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Ecological winners and losers of extreme drought in California

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An unprecedented era of climatic volatility is altering ecosystems across our planet[1]. The potential scale, pace and consequences of this global change have been modelled extensively[2], yet little empirical research has quantified the impacts of extreme climate events on the composition of contemporary ecological communities. Here, we quantified the responses of 423 sympatric species of plants, arthropods, birds, reptiles and mammals to California's drought of 2012–2015—the driest period in the past 1,200 years[3] for this global biodiversity hotspot. Plants were most responsive to one-year water deficits, whereas vertebrates responded to longer-term deficits, and extended drought had the greatest impact on carnivorous animals. Locally rare species were more likely to increase in numbers and abundant species were more likely to decline in response to drought, and this negative density dependence was remarkably consistent across taxa and drought durations. Our system-wide analysis reveals that droughts indirectly promote the long-term persistence of rare species by stressing dominant species throughout the food web. These findings highlight processes that shape community structure in highly variable environments and provide insights into whole-community responses to modern climate volatility.

The frequency, severity and duration of droughts is increasing due to global warming[4–6]. High socioeconomic costs of severe droughts are among the most worrisome of climate change impacts, and effects on natural ecosystems may likewise be substantial[7]. Predicting the ecological impacts of drought is complicated by the fact that species can be impacted through multiple pathways. Drought affects communities directly through physiological impacts on species' survival and growth rates, and indirectly by altering species interactions such as competition[8,9]. Some theoretical models show that droughts can increase coexistence probabilities through selective mortality on dominant species[8,10], while others predict that drought can increase dominance through increased competitive intensity[9]. Here, we tested these conflicting predictions regarding the pathways through which drought impacts ecosystems, while broadly characterizing the response of a community to a once-in-a-millennium climate-induced disturbance.

Theoretical predictions of drought effects are rooted in plant ecology[11], and it is not known whether they apply to animal populations that may primarily be indirectly affected by soil moisture deficits. Drought may affect all trophic levels similarly via generalized processes of disturbance or competition. Alternatively, drought

effects may move up the food web with time lags or opposing effects. For example, droughts in sub-Saharan east Africa have led to ungulate die-offs[12], resulting in a short-term resource pulse for scavengers[13]. Thus, the effects of drought on resource availability differ among trophic levels and over time. Emerging studies indicate that droughts can strongly affect the dynamics of animal populations[14,15], but community-wide studies of drought impacts across plant, invertebrate and vertebrate species are lacking. Predicting which species will 'win' (that is, increase in abundance) and 'lose' (that is, decline) in an era of increasingly extreme weather events remains a foremost challenge in global change biology.

We used a comprehensive survey dataset from the Carrizo Plain National Monument, California, USA (CPNM) to examine the responses of 423 species within a semi-arid grassland community to a record-breaking drought. Located within a global biodiversity hotspot[16], the Carrizo Plain is a key conservation area for more than 30 at-risk species (Supplementary Fig. 1)[17]. This region was at the epicentre of the region's worst drought in the past 1,200 years, which occurred from 2012–2015[3]. We monitored the abundance of plants, arthropods, reptiles, birds and mammals from 2007–2015 (that is, before and during the drought) to identify winners and losers, and examined whether the pre-drought abundance, maximum observed population growth rate, body mass, trophic level or functional group predicted species' responses.

Annual precipitation varied more than fivefold during our study, and the drought years transformed the landscape from a verdant grassland to a barren plain nearly devoid of vegetation (Fig. 1). We calculated drought indices over one, two or three growing seasons (DI_1, DI_2 and DI_3, respectively) and classified each species as a winner, loser or neither in response to drought based on the slope from the best-fitting linear regression (normalized log abundance $\sim DI_x$). Species present for 1 year only were excluded ($n = 87$ excluded species; 336 included species). Some 85 species (25%) were classified as losers, 12 (4%) were winners and 239 (71%) did not have a significant response to drought at the $\alpha = 0.05$ level (Fig. 2a). Winners consisted of seven insects (six beetle species and the ant species *Cyphomyrmex*), one plant (the native forb red maids *Calandrinia menziesii*), one reptile (the common side-blotched lizard *Uta stansburiana*), two birds (the killdeer *Charadrius vociferous* and greater roadrunner *Geococcyx californianus*) and one rodent (the short-nosed kangaroo rat *Dipodomys nitratoides brevinasus*). At the $\alpha = 0.10$ level, proportions were 34% losers, 10% winners and 56% of species with no significant response (Supplementary Table 1). Thus, despite strong declines in the total abundance and species

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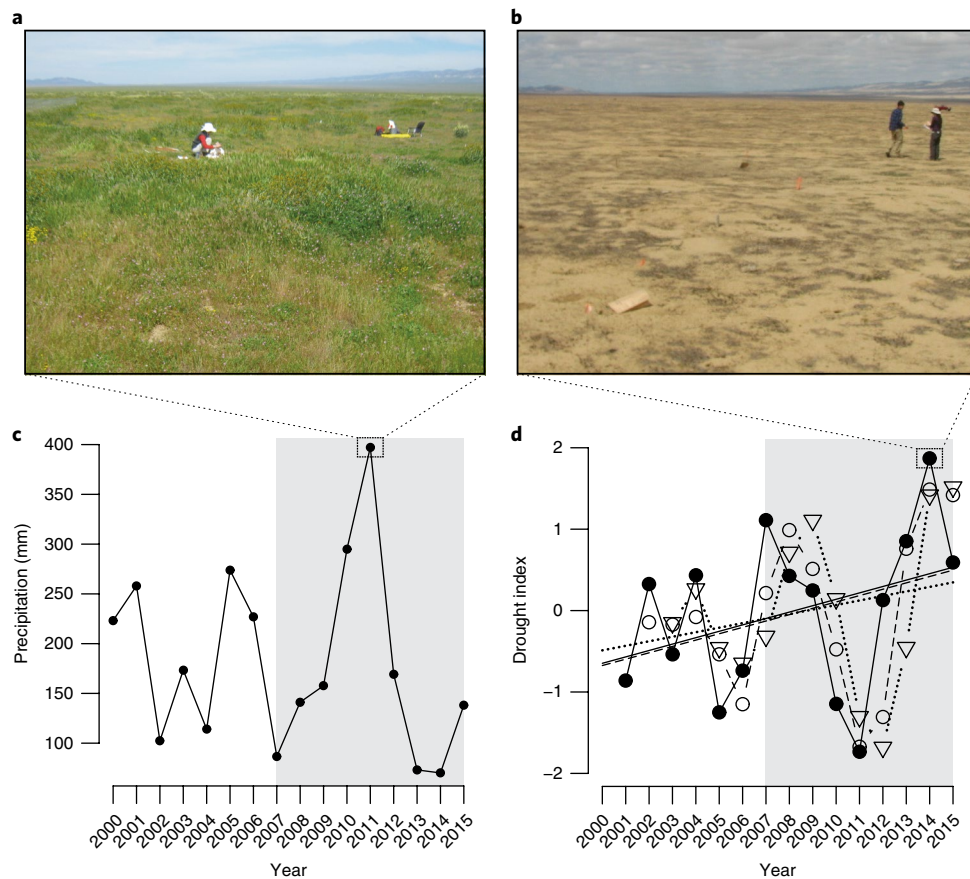
Fig. 1 | Precipitation patterns in the CPNM (2000–2015). a,b, Photographs taken from the 'Center Well 2' study plot in 2011 (**a**) and 2014 (**b**) show how the drought affected the landscape. Both photos were taken in late March (30 March 2011 and 27 March 2014) when plant biomass is at peak levels in this system. **c,d**, Total growing season (October to April) precipitation (**c**) and drought indices (**d**). The 2007–2015 study years are shaded in grey. The SPEI was used to calculate the climatic water balance, and we used its inverse as a drought index (DI = −1 × SPEI) that increased with drier conditions. DI_1 (solid line, filled circles), DI_2 (long dashed line, open circles) and DI_3 (short dashed line, triangles) in **d** represent drought indices calculated over one, two or three growing seasons, respectively. Linear trend lines show increasing aridity over time. Images courtesy of J. Chesnut.

richness for most taxonomic groups (Supplementary Table 2 and Supplementary Fig. 2), the extreme drought did not result in overwhelming declines at the level of individual species.

Pre-drought abundance (N_{pre}) and functional group (animal diet type or plant growth form) were significant predictors of drought responses across taxonomic groups and drought durations, and the maximum population growth rate (r_{max}) was a significant predictor of responses to two- and three-year droughts (Supplementary Table 2). Trophic level (1 = plants; 2 = herbivores; 2.5 = omnivores; and 3 = insectivores and carnivores) and animal body mass were not significant predictors of responses to any drought measures. Abundant species were more likely to lose and rare species were more likely to win, and the strengths and slopes of these negative density-dependent drought responses were remarkably consistent across taxonomic groups (Fig. 2b–d). In addition, there was a spike in the number of rare species during the last year of the drought: 27 of the 87 species (31%) that occurred during one year only were present in 2015—far more than expected by chance (binomial test $P < 0.001$). These findings support the role of drought as a disturbance agent that opens niche space by stressing dominant species and allowing competitively inferior species to increase in abundance[18]. For example, the only plant that increased in absolute abundance during the drought (red maids) thrives under reduced competition[19].

We further tested this competitive release hypothesis by assessing the response of nocturnal rodents to drought, because species within this guild are known to compete for resources in semi-arid systems[20]. The giant kangaroo rat *D. ingens* excluded or greatly outnumbered other rodent species before the drought, but this dominance weakened as the drought ensued: four species colonized the system during the drought, and the abundance of the short-nosed kangaroo rat increased fivefold (Fig. 3a). A structural equation model (SEM) showed that the effect of drought on rare nocturnal rodents was mediated primarily through dominant rodent (that is, giant kangaroo rat) abundance the previous year (Fig. 3b). The giant kangaroo rat population crash allowed smaller-bodied rodents with lower per-capita resource requirements to colonize the system (Fig. 3c), markedly increasing species richness (Supplementary Fig. 2). A supplemental feeding experiment provided evidence that resources were limiting for the large-bodied giant kangaroo rat during the drought (Fig. 3d).

Species with slower population growth rates were more likely to lose and species with higher growth rates were more likely to win during extended drought. When separate regressions were conducted for each taxonomic group, r_{max} was not a significant predictor of plant responses, but it was a significant predictor for birds, mammals and arthropods (Supplementary Fig. 3). This pattern may occur because animals with higher population growth rates tend to be smaller bodied and have lower per-capita resource requirements[21]. Indeed, r_{max} and log[body mass] were weakly negatively correlated for animal species in our dataset ($r = −0.20$, $n = 224$,
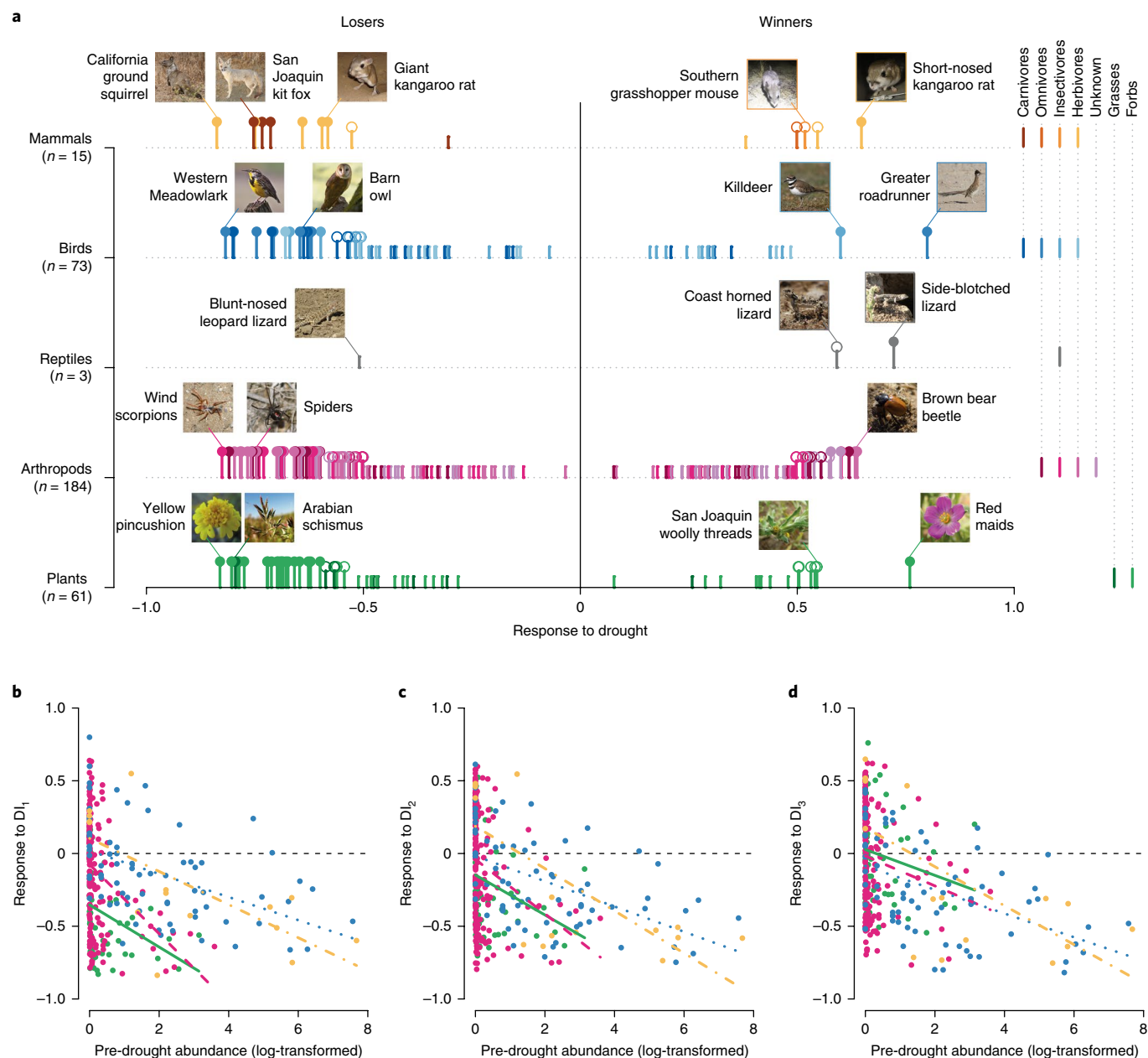
Fig. 2 | Winners and losers in response to drought. Responses of 336 species to drought in the CPNM. **a**, Values on the *x* axis are slope coefficients from the best-fitting of three linear models examining drought effects on the absolute abundance of each species from 2007–2015. Winners increased in abundance in response to drought, whereas losers decreased in abundance. Lines with filled circles indicate significant responses at the $\alpha = 0.05$ level. Open circles indicate significant responses at the $\alpha = 0.10$ level. Lines with no circles indicate non-significant relationships. **b–d**, The effects of pre-drought abundance on responses to drought were measured over one growing season (DI_1; **b**), two seasons (DI_2; **c**) or three seasons (DI_3; **d**). The effects of pre-drought abundance on responses to drought were similar for all taxonomic groups (plants, green solid line; pink, arthropods, dashed line; birds, blue dotted line; and mammals, purple dash-dotted line). Photo credits: Colin Morita (California ground squirrel), J. Roser (San Joaquin kit fox, giant kangaroo rat), A. Semerdjian (southern grasshopper mouse, short-nosed kangaroo rat), B. Gunderson (western meadowlark), R. Schell (barn owl), J. Gross (killdeer, greater roadrunner), C. Frock (blunt-nosed leopard lizard, spiders), A. Metea (coast-horned lizard), L. Prugh (side-blotched lizard), N. Deguines (wind scorpions), D. Daniels (brown bear beetle), G. Butterworth (red maids), J. Chesnut (all other plants).

$P = 0.002$). However, log[body mass] was not retained as a significant predictor for any taxonomic or functional groups except rodents (Fig. 3c). Thus, rapid population growth may in itself be a key life-history trait enabling locally rare species to capitalize on niche space vacated by the decline of dominant species.

Community-wide linear mixed-effects models showed that drought effects moved up the food web over time, with plants responding most strongly to water balance over one growing season;

herbivores, omnivores and insectivores responding similarly to shorter- and longer-term droughts; and carnivores (meat-eating vertebrates) responding most strongly to water balance over three growing seasons (Fig. 4). Drought effects did not attenuate or amplify as they moved up the food web, and instead were strongest at both the bottom (plants) and top (carnivorous birds and mammals), and weakest in the middle (Fig. 4). The strong response of carnivorous animals despite weaker responses from many prey
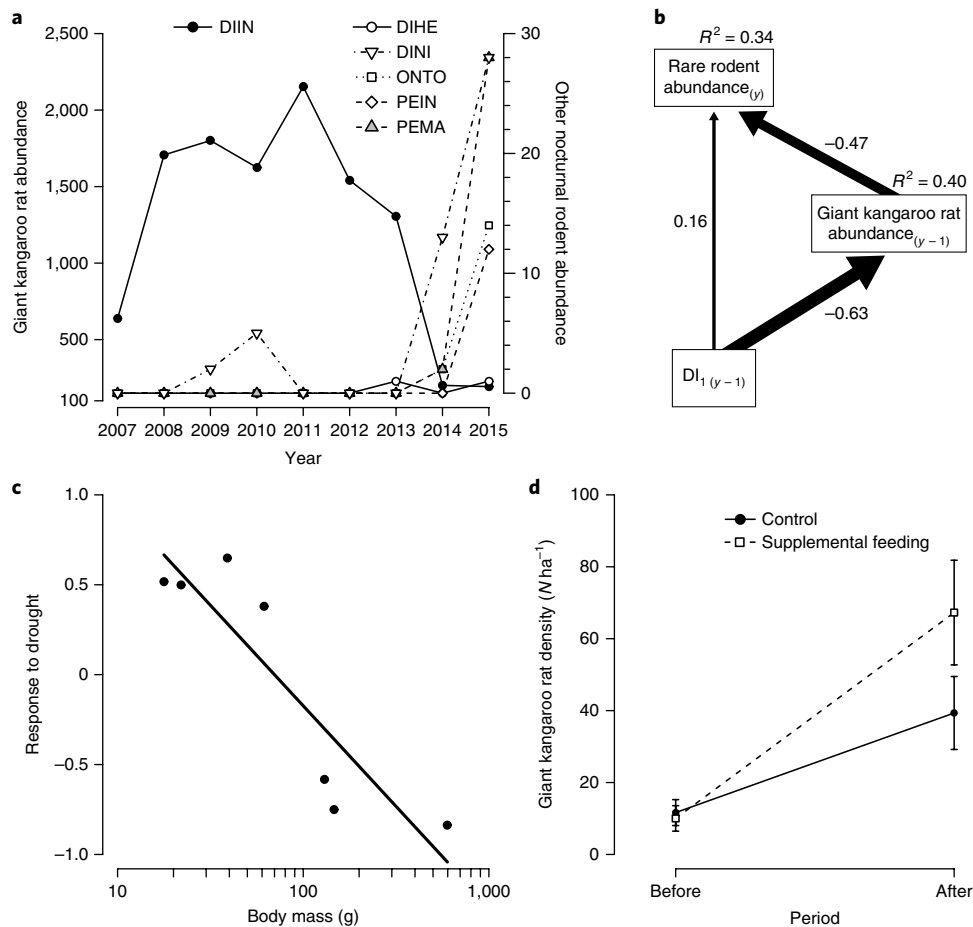
Fig. 3 | Competitive release of rare nocturnal rodents in response to the drought-induced crash of the dominant giant kangaroo rat (*D. ingens*) population. a, Time series of nocturnal rodent abundance, measured as the total number of unique individuals captured during spring and summer mark–recapture sessions on 30 1 ha plots. DIHE, *D. heermanni* (Heerman's kangaroo rat); DIIN, *D. ingens* (giant kangaroo rat); DINI, *D. nitratoides brevinasus* (short-nosed kangaroo rat); ONTO, *Onychomys torridus tularensis* (southern grasshopper mouse); PEIN, *Perognathus inornatus* (San Joaquin pocket mouse); PEMA, *Peromyscus maniculatus* (deer mouse). **b**, Partial mediation SEM showing how the rare nocturnal rodents (all species from **a** except DIIN) were affected directly and indirectly (through the giant kangaroo rat) by drought with a one-year lag ($DI_{1(y-1)}$). Numbers on arrows indicate standardized path coefficients and R^2 values indicate the amount of variance in rodent abundance explained by predictors. All paths were significant ($\alpha < 0.05$). **c**, Larger-bodied rodents were losers and smaller-bodied rodents were winners in response to drought ($R^2 = 0.80$, $F_{1,5} = 20.15$, $P = 0.007$). The response to drought was measured as the coefficient of the best-fitting abundance ~ DI_x regression. **d**, Effect of supplemental feeding on giant kangaroo rat density following extreme drought. Mean densities from nine paired control (filled circles and solid line) and treatment (open squares and dashed line) plots are shown, with standard error bars, before and after supplemental feeding on treatment plots during winter 2015–2016.
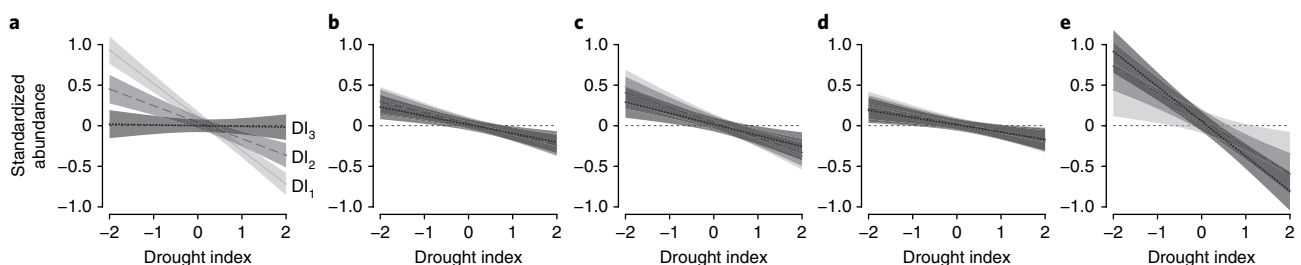
Fig. 4 | Drought effects move up the food web over time. a–e, Responses of plants (**a**), herbivores (**b**), omnivores (**c**), insectivores (**d**) and carnivores (**e**) to drought occurring over one year (DI_1, solid light grey line), two years (DI_2, dashed medium grey line) or three years (DI_3, dotted dark grey line). Regression lines and 95% confidence intervals are shown ($n = 336$ species). Statistical results are summarized in Supplementary Table 3.

species indicates that the responses of a few keystone prey may have disproportionately affected higher trophic levels. For example, the giant kangaroo rat comprised 99.8% of nocturnal rodent biomass and 86.8% of all rodent biomass; unsurprisingly, it is an important

prey item for nearly all of the mammalian and avian carnivores in the Carrizo Plain[17]. Giant kangaroo rats were resistant to one-year water deficits, probably because their large seed caches provided a buffer against short-term resource shortages[22]. However, they

experienced an 11-fold decline in response to extended drought (Fig. 3a). Thus, drought effects may flow through food webs in direct proportion to interaction strengths, operating primarily through highly connected hub species[23]. The drought resistance of hub species may thus be critical in determining community-wide effects.

Biotic interactions are often regarded as less important than abiotic drivers in dryland systems, where variation in rainfall drives dramatic fluctuations in flora and fauna[24,25]. However, recent studies of plant communities indicate that climate variability, including drought, increases long-term niche space by favouring different species in different years and preventing competitive exclusion[26]. Here, we show that abiotic conditions indeed have strong effects on dominant species, but rare species may respond primarily to shifts in the competitive landscape rather than abiotic conditions per se. Animals that were absent from our study area before the drought probably colonized from surrounding areas. Our study area was relatively flat and lacked shrubs, whereas the surrounding areas were characterized by more heterogeneity in topography and habitat structure, and these areas may have served as refugia for 'fugitive' species in non-drought years. The increase in abundance of plant species, most of which have an annual life history, was probably due to germination from a long-lived seed bank that allowed for persistence. Thus, the primary mechanism facilitating the increase of rare species is consistent with spatial source–sink dynamics for animal populations and a temporal storage effect for plant populations, but testing these mechanisms would require additional metrics that we lacked (for example, reproduction, survival and dispersal rates). Although we were not able to test the role of competitive release across all guilds, the compelling evidence within the nocturnal rodent guild combined with the strength and consistency of negative density dependence across taxonomic groups indicates that biotic interactions such as competition are fundamentally important, even in—or perhaps especially in—highly variable environments.

Most climate projection models predict that dry regions will become drier and wet regions will become wetter in the future, with anticipated increases in the frequency and severity of droughts and floods[4,6]. Our analysis may give cause for optimism in the face of these alarming trends, because the responses of most species were surprisingly weak despite strong community-aggregated responses. Weak and variable responses to major disturbances have similarly been reported in studies of bird and plant communities[27,28]. However, our results indicate that animals at the top of the food chain will probably be the biggest losers as drought durations increase. Mammals were more sensitive to drought than plants (Supplementary Table 1), indicating that aridity may affect animals directly in addition to the indirect plant-mediated effects typically assumed to be the primary mechanism of drought effects on animals[29]. The response of keystone or hub species should be a priority for monitoring, because their level of resistance may determine whether system-wide drought impacts are buffered or amplified. An obvious next step is to determine whether the system is resilient, recovering to the same pre-drought state, or whether it transitions to a new post-drought state[30]. While extreme droughts can lead to substantial short-term declines in the abundance and diversity of species across taxonomic groups, our findings indicate that these disturbances may play a vital role in the long-term maintenance of biodiversity by inducing periodic die-offs of dominant species and subsequent opportunities for rare, yet fast-growing, species.

Methods

Methods, including statements of data availability and any associated accession codes and references, are available at https://doi.org/10.1038/s41558-018-0255-1.

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Author contributions

L.R.P. and J.S.B. designed the study. L.R.P., J.S.B., N.D., J.B.G., W.T.B. and R.S. collected the data. L.R.P., N.D. and J.B.G. conducted the statistical analyses. All authors wrote the paper.

Competing interests

The authors declare no competing interests.

Additional information

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Methods

Study area. This study took place in the CPNM—a 1,012 km² natural area. The CPNM is the largest remnant of the San Joaquin Valley ecosystem that historically extended throughout the central valley of California (Supplementary Fig. 1). The CPNM is a semi-arid grassland that receives an average of 232 mm of precipitation per year, falling almost exclusively as winter rain (https://cdec.water.ca.gov/snow_rain.html). Historically, the CPNM was dominated by perennial bunchgrasses and native annual forbs, but today the vegetative cover is dominated by European annuals such as barley (*Hordeum murinum*), red brome (*Bromus madritensis rubens*) and red-stemmed filaree (*Erodium cicutarium*)[31].

Drought index. We calculated a standardized precipitation evapotranspiration index (SPEI) to estimate drought severity based on a 16-year time series (2000–2015) of hourly records from a weather station in our study area (MesoWest; station ID = CAZC1). SPEI is a multi-scalar measure of climatic water balance that accounts for atmospheric evaporative demand in addition to precipitation[32]. SPEI values indicate the number of standard deviations by which the observed water balance deviates from the long-term mean. We used the FAO-56 Penman–Monteith equation implemented in the 'SPEI' R package to calculate atmospheric evaporative demand (ETo) each month based on average daily minimum and maximum temperatures, average daily relative humidity, dew-point temperature, solar radiation and wind speed[32]. SPEI was then calculated as precipitation minus ETo. SPEI can be calculated over different time intervals to measure short- or long-term droughts[33]. To understand aridity in April at the peak of primary production, we calculated 7-, 19- and 31-month SPEI values, which estimated water balance over 1, 2 and 3 growing seasons, respectively, before the current time point. We used the reverse of these SPEI values as a drought index, such that $DI_x = -1 \times SPEI_x$ to calculate DI_1, DI_2 and DI_3, respectively from 2000–2015. Winner species thus had positive abundance–drought index relationships and loser species had negative relationships. All three drought indices showed a trend of increasing aridity over time (Fig. 1).

Surveys. In 2007, stratified randomization was used to place 30 2 ha (140 m × 140 m) sites within a 112 km² study area in the CPNM (Supplementary Fig. 1). Replicated surveys were conducted on each site annually from 2007–2015 to estimate the abundance and species composition of plants, rodents, reptiles and arthropods. Plant cover was estimated using the pin frame method on 400 1 m² plots in April (the peak of the growing season)[34]. Nocturnal rodent abundance was estimated using 3–5 night mark–recapture sessions in April and August on each of the 30 study sites. Rodents were captured in Sherman traps (*n* = 60 per 1 ha trapping grid on each site), individually marked with passive integrated transponder and ear tags, and released. Squirrel abundance was estimated using five-day mark–recapture sessions in May on each study site. Squirrels were captured in Tomahawk traps, individually marked with passive integrated transponder tags and released. Rodent abundance was estimated as the number of unique individuals captured per year for each species. Reptile abundance was estimated using visual line transect surveys in June on each study site. Observers walked along 7 140-m-long transects spaced 20 m apart and recorded each reptile sighting. Three surveys were conducted on each site per year (*n* = 90 in total).

Arthropods were sampled using pitfall traps placed on each plot for 2 weeks each year in June (*n* = 8 traps per plot; 240 in total). Individuals within each sample were identified to order, and the number of individuals within each unique morphospecies was counted. Species richness was calculated for each sample. Beetles (order Coleoptera), ants (family Formicidae), and grasshoppers and crickets (order Orthoptera) were identified to genus or species when possible, and a reference collection was maintained to facilitate consistent species identification across samples. Thus, abundance patterns of beetles, ants and orthopterans were examined at the species level, and abundance patterns of other invertebrate taxa were examined at the order level.

Mammalian carnivore and lagomorph abundances were estimated from road-based spotlight surveys conducted each season (*n* = 4 per year; quarterly) along the two main roads through the CPNM—Soda Lake Road and Elkhorn Road (total distance = 116.9 km). Carrizo Plain Christmas Bird Count data were used to estimate bird abundance and species composition from 2007–2015. Bird counts were adjusted by the distance surveyed each year (range = 220–397 km) to create an index of birds counted per 100 km surveyed. Tule elk (*Cervus elaphus nannodes*) abundance was estimated from aerial surveys conducted annually. Pronghorn antelope (*Antilocapra americana*) abundance was estimated from sightings that were systematically recorded by field workers from April through August each year, adjusted by the total hours of effort (range = 638–1,208 h per year) to create an index of pronghorn counted per 100 h of search effort. Aerial pronghorn surveys were conducted during 6 of the 9 study years, and our sighting index was positively correlated with survey numbers during these years (*r* = 0.78).

During surveys from 2007–2015, we recorded 99,268 sightings of 94 bird species, 31,139 captures or sightings of 16 mammal species, 3,430 sightings of 5 reptile species and 575,627 captures of arthropods from 25 orders (including 206,140 individuals from 205 species of ant, beetle and orthopteran). Although not all arthropod taxa were identified to species level, we refer to all taxa as 'species' for simplicity. The percentage cover was recorded for 74 plant species (65 forbs and 9 grasses).

Supplemental feeding experiment. We tested the role of resource limitation in the response of giant kangaroo rats to drought by conducting a replicated supplemental feeding experiment. The global range of this federally endangered rodent is restricted to five remnant populations in central California[18]. We used a before–after–control–impact (BACI) design in three of the five areas with extant populations (Supplementary Fig. 1): CPNM (San Luis Obispo and Kern counties), Lokern Ecological Reserve (Kern County) and the Ciervo-Panoche Natural Area (San Benito and Fresno counties). Experimental blocks consisted of paired 1 ha plots spaced 100 m apart, and 3 blocks were established in each area spaced at least 500 m apart (*n* = 9 blocks). One plot in each block served as a control, and the other plot received supplemental food. Feeding stations were placed at each trap station on treatment plots (*n* = 60 stations per plot). Stations were constructed with two sections of 30-cm-long polyvinyl chloride tube connected by a 5 cm conduit box containing bird seed. Seed was provided ad libitum for six weeks during the autumn of 2015, which immediately followed the extreme drought period. In total, approximately 45 kg of bird seed was provided on each treatment plot. Each plot was trapped for 3–5 consecutive nights in summer 2015 ('before') and summer 2016 ('after'), and all captured rodents were individually tagged and released. Closed capture–mark–recapture modelling was used to estimate giant kangaroo rat densities[35]. No individuals were found to have moved between plots, consistent with findings that giant kangaroo rats maintain home ranges of approximately 100 m² and are strongly territorial[36].

Statistical analyses. To examine species' responses to drought, we conducted analyses that included all species' individual responses, followed by separate analyses for each species. Annual abundance estimates (*n* = 9 years) of each species were log-transformed and normalized using the z-transformation. Species present during only one year were excluded. Community-wide assessments were conducted with repeated-measures linear mixed-effects models that included species identity as a random effect, abundance as the dependent variable, and drought measure and broad functional grouping (plant, herbivore, omnivore, insectivore or carnivore) as fixed effects, as well as their interaction term:

$$N = FG \times DI_x + (random = speciesID)$$

Where *N* is the abundance, FG is the functional group, DI_x is the drought index calculated over *x* growing seasons and speciesID is the unique identifier for each species. Separate repeated-measures linear mixed-effects models were conducted for each drought index (DI_1, DI_2 and DI_3), and all models had a total of 3,024 observations from 336 species (9 observations per species). Models included a temporal autocorrelation term (CAR1) to account for the repeated-measures nature of the data. To find models with optimal fit, we used the Akaike information criterion (AIC) to compare models with random intercepts versus random intercepts and slopes, and then to compare models with different variance structures (fixed, power and exponential structures for the drought index, and identity structure for functional grouping) to account for violations of equal variance of the residuals[37]. The random effect on the intercept only was supported by AIC in all cases. Exponential variance structure was supported for DI_1 and DI_2 (the variance increasing as an exponential function of the drought index), and no structure (equal variances) was supported for DI_3. Model selection was not conducted on fixed effects (drought index and functional group). We performed marginal *F*-tests with univariate analysis of deviance to assess the significance of the fixed effects (Supplementary Table 3).

At the individual species level, separate linear regressions were conducted using each species' abundance as the response variable and DI_1, DI_2 and DI_3 as predictors in three univariate regressions per species. Abundance data were log-transformed and normalized using the z-transformation before analyses. Thus, the slope of each linear regression measured the strength of each species' response as an order-of-magnitude change in abundance per unit change in the drought index. The slope coefficient, standard error of the coefficient, coefficient of determination (R^2) value and *P* value of each regression were recorded. R^2 values were compared among the three regressions for each species to identify the drought index that explained the greatest amount of variation in abundance (best R^2). The *P* value and slope coefficient of the best model were used to classify each species as a 'winner' (*P* < 0.05, positive slope coefficient), 'loser' (*P* < 0.05, negative slope coefficient) or not significantly affected (*P* > 0.05). This *P* value cut-off was associated with R^2 values of 45–50%.

To examine factors affecting the response of species to drought, we constructed a weighted linear mixed-effects model:

$$\text{Response to } DI_x = N_{pre} \times FG + r_{max} \times FG + (random = taxa)$$

where 'taxa' is the taxonomic group, N_{pre} is the pre-drought abundance (measured as the log-transformed abundance in 2011) and r_{max} is the maximum population growth rate (see below for the method of calculation). We used slopes from the abundance ~ DI_x regressions for each species as response variables and the inverse of associated standard errors as weighting values. This approach is analogous to a weighted meta-analysis. Taxonomic group was included as a random effect. Reptiles were excluded because there were only three species. Functional group

was classified, based on each animal species' primary source of energy, as carnivore (meat eating), omnivore (consuming species from multiple trophic levels), insectivore or herbivore. Plant functional groups were based on the growth form and classified as forbs or grasses. We used AIC to compare models with random intercepts with models with random intercepts and slopes, and then compared models with different variance structures (fixed, power and exponential structures for N_{pre}, r_{max} and fitted values, and identity structure for functional group)[37]. The random effect on the intercept only was the best model structure for all three drought indices, indicating that the effects of predictors did not differ between taxonomic groups.

We used separate weighted general linear models for each taxonomic and functional group to examine additional taxon-specific predictors. The full model for plants was:

$$\text{Response to DI}_x = N_{pre} \times \text{FG} + r_{max} \times \text{FG} + \text{origin} \times \text{FG}$$

where 'origin' is native or exotic. Nearly all plants were annuals. The full model for each animal taxonomic group (arthropod, bird and mammal) was:

$$\text{Response to DI}_x = N_{pre} \times \text{FG} + r_{max} \times \text{FG} + \text{mass} \times \text{FG}$$

where 'mass' is log[body mass]. Functional group was included as an additive factor in the model for mammals because the sample size was too low ($n = 15$ species) to include interactions. The full model for each animal functional group (herbivore, omnivore, insectivore and carnivore) was:

$$\text{Response to DI}_x = N_{pre} \times \text{taxa} + r_{max} \times \text{taxa} + \text{mass} \times \text{taxa}$$

We used backwards deletion of non-significant predictors to obtain final models that included significant predictors only (Supplementary Table 4).

For species in all taxonomic groups, we calculated the maximum growth rates observed during our nine-year study as:

$$r_{max} = \max\left[\ln\left(\frac{N_{t+1}}{N_t}\right)\right]$$

Body masses of arthropod species were obtained when possible during the processing of samples. Rodent body masses were calculated from our live-trapping records and masses of other mammals were obtained from the panTHERIA database[38]. Bird body masses were provided by Dunning[39].

We tested the role of drought on releasing rare species from competition with dominant species using the nocturnal rodent community data in mediation analyses with SEMs. We compared the AIC of three SEMs modelling how the total abundance of rare nocturnal rodent species was affected by the drought index: solely directly (no mediation), solely indirectly through the dominant giant kangaroo rat species (that is, complete mediation) or both directly and indirectly (partial mediation)[40]. We ran these three SEMs with either DI_1, DI_2 or DI_3, and with or without a one-year lag in the effect of DI_x and giant kangaroo rat abundance on the abundance of rare rodents. Abundances in the SEM were log-transformed. Sample sizes for the lagged and non-lagged SEMs were 240 and 270, respectively, corresponding to data from 30 sites in 2008–2015 (lagged) or 2007–2015 (non-lagged). The results using DI_1 with a one-year lag are presented in Fig. 3b because this model had the best fit to the data. The results from the other models (which had qualitatively similar results) are presented in Supplementary Fig. 4.

To test the effect of supplemental feeding on the giant kangaroo rat population density, a linear mixed-effects model was used to conduct a BACI analysis, with population density as the response variable; time period (before versus after), treatment (fed versus control) and a period × treatment interaction as fixed effects; and block as a random effect[41]. The interaction term represents the BACI contrast, which is interpreted as the effect of the experiment. Giant kangaroo rat density was similar on control and treatment plots in summer 2015, before supplemental feeding. The density increased on both the control and treatment plots in summer 2016 ('period' factor $F_{1,24} = 33.5$, $P < 0.001$), probably due to a break in the drought and the resulting increase in natural food resources. However, densities on treatment plots (which received supplemental food) increased 71% more than densities on control plots in summer 2016 (after feeding: control plot density = 39 animals ha^{-1}; treatment plot density = 67 animals ha^{-1}; period × treatment $F_{1,24} = 4.05$, $P = 0.055$).

All analyses were carried out using R, and linear mixed-effects models were conducted using the nlme package[42].

Data availability. All data supporting the findings of this study are available in Supplementary Data 1.

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