpublished data). We used the temperature and precipitation values to calculate SPEI for six-month spans as above for each scenario × year × season (spring or monsoon) combination, using the historic data from the two on-site meteorological stations for the reference period specified in the calculation⁶⁹.

Next, for each bee population (species × ecosystem combination), we obtained the CSF equation that best described the relationship between bee abundance and SPEI in our long-term data (2002–2019; see above). Separately for each GCM, we used the future SPEI values from ClimateNA in each CSF equation to predict bee population abundance in each year from 2020–2100. We eliminated unrealistically high (outlier) predicted bee abundance values that were greater than five times the maximum abundance recorded in the historic data on a transect × year combination. Other outlier removal methods produced similar results in subsequent statistical analyses. Then, for each species × year, we calculated transect-level mean predicted abundance across GCMs, summed abundance across sites, and regressed abundance against year to evaluate change over time from 2002–2100⁷⁶. We also completed this step using predicted future bee abundance data from each GCM separately. Finally, to consider if life history traits predicted winners or losers under climate change, we used Pearson chi-squared tests with Monte Carlo simulation for *P* values to examine relationships between traits and projected future trends (increase, decrease, no change) from the regressions of mean predicted abundance averaged over the individual GCMs, for the subset of species for which trait data were available. Traits considered were sociality (levels: social, solitary, parasitic), diet breadth (levels: specialist, generalist, parasitic), and overwintering life stage (levels: adult, prepupae).

Thermal and desiccation tolerances

To assess thermal tolerance, we measured CTMax on individual bees from June–October 2020 and May–October 2021. Bees were collected via aerial netting and immediately placed in individual wells within a field-portable environmental chamber covered with a shading tent (Extended Data Fig. 2). Bees were held initially at 25 °C for 10 min. We then increased the temperature at a rate of 0.5 °C min^{−1}, periodically applying a puff of air to each bee to test its responsiveness. CTMax was determined as the temperature at which each bee lost responsiveness. We used iButtons adhered to alternating wells in the chamber to record temperature and humidity once per minute for the duration of each trial. After losing responsiveness, each bee was immediately removed from the chamber. Prior to analyses, we removed low outliers (bees with thermal tolerances less than 38 °C) that may have resulted from compromised health.

We acknowledge the caveats associated with our method for establishing CTMax; in insects, measured CTMax can vary with factors including experimental ramping rate, developmental stage, acclimation temperature, age, and feeding status^{47,77}. However, the latter three factors did not alter CTMax in studies of honeybees or bumblebees^{25,77}. In addition, we chose a ramping rate of intermediate value to minimize biases associated with both high and low ramping rates, according to published recommendations⁷⁷. We recognize that other tolerance assays are available^{18,47,78}; however, we focus on CTMax as a prevalently calculated metric that has been shown to relate to species’ responses to urban and experimental warming^{24,79}. We emphasize that we examined whether intergeneric differences in CTMax relate to patterns in long-term data, rather than interpreting CTMax values in absolute terms. Sample sizes: 133 bee individuals representing 12 genera (*Agapostemon*: *n* = 2, *Anthidium*: *n* = 5, *Anthophora*: *n* = 4, *Anthophorula*: *n* = 3, *Colletes*: *n* = 6, *Diadasia*: *n* = 31, *Lasioglossum*: *n* = 38, *Macrotera*: *n* = 8, *Megachile*: *n* = 1, *Melissodes*: *n* = 21, *Perdita*: *n* = 11, *Svastra*: *n* = 3).

To measure desiccation tolerance, we collected bees as above, first placing them in individual vials that each contained a small piece of sponge soaked in water to prevent bee dehydration during transport. Vials containing bees were placed in a cooler and transported to Albuquerque, NM, where the bees were weighed to the nearest 0.0001 g and placed in individual wells (with no water source) of the same environmental chamber described above, this time situated indoors. We held the bees for a maximum of 3 h prior to testing, and only tested bees that showed no visible signs of stress. For each trial, we held the bees at 25 °C (far below CTMax), and measured temperature and humidity using iButtons as above. We checked each bee every 20 min for the first 8–9 h, held them overnight for ~6 h, and then again checked each one every 20 min until it lost responsiveness, which we assessed using a puff of air as above. Time to loss of responsiveness was recorded as a desiccation tolerance metric, following evidence that dehydration occurs much more quickly than starvation^{27,80}. Statistical results were robust to use of critical water content²⁷ as an alternative desiccation tolerance metric. We immediately removed each bee after it lost responsiveness and weighed it to the nearest 0.0001 g. To determine dry mass, we placed each bee in a drying oven at 60 °C for 72 h, and immediately weighed it. Sample sizes: 188 bee individuals representing 12 genera (*Agapostemon*: *n* = 11, *Anthidium*: *n* = 6, *Anthophora*: *n* = 14, *Anthophorula*: *n* = 3, *Colletes*: *n* = 17, *Diadasia*: *n* = 22, *Lasioglossum*: *n* = 46, *Macrotera*: *n* = 6, *Megachile*: *n* = 10, *Melissodes*: *n* = 7, *Perdita*: *n* = 39, *Svastra*: *n* = 7). For 24 individuals, loss of responsiveness occurred during the ~6-h lapse period; for these, we assigned end time as the midpoint between the lapse period’s start and end times; statistical results were unchanged when we instead either removed these individuals or included time discovered unresponsive as the end point.

For each bee genus, we modelled the magnitude (slope) of change in abundance over time for the tested species as a function of mean thermal or desiccation tolerance, incorporating phylogeny as a random

effect⁸¹. We built similar models with linear parameter estimate from CSFs as the response variable. We constructed the phylogeny using genus-level tree data⁸², adding species as polytomies^{83,84}. To consider how thermal and desiccation tolerances together related to abundance change, we first z-scored the genus-level thermal and desiccation tolerance data (standardized each dataset to a mean of zero and standard deviation of one). We then added the z-scored thermal and desiccation values for each genus to create a combined metric of the two.

Because humidity decreased during the thermal tolerance trials, we also calculated vapour pressure deficit tolerance (VPD at the time of loss of responsiveness)⁸⁵. We then used the Akaike information criterion to compare models that respectively contained thermal, desiccation, combined thermal and desiccation, or VPD tolerance metrics to determine which best predicted change over time or linear CSF parameter, respectively. We tested for phylogenetic signal in abundance change over time across GCMs, linear CSF parameter, and physiological tolerance using $\langle \text{phylosignal} \rangle$ ⁸⁶. Models were built at the genus level to enable inclusion of data from species for which we were able to collect thermal but not desiccation tolerance data, or vice-versa.

Relation of bee body size to climate over time and changes expected under future climate scenarios

We measured intertegular distance (ITD), a standard bee body size metric^{87,88}, on female individuals of 256 species for which specimens were available. These species represented ~99% of total abundance in the long-term dataset. We measured a minimum of three individuals per species whenever possible, and measured males when no females were available for a given species. We photographed the thorax of each bee from above and measured the distance between the wing bases (tegulae) using ImageJ v. 1.52⁸⁹ or a microscope imaging system with an integrated measurement capability (VHX-S650E free-angle observation system, Keyence). We then estimated total body mass (mg) using established allometric equations^{87,88}. After calculating mean body mass for each species, we determined community-weighted mean (CWM) body mass for each transect $\times$ year combination in the historic and predicted future data from each GCM separately by multiplying each species' mean body mass by its fractional contribution to total abundance. Then, using mixed effects models⁹⁰, we tested for change in CWM body mass as a function of year in each ecosystem, running models separately for each GCM and including the random effect of transect. We used the same framework to model CWM body mass as a function of monsoon SPEI in each ecosystem, including the random effects of transect and year, and comparing models with or without the quadratic effect of SPEI based on AICc. When models were within two AICc values of one another, we chose the simplest model for presentation. For just the historic data pooled across ecosystems, we separately modelled CWM body mass as a function of monsoon SPEI, including ecosystem as a fixed effect that interacted with SPEI and the random effects of year and transect, and visualized the result using visreg⁹¹.

We took additional body mass measurements to validate the interpretation that community-level body mass shifts were driven by species' relative abundance changes rather than within-species evolution or phenotypic plasticity. For 16 of the most abundant species, we measured ITD on a minimum of 10 individuals per species whenever possible from each of at least 5 years spaced throughout the dataset, using specimens stored within our collections. We then regressed body mass (estimated from ITD above) on year for each species. No species changed in body mass over time (Extended Data Fig. 6). Number of individuals measured per species: *Agapostemon angelicus*: 57, *Anthophora affabilis*: 239, *Anthophora lesquerellae*: 61, *Anthophora montana*: 176, *Ashmeadiella meliloti*: 159, *Diadasia australis*: 219, *D. rinconis*: 331, *Halictus ligatus*: 112, *H. tripartitus*: 80, *Lasioglossum*

sp. A: 119, *L. deludens*: 180, *L. hudsoniellum*: 341, *L. semicaeruleum*: 118, *L. sisymbrii*: 199, *Osmia watsoni*: 77, *Perdita callicerata*: 45.

Ecosystem transitions and bee vulnerabilities to future climates

We examined how bee species' climate sensitivities and population trends differed among ecosystems to consider how the expansion of some ecosystem types and contraction of others could influence vulnerability to aridity. For 143 bee species with sufficient data in 2 or more ecosystems, we calculated the proportion of species for which the best CSF, determined above, differed among ecosystems in shape (linear, quadratic or cubic) and/or direction (positive versus negative linear parameter estimate). Then, within each ecosystem, we calculated the proportion of species with positive versus negative linear parameter estimates from the best CSF.

Reporting summary

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

Data availability

All datasets generated and/or analysed during the current study are publicly available. Long-term bee monitoring data are available via the Environmental Data Initiative (EDI) at <https://doi.org/10.6073/pasta/cdc8381b8b2be97188daeffcd6310e9b>. Also available via EDI are the SEV-LTER meteorological data (<https://doi.org/10.6073/pasta/decdaa0c695cb2070c73f5b684a32e73>), plant phenology data (<https://doi.org/10.6073/pasta/ceb693495ef57b8b1ba075calee0f7ed>), and plant biomass data (<https://doi.org/10.6073/pasta/5d6fa085c3d31bc1bc352081ec9e839a>). Bee body mass, life history trait, and physiological tolerance data are available via the Open Science Framework (OSF) at <https://doi.org/10.17605/OSF.IO/H2YV6>. Projected future climate data are available from ClimateNA at <https://climatena.ca/>.

Code availability

Computer code used in the analyses is available via Zenodo at <https://doi.org/10.5281/zenodo.8412361> (ref. 92).

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Author contributions M.R.K. created the conceptual framework, collected bee physiology and morphology data, analysed the data, and wrote the manuscript. K.W.W. designed the long-term bee monitoring study and completed specimen collection and identification. T.G. provided taxonomic expertise. J.A.R. and K.D.W. contributed to conceptualization, statistical analyses and writing. All authors helped to revise the manuscript.

Competing interests The authors declare no competing interests.

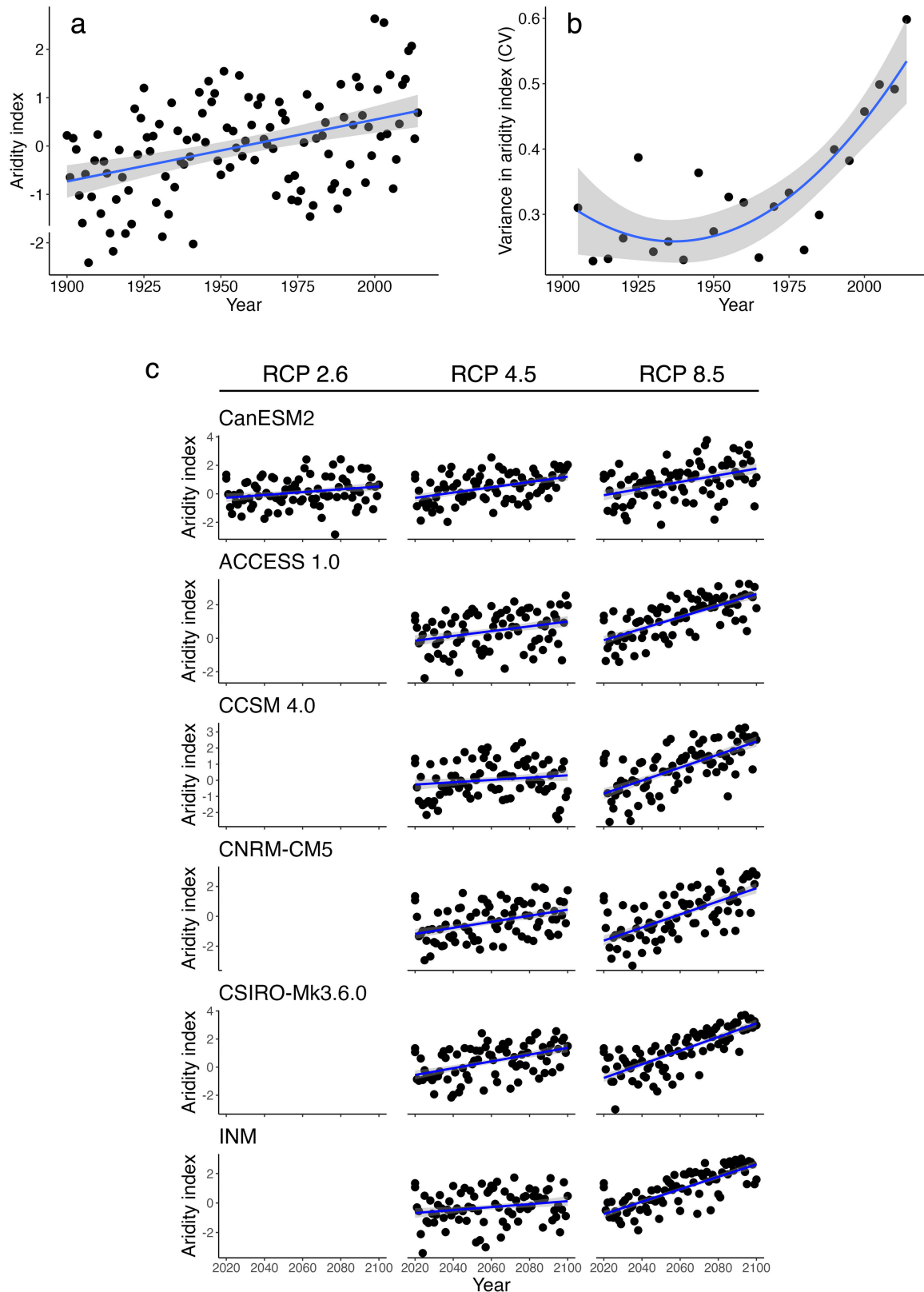
Additional information

Supplementary information The online version contains supplementary material available at <https://doi.org/10.1038/s41586-024-07241-2>.

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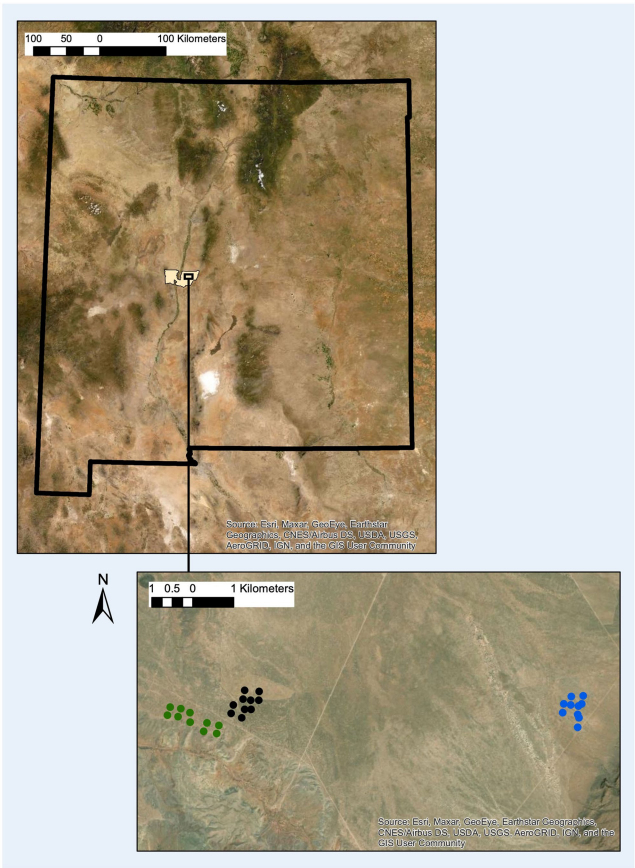
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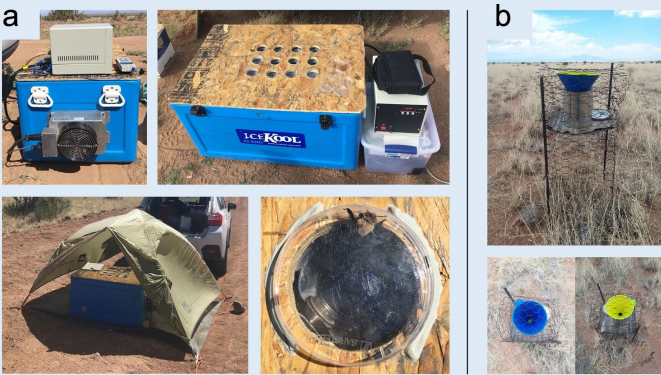
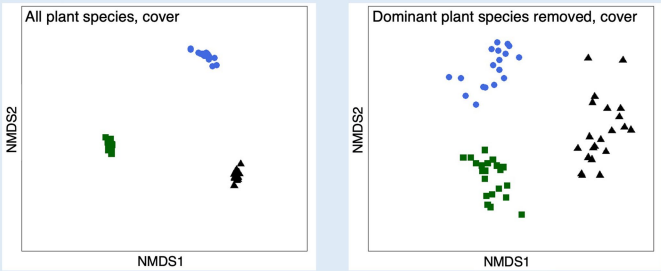
Extended Data Fig. 1 | Temporal trends in historic and predicted future aridity (inverse *SPEI*). (a, b) Trends for the monsoon season in Socorro, NM, USA. In (a), points show the 6-month integrated aridity index, calculated from temperature and precipitation data recorded since 1900, with positive values indicating hotter and drier conditions relative to the mean. In (b), points show the coefficient of variation (CV) in the aridity index for non-overlapping 5-yr time windows (adapted from Rudgers et al., Ecology, 2018). (c) Predicted future monsoon season aridity trends for the Sevilleta National Wildlife Refuge

(NM, USA) under low, moderate, and high CO₂ emissions scenarios (RCP 2.6, 4.5, and 8.5, respectively), using projected future climate data from six General Circulation Models (ACCESS 1.0, CanESM2, CCSM 4.0, CNRM-CM5, CSIRO-Mk3.6.0, and INM-CM4). RCP 2.6 data were only available for the CanESM2 GCM. Positive and negative values indicate hotter/drier and cooler/wetter conditions relative to the historic mean (2002–2019), respectively. In all panels, error bands represent 95% confidence intervals.

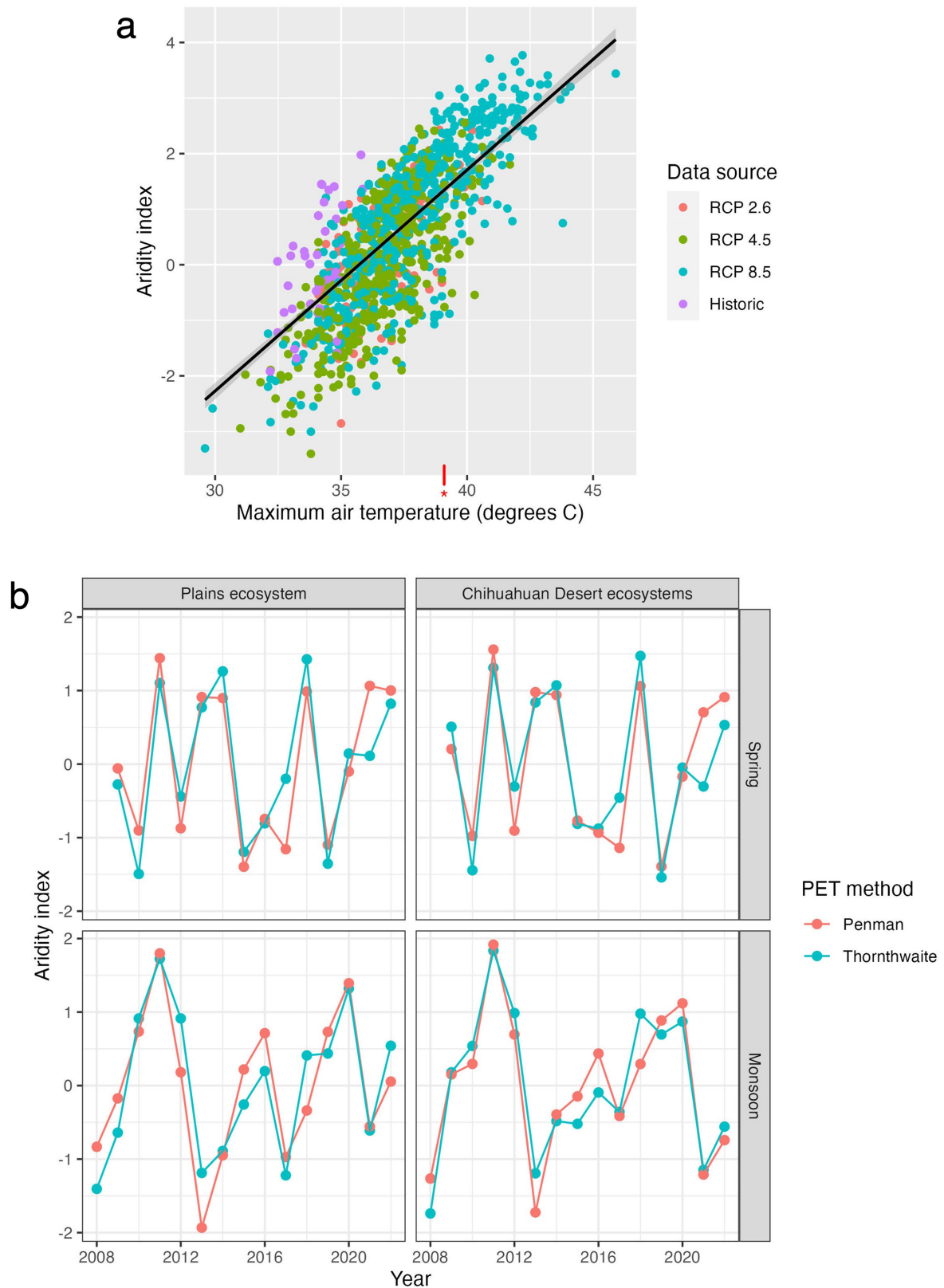


Extended Data Fig. 2 | Research sites and equipment. *Left:* Map of sampling sites at the Sevilleta National Wildlife Refuge, NM, USA (beige polygon in upper map). Bees were sampled in three focal ecosystem types: Chihuahuan Desert shrubland (green points), Chihuahuan Desert grassland (black points), and plains grassland (blue points). To sample bees, we installed one passive funnel trap at each end of five 200 m transects/site; traps are indicated by colored points in the lower panel. Maps were generated via ArcGIS v.10.1 (ESRI 2012, Redlands, CA) using the World Imagery basemap⁹³ (sources: Esri, Maxar, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community; accessed 23 February 2022 via <https://www.arcgis.com/home/item.html?id=10df2279f9684e4a9f6a7f08febac2a9>). *Upperright:* Differences between sites in climate conditions (table) and plant community composition (figures). Table values are results from paired, two-sided *t*-tests comparing temperature and precipitation metrics from the month of greatest difference between the Plains and Chihuahuan Desert meteorological stations.

Metric	Month	df	t	P	Plains		Desert	
					Mean	SE	Mean	SE
Maximum temperature	November	20	-3.20	0.0045	24.40	0.36	23.80	0.29
Minimum temperature	October	20	-3.32	0.0034	-0.34	0.79	-1.75	0.79
Mean temperature	January	20	-12.99	< 0.0001	3.78	0.36	2.60	0.35
Total precipitation	July	20	-1.76	0.0945	56.60	6.96	49.00	5.72

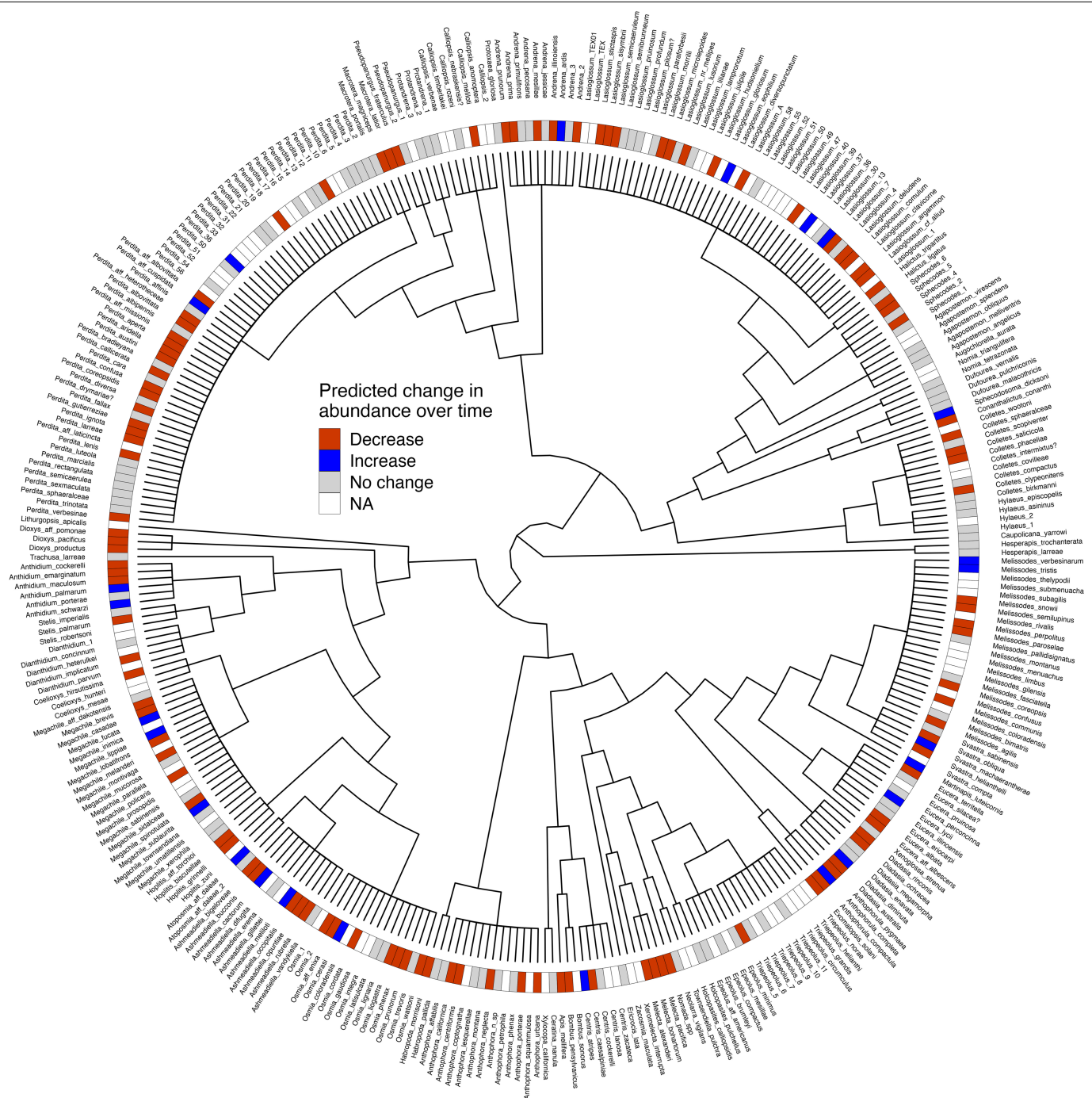


Figures are NMDS plots⁹⁴ illustrating differences among ecosystems in plant cover for all species, and with the dominant species removed. **Lower right:** (a) Images of the environmental chamber used to assess thermal and desiccation tolerances of bees. The chamber consisted of an insulated ice chest (IceKool, Queensland, Australia). In the chamber, air temperature was controlled using a 162-W Peltier device (model AC-162, TE Technology, Traverse City, MI) and a custom-built controller that incorporated a TE Technology digital display (MP-2986) and control card (TC-36-25-RS486). (b) Traps used for bee collection. Each consisted of a 946 mL paint can filled with ~275 mL of propylene glycol and topped with a plastic automotive funnel (funnel height = 10 cm, top diameter = 14 cm, bottom diameter = 2.5 cm). The funnels' interiors were painted with either blue or yellow fluorescent paint (Krylon, Cleveland, OH or Ace Hardware, Oak Brook, IL). Each trap was placed on a 45 cm high platform that was surrounded by a 60 cm high chicken wire cage to prevent wildlife and wind disturbance.



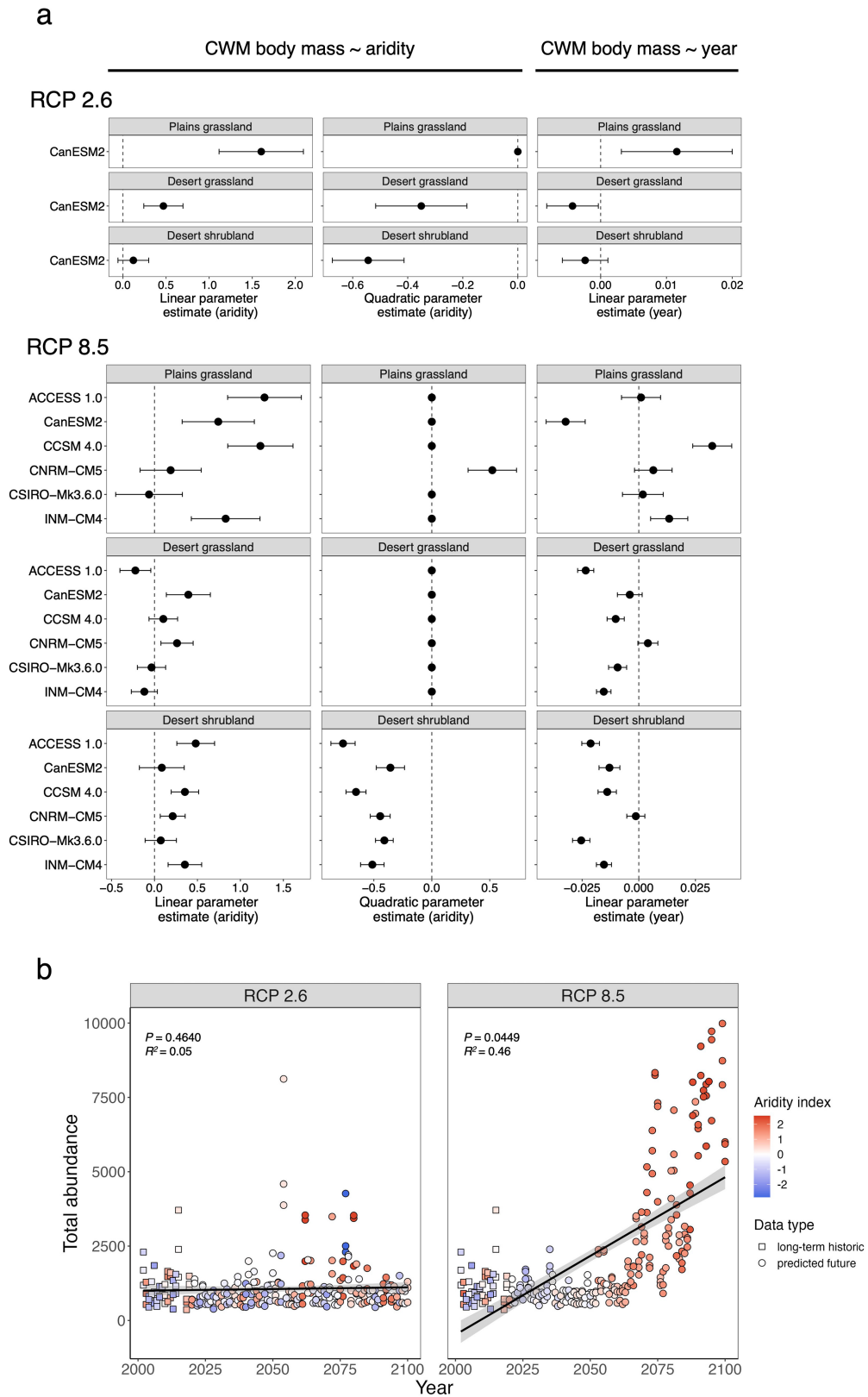
Extended Data Fig. 3 | Relationship between air temperature and aridity, and alternate aridity index calculations. (a) Aridity index (inverse *SPEI*) as a function of maximum air temperature for the period leading up to the monsoon season (April–September), for the historic period (2002–2020) in the plains and Chihuahuan Desert ecosystems, and for 2021–2100 under three predicted future climate scenarios (RCP 2.6, 4.5, and 8.5) for the midpoint between ecosystems, using data from six General Circulation Models (ACCESS1.0,

CanESM2, CCSM4.0, CNRM-CM5, CSIRO-Mk3.6.0, and INM-CM4). The red bar with an asterisk on the x-axis indicates the critical thermal maximum (*CTMax*) of the least thermally tolerant bee taxon in the dataset. The error band represents the 95% confidence interval. (b) Year-to-year variation in the aridity index calculated using two different PET estimation methods (Thornthwaite and Penman) for the spring and monsoon seasons in the plains ecosystem and Chihuahuan Desert ecosystems.



Extended Data Fig. 4 | Bee phylogeny and predicted change in abundance over time. Phylogeny of the 339 bee species collected at the Sevilleta National Wildlife Refuge (NM, USA) from 2002–2019, with direction of predicted future

change in abundance from 2002–2100 based on averaged projections from six General Circulation Models of global climate (white = insufficient data).

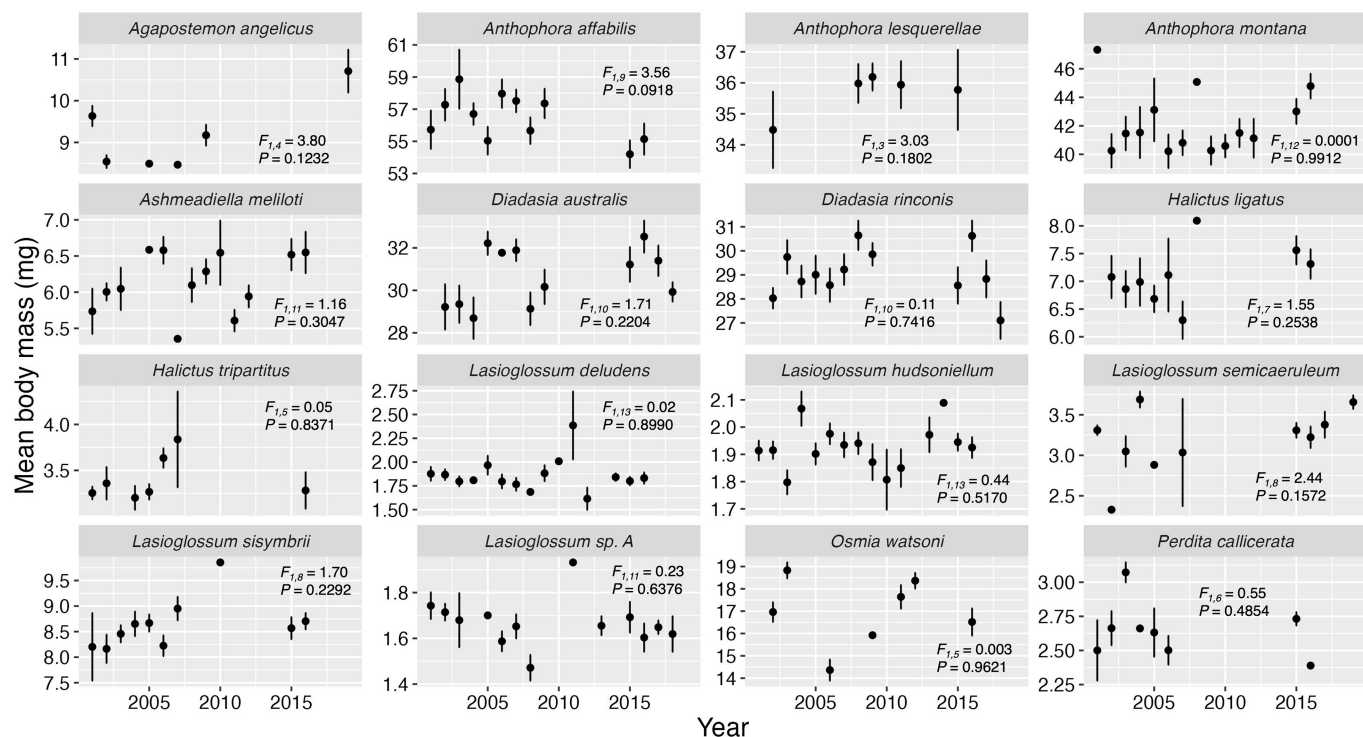


Extended Data Fig. 5 | See next page for caption.

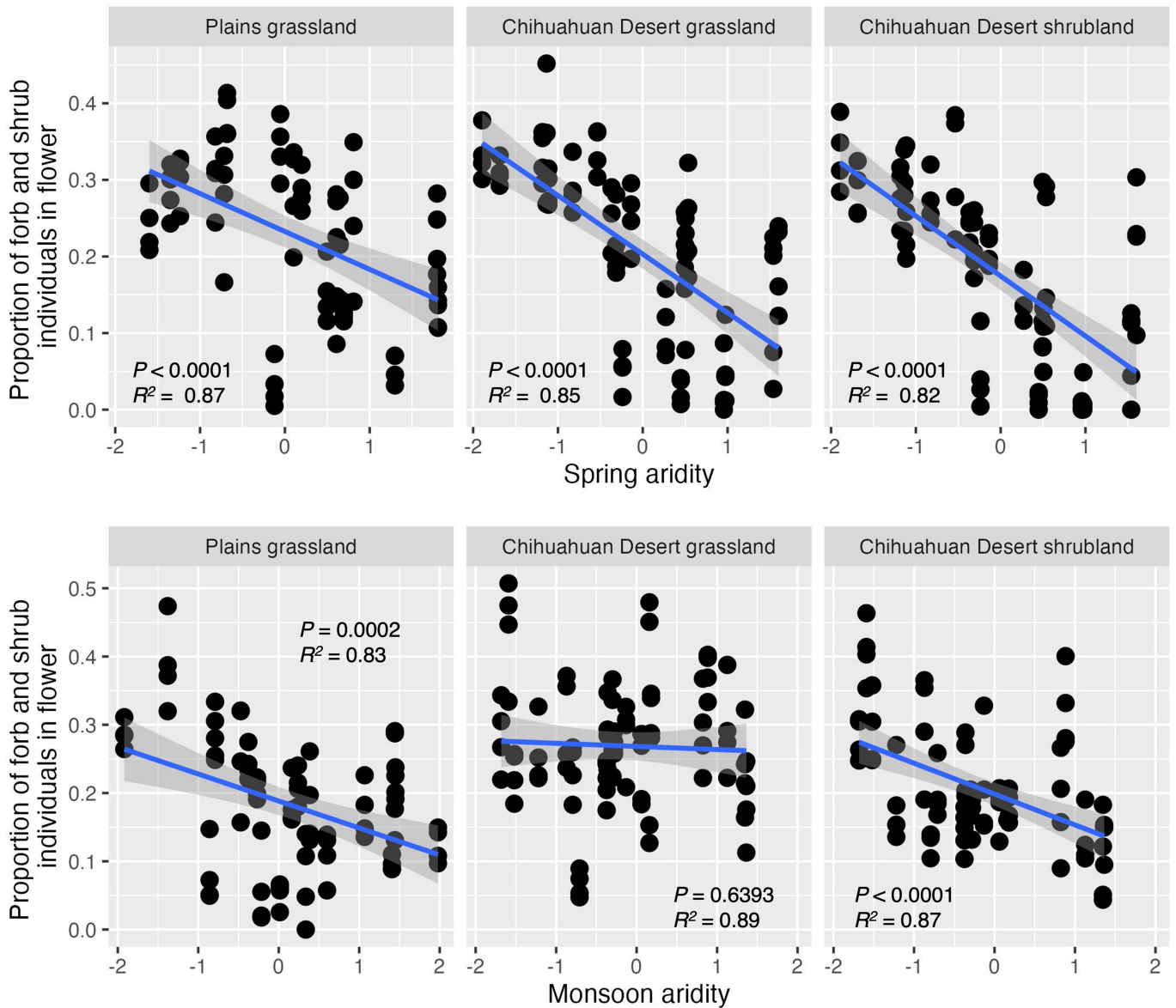
Extended Data Fig. 5 | Projected trends in community-weighted mean body mass and total abundance under low and high climate change scenarios.

(a) Change in community-weighted mean (CWM) bee body mass with monsoon season aridity (inverse *SPEI*) and over time in the combined historic and predicted future datasets, for low (RCP 2.6) and high (RCP 8.5) climate change scenarios. Points represent means and error bars indicate s.e.m. for the linear or quadratic effect of aridity or year on CWM body mass using results from each of six General Circulation Models (GCMs; listed on y-axis). RCP 2.6 data were only available for the CanESM2 GCM. Positive and negative aridity values indicate hotter/drier and cooler/wetter conditions relative to the historic mean (2002–2019), respectively. Statistical results are from mixed effects models

(see Methods). (b) Change over time in total bee abundance across study sites, using long-term historic data and predicted future data for low and high climate change scenarios (RCP 2.6 and 8.5). Each point represents the sum for each ecosystem × year combination of all species-level mean predicted abundance values that were calculated by averaging across predictions from the six GCMs. Points are colored by monsoon aridity averaged across the six GCMs. Positive and negative aridity values indicate hotter/drier and cooler/wetter conditions relative to the historic mean (2002–2019), respectively. Error bands represent 95% confidence intervals. Statistics are from linear regression analysis.

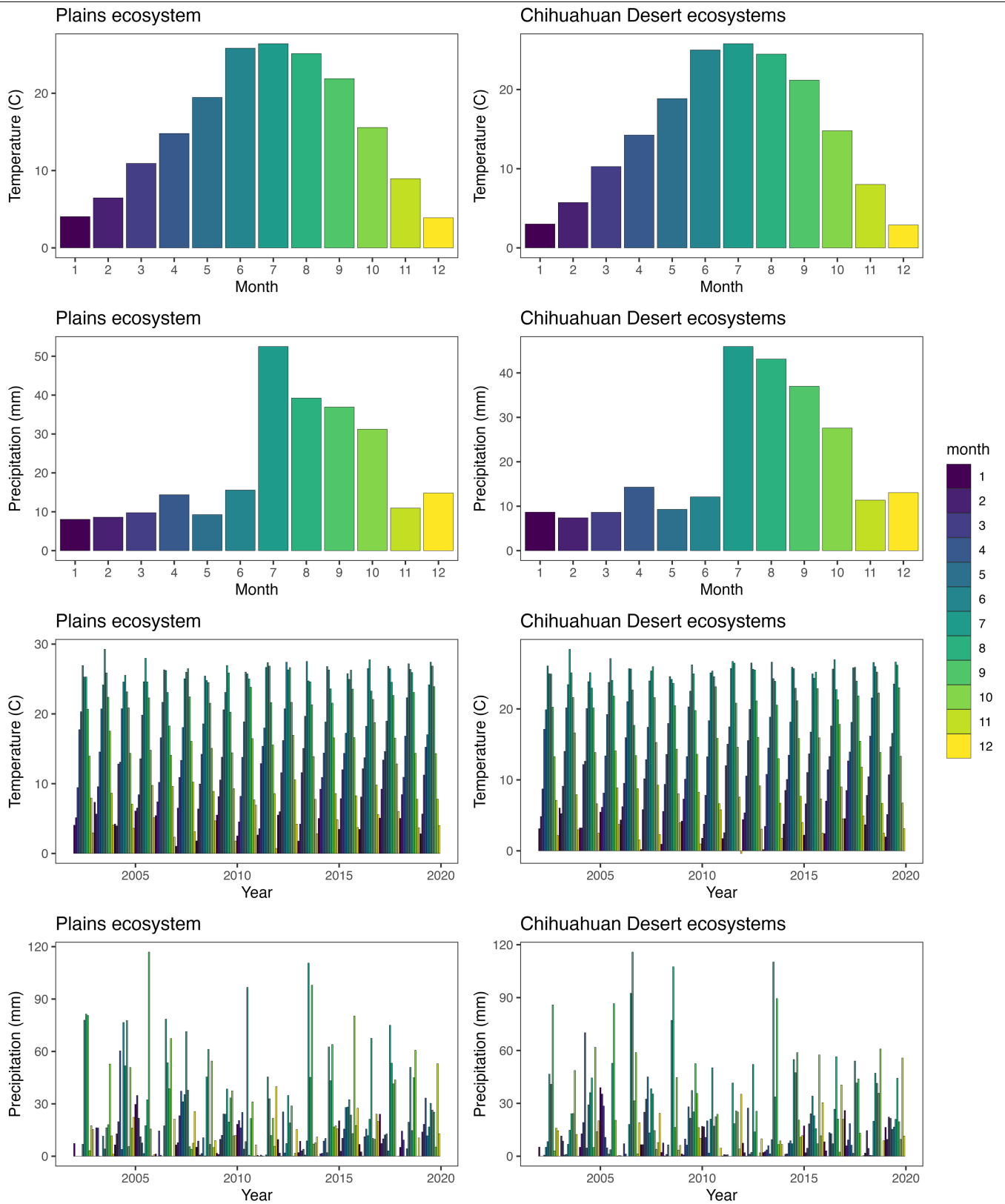


Extended Data Fig. 6 | Body mass of 16 bee species as a function of time. Points represent means and error bars indicate s.e.m. (mean $n = 15$ bee individuals/species/year; see Methods for sample sizes per species). Statistical results are from linear regressions. Mean body mass did not change over time within any species.



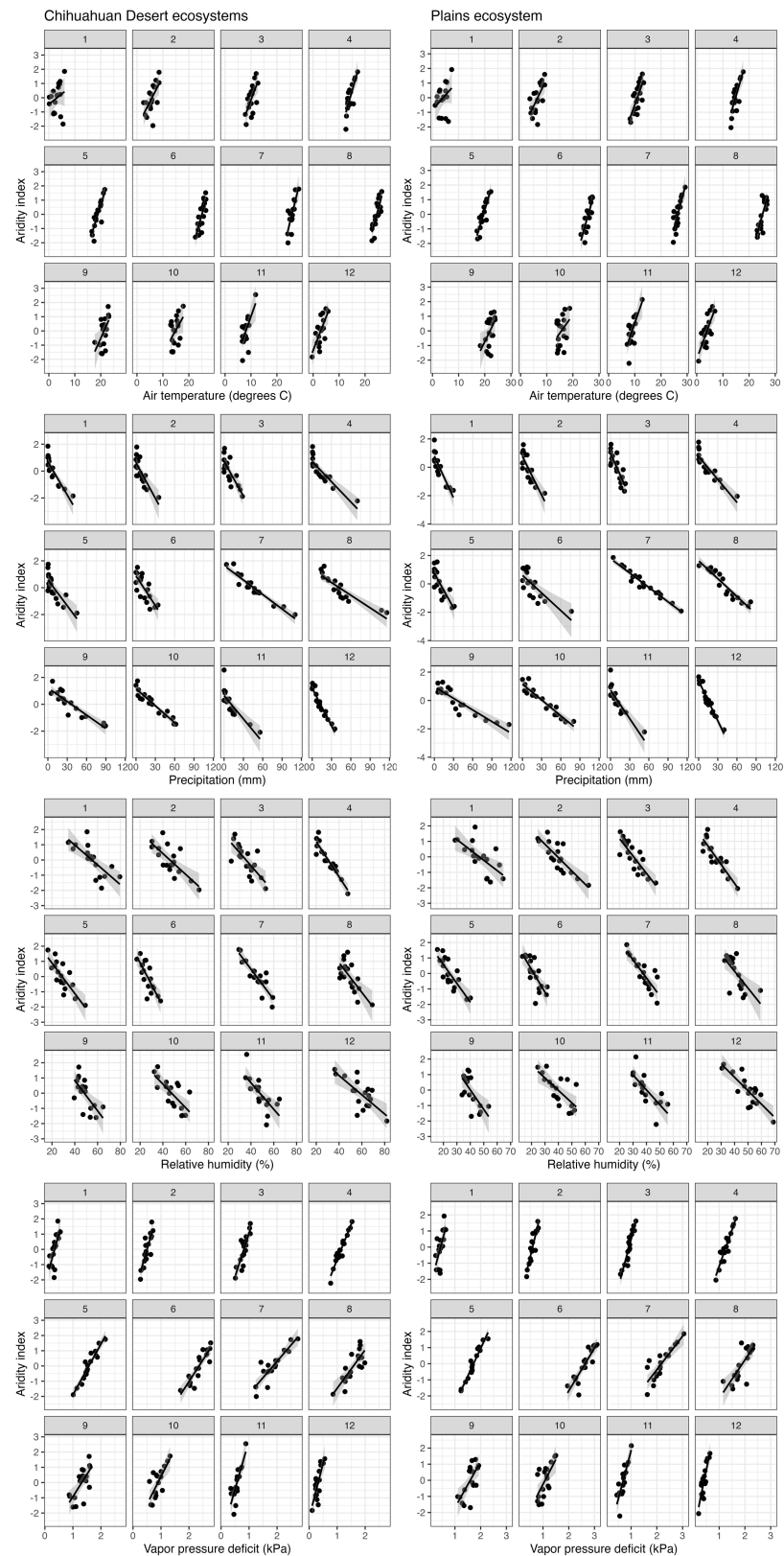
Extended Data Fig. 7 | Aridity predicts floral availability. Relationship between spring or monsoon season aridity and proportion of forb and shrub individuals in flower from long-term plant phenology data (2002–2019), in three focal ecosystem types. Positive and negative aridity values indicate

hotter/drier and cooler/wetter conditions relative to the mean, respectively. Error bands represent 95% confidence intervals. Statistical results are from mixed effects models.



Extended Data Fig. 8 | Monthly climate trends. Mean air temperature and total monthly precipitation trends for the plains ecosystem and Chihuahuan Desert ecosystems (grassland and shrubland) at the Sevilleta National Wildlife

Refuge, for each month averaged across the years 2002–2019 (top) and for each month within each year (bottom).



Extended Data Fig. 9 | Relationships between aridity and other climate variables. Monthly aridity index (inverse *SPEI*) as a function of four other climate variables (temperature, precipitation, relative humidity, and vapor

pressure deficit) for each month of the year (1–12). Data are from two meteorological stations at the Sevilleta National Wildlife Refuge (Chihuahuan Desert and Plains). Error bands represent 95% confidence intervals.

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Software and code

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Data collection	To estimate bee body size, we photographed the thorax of each bee from above and measured the distance between the wing bases (tegulae) using ImageJ v. 1.52 software or a microscope imaging system with an integrated measurement capability (VHX-S650E free-angle observation system, Keyence Corporation, Ithaca, IL). We obtained projected mean monthly temperature and total monthly precipitation data for 2021–2100 from the ClimateNA v. 5.21 software package. No other software was used for data collection.
Data analysis	Analyses were conducted in R v. 4.2.2 (2022) and PRIMER v. 7 (2015). Maps were generated via ArcGIS v. 10.1. DOIs for computer code used in analyses are provided in the manuscript.

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All datasets generated and/or analyzed during the current study are publicly available. Long-term bee monitoring data are available via the Environmental Data Initiative (EDI) at <http://doi.org/10.6073/pasta/cdc8381b8b2be97188daeffcd6310e9b>. Also available via EDI are the SEV-LTER meteorological data (<https://doi.org/10.6073/pasta/decdaa0c695cb2070c73f5b684a32e73>), plant phenology data (<https://doi.org/10.6073/pasta/ceb693495ef57b8b1ba075ca1ee0f7ed>), and

plant biomass data (<https://doi.org/10.6073/pasta/5d6fa085c3d31bc1bc352081ec9e839a>). Bee body mass, life history trait, and physiological tolerance data are available via the Open Science Framework (OSF) at <https://doi.org/10.17605/OSF.IO/H2YV6>. Projected future climate data are available from ClimateNA at <https://climatenas.ca/>.

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Ecological, evolutionary & environmental sciences study design

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Study description	For long-term bee monitoring, we used passive traps to collect bees at three sites, each representing a key ecosystem type of the southwestern USA: Chihuahuan Desert shrubland, Chihuahuan Desert grassland, and plains grassland. Each site contained 10 bee traps. Traps were opened for 2 weeks/month from March through October of each year. To measure the physiological tolerances of bees, we collected bees with aerial nets, placed them in an environmental chamber, and assessed either their thermal or desiccation tolerance.
Research sample	Adult bees (Hymenoptera: Apoidea: Anthophila), both female and male, were captured at the Sevilleta National Wildlife Refuge (Socorro, NM, USA), at three sites. The samples were meant to represent the bee populations present in these three locations.
Sampling strategy	For the long-term monitoring study, all bee individuals collected in the traps during each sampling period were included in the study. For the physiological tolerance trials, to align with best practices for the collection of trait data, we aimed to measure at least 10 individuals per taxon whenever possible, and at least 3 individuals for taxa with low abundance.
Data collection	For the long-term bee monitoring dataset, bee specimens were collected from the traps by K.W.W., M.R.K., and research staff. All bee individuals were identified to species by K.W.W. and T.G. For the thermal and desiccation tolerance trials, M.R.K. completed all data collection. Individual bees were placed in wells within an environmental chamber. To measure thermal tolerance, the chamber's temperature was increased at a rate of 0.5°C/min, and thermal tolerance was determined as the temperature at which each bee lost responsiveness. To measure desiccation tolerance, we held the bees at 25°C, and recorded time to loss of responsiveness as a desiccation tolerance metric. K.W.W. identified all bee specimens from the thermal and desiccation tolerance trials.
Timing and spatial scale	For long-term bee monitoring, collection traps were opened for 2 weeks/month from March–October in 2002 through 2019. March–October is the portion of the year during which adult bees are active in the study system. Opening the traps for 2-week periods enabled collection of a sufficient number of bee individuals to capture the area's bee diversity. For the thermal and desiccation tolerance trials, data were collected from June–October 2020 and May–October 2021, which allowed us to measure physiological tolerance on representatives of 12 focal bee genera present throughout the bee activity season. Spatially, the two Chihuahuan Desert sites are separated by ~3 km and are ~10 km from the plains grassland site.
Data exclusions	Long-term bee monitoring data from 2016 and 2017 were excluded from analyses due to a temporary reduction in sampling effort during those two years. Prior to analyzing trends in predicted future bee abundance, we eliminated unrealistically high (outlier) predicted bee abundance values that were greater than 5x the maximum abundance recorded in the historic data on a transect x sampling date combination. From the thermal tolerance data, we removed low outliers (bees with thermal tolerances less than 38°C) that may have resulted from bees with compromised health. From one statistical analysis related to how physiology predicts the quadratic parameter estimate of climate sensitivity functions, we excluded one bee genus that was a very high outlier.
Reproducibility	For reproducibility, thermal and desiccation tolerance trials were conducted on a minimum of 3 individuals per taxon for >80% of taxa (mean n = 11 for thermal tolerance and 16 for desiccation tolerance). For the remaining taxa, this level of reproducibility was not possible due to low catch rates in the field during the study.
Randomization	In the thermal and desiccation tolerance trials, bee individuals were randomly assigned to wells within the experimental chamber during the trials. Other data collection methods were observational and did not entail randomization.
Blinding	Blinding did not occur in the study. In the thermal and desiccation tolerance trials, blinding of bee species identity was not possible, as each bee needed to be visually checked for responsiveness. Field collection of bees was observational and thus did not involve blinding.
Did the study involve field work?	☒ Yes ☐ No

Field work, collection and transport

Field conditions	For the long-term bee monitoring dataset, bee collection traps were open continuously for 2 weeks/month, across the full range of weather conditions that occurred during those periods. Collection of bees for the thermal and desiccation tolerance trials occurred during conditions known to be conducive to bee activity (temperatures above 15°C, wind speeds below 25 kmh, and low cloud cover).
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Location	Field work was conducted at the Sevilleta National Wildlife Refuge (Socorro, NM, USA), at three sites, each of which represented a distinct ecosystem type: Chihuahuan Desert shrubland, Chihuahuan Desert grassland, and plains grassland.
Access & import/export	All site visits and data collection were made pursuant to research permits issued by the Sevilleta National Wildlife Refuge, U.S. Fish and Wildlife Service to K.W.W., M.R.K., and J.A.R.
Disturbance	Movement around sites was confined to established roads and paths whenever possible to minimize disturbance. Long-term bee monitoring infrastructure consists solely of minimalist traps that will be removed when the ongoing study is discontinued.

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Materials & experimental systems

n/a	Involved in the study
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☒	☐ Eukaryotic cell lines
☒	☐ Palaeontology and archaeology
☐	☒ Animals and other organisms
☒	☐ Human research participants
☒	☐ Clinical data
☒	☐ Dual use research of concern

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
☒	☐ MRI-based neuroimaging

Animals and other organisms

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Laboratory animals	No laboratory animals were used in the study
Wild animals	Adult bees (Hymenoptera: Apoidea: Anthophila), both female and male, were captured using two methods: passive trapping (for the long-term bee monitoring study) and aerial netting (for thermal and desiccation tolerance trials). In the passive traps, bees were caught and killed in propylene glycol. Following the thermal and desiccation tolerance trials, all bee individuals were euthanized via freezing at -20°C. All bees were pinned, labeled, and archived in permanent museum collections. Species-level identification of most bee species requires microscopy on non-living specimens, necessitating the euthanasia of bees in our study. All transport of bees occurred by car, with bees held in vials (see below for further detail). Bee individuals are estimated to have ranged in age from several days to 6 weeks.
Field-collected samples	For thermal tolerance trials, bees were collected via aerial netting, weighed, and immediately placed in individual wells within a field-portable environmental chamber covered with a shading tent. Bees were held at 25°C for 10 min prior to the start of each thermal trial. For desiccation tolerance trials, bees were collected via aerial netting and placed in individual vials that each contained a small piece of sponge soaked in water to prevent bee dehydration during transport. The vials were placed in a cooler and transported by car to Albuquerque, NM, where the bees were weighed and placed in the environmental chamber for the desiccation trial, this time situated indoors. Bees were held for a maximum of 3 hours prior to desiccation tolerance testing, and we only tested bees that showed no visible signs of stress. No other housing or maintenance of animals occurred in this study. Following the thermal and desiccation tolerance trials, all bee individuals were euthanized via freezing at -20°C.
Ethics oversight	The study did not require ethical approval, as no vertebrate animals were involved

Note that full information on the approval of the study protocol must also be provided in the manuscript.