Precipitation alters interactions in a grassland ecological community

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Abstract

1. Climate change is transforming precipitation regimes world-wide. Changes in precipitation regimes are known to have powerful effects on plant productivity, but the consequences of these shifts for the dynamics of ecological communities are poorly understood. This knowledge gap hinders our ability to anticipate and mitigate the impacts of climate change on biodiversity.

2. Precipitation may affect fauna through direct effects on physiology, behaviour or demography, through plant-mediated indirect effects, or by modifying interactions among species. In this paper, we examined the response of a semi-arid ecological community to a fivefold change in precipitation over 7 years.

3. We examined the effects of precipitation on the dynamics of a grassland ecosystem in central California from 2007 to 2013. We conducted vegetation surveys, pitfall trapping of invertebrates, visual surveys of lizards and capture–mark–recapture surveys of rodents on 30 plots each year. We used structural equation modelling to evaluate the direct, indirect and modifying effects of precipitation on plants, ants, beetles, orthopterans, kangaroo rats, ground squirrels and lizards.

4. We found pervasive effects of precipitation on the ecological community. Although precipitation increased plant biomass, direct effects on fauna were often stronger than plant-mediated effects. In addition, precipitation altered the sign or strength of consumer-resource and facilitative interactions among the faunal community such that negative or neutral interactions became positive or vice versa with increasing precipitation.

5. These findings indicate that precipitation influences ecological communities in multiple ways beyond its recognized effects on primary productivity. Stochastic variation in precipitation may weaken the average strength of biotic interactions over time, thereby increasing ecosystem stability and resilience to climate change.

Key-words: arthropods, conditional outcomes, *Dipodomys ingens*, dryland, ecological non-monotonicity, food web, path analysis, rain, San Joaquin antelope squirrel

Introduction

A major challenge for ecologists of the 21st century is understanding how climate influences interactions among species within ecological communities. Precipitation is a limiting resource in many terrestrial ecosystems and can alter ecosystem functioning through several pathways (Webb *et al.* 1983; Adler *et al.* 2006; Gerten *et al.* 2008). Water is critical for plant growth, photosynthesis and survival, and this dependence leads to strong effects of

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precipitation on regional primary productivity (Knapp, Briggs & Koelliker 2001; Hsu, Powell & Adler 2012). However, much less is known about the strength and mechanisms of precipitation effects on faunal communities. Climate change is altering both the mean and variability of precipitation levels world-wide (IPCC 2014), and a better understanding of the system-wide effects of this critical resource is needed to predict the response of ecosystems to future precipitation regimes.

Precipitation could have pervasive effects on animals in addition to its well-understood effects on plants (Yahdjian, Gherardi & Sala 2011; Sala *et al.* 2012). Precipitation

may directly affect the survival and reproduction of animals (Hagstrum & Milliken 1988; Warner & Andrews 2002) or influence their behaviour and physiology to maintain water balance (McCluney & Sabo 2009; Takei *et al.* 2012). Beyond these direct species-level effects, indirect effects of precipitation via plant productivity can influence herbivore and predator densities through changes in feeding or habitat resources (Morris 2000; Suttle, Thomsen & Power 2007). Additionally, abiotic factors such as precipitation may modify the strength or sign of species interactions (Holland & DeAngelis 2009). Precipitation has been shown to alter consumer–resource interactions among pairs of invertebrate and vertebrate species through both density- or trait-mediated effects (Loveridge *et al.* 2006; McCluney & Sabo 2009). However, the modifying effect of precipitation on community dynamics remains poorly understood despite a recent review highlighting its importance (McCluney *et al.* 2012).

Direct, indirect and modifying effects of precipitation on flora and fauna occur simultaneously in ecosystems, but the three have seldom been considered in networks of interactions among multiple trophic and functional groups, thereby precluding assessment of their relative importance. The effects of precipitation on ecosystems may differ fundamentally when multiple interactions are examined simultaneously rather than in isolation, because strong effects could attenuate rapidly, be neutralized by opposing pathways, or be amplified by synergistic effects (Werner & Peacor 2003; Duffy *et al.* 2007; Aschehoug & Callaway 2015). A recent meta-analysis suggested that climate impacts on ecosystems were greater through alterations of biotic interactions than direct effects on organisms, and the authors stressed that simultaneous monitoring of species from multiple trophic levels within a single ecosystem is needed to predict community-wide effects of climate change (Ockendon *et al.* 2014). Here, we quantify the direct, indirect and modifying effects of precipitation on plants, rodents, invertebrates and lizards in a semi-arid grassland during a 7-year period.

Dryland ecosystems, which cover 41% of Earth's terrestrial surface and provide critical ecosystem services to over two billion people (MEA 2005), are particularly suitable for examining the role of precipitation on ecological communities. Characterized as systems driven by annual variation in precipitation (Noy-Meir 1973), arid and semi-arid ecosystems are expected to be particularly sensitive to climate change (Gerten *et al.* 2008; IPCC 2014). Frequent record-breaking droughts, such as those documented in California during the past decade (Griffin & Anchukaitis 2014), could disrupt ecosystem stability beyond thresholds and induce state transitions such as desertification or invasion by exotic species (Scheffer *et al.* 2001; Suding, Gross & Houseman 2004; Bradley *et al.* 2010). The dynamics of arid and semi-arid grasslands are also strongly affected by burrowing mammals through their soil disturbance, habitat creation, competitive interactions and foraging activities (Whitford & Kay 1999; Davidson,

Detling & Brown 2012; Prugh & Brashares 2012). Our study system in the Carrizo Plain National Monument (California, USA) harbours the largest remaining population of the giant kangaroo rat (*Dipodomys ingens*), an abundant burrowing rodent. The Carrizo Plain, as a typical semi-arid grassland in terms of soils, precipitation patterns, vegetation and fauna (Germano *et al.* 2011), may be representative of how precipitation affects the dynamics of arid ecological communities.

We developed a conceptual model of our study system based on our own expertise (e.g. Prugh & Brashares 2012; Bean *et al.* 2014; Gurney, Prugh & Brashares 2015) and the literature (Fig. 1). We parameterized the model using data from surveys of plants, invertebrates, kangaroo rats, ground squirrels and lizards conducted on 30 plots across our 112-km^2 study area from 2007 to 2013. Precipitation fluctuated dramatically during our 7-year study with a fivefold difference between the minimum and maximum annual rainfall amounts (7·3–39·7 cm, Fig. 1). We used this large dataset to assess the multiple effects of precipitation on the Carrizo Plain ecological community. Specifically, we examined precipitation's (i) direct effects on abundance, (ii) indirect effects on the fauna via plant productivity, and (iii) modifying effects on interactions. We expected (i) a strong direct effect of precipitation on plant productivity because water is a critical limiting resource for plants in drylands (Noy-Meir 1973; Yahdjian, Gherardi & Sala 2011), and (ii) stronger indirect, plant-mediated effects of precipitation on fauna than direct effects. We expected strong indirect effects because animals in our semi-arid system, such as kangaroo rats, are adapted to dry conditions and may therefore respond more to variation in food resources (which can yield metabolic water) than to changes in rainfall itself. We statistically evaluated direct, indirect and modifying effects of precipitation using a structural equation modelling approach (Shipley 2009; Grace, Scheiner & Schoolmaster 2015).

Materials and methods

STUDY AREA AND DESIGN

We studied the ecological community of a semi-arid grassland located in the Carrizo Plain National Monument (CPNM; latitude = 35·35438, longitude = −120·04001, ca. 700 m above sea level) in California, USA, from 2007 to 2013. The CPNM has been designated as a 'Biogem' by the Natural Resources Defense Council and is a key conservation area for more than 30 at-risk species (U.S. Fish and Wildlife Service 1998). It is the largest remnant of the San Joaquin Valley ecosystem that historically extended throughout the central valley of California and has largely been converted to industrial agriculture. Over the past 20 years, mean annual precipitation in the CPNM was 21·7 cm (95% CI = 16·3–27·1 cm), with most rain events occurring during the growing season from October to April (California Data Exchange Center 2015). During our study, there were 4 years of below average precipitation (7·3–15·8 cm, 2007–2009 and 2013),
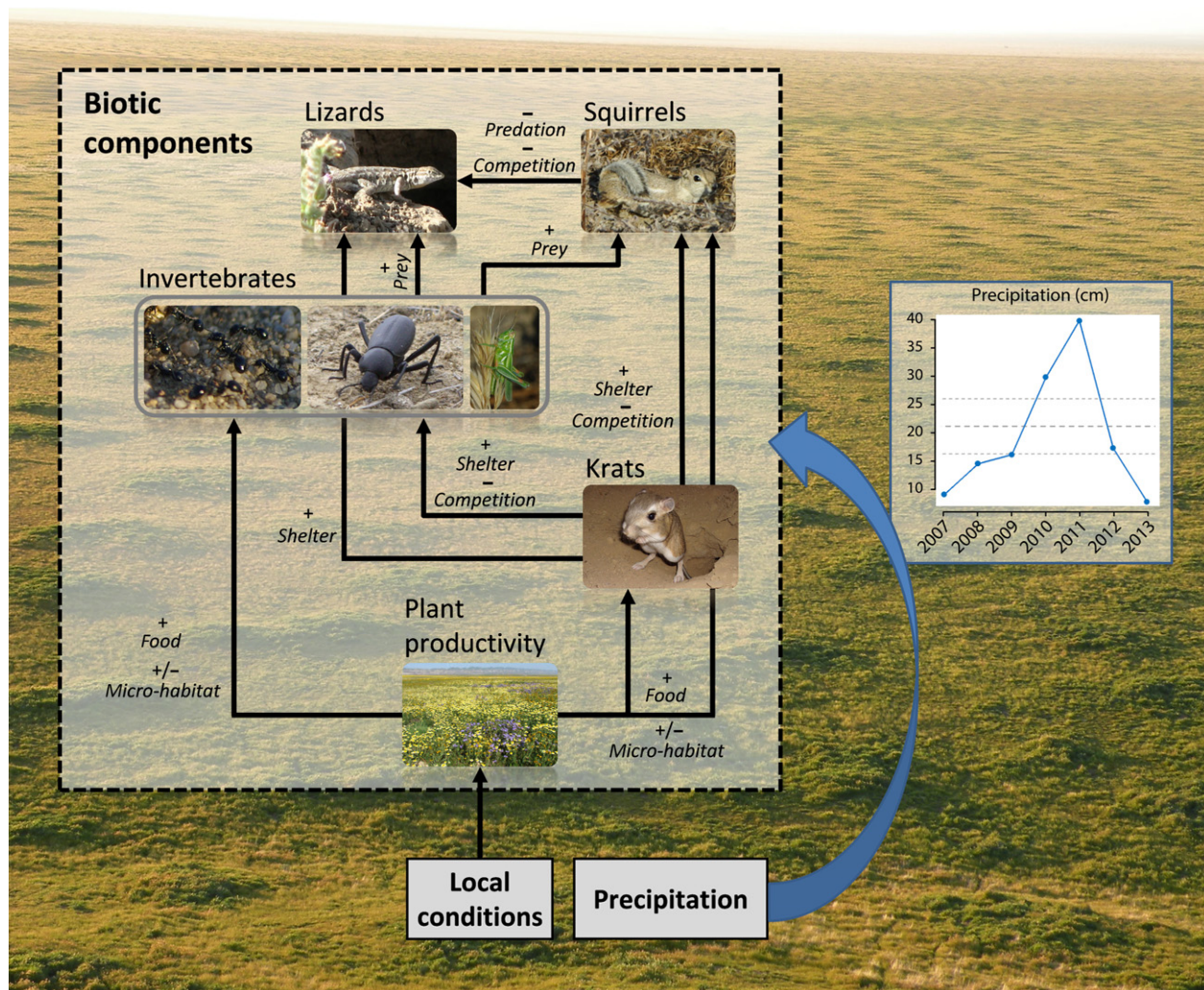
Fig. 1. Conceptual model of the Carrizo Plain ecological community. The background picture shows the landscape of our study area in the Carrizo Plain National Monument, with burrow mounds dug by giant kangaroo rats clearly visible. The right panel shows annual growing-season precipitation during our 7-year study period with both below- and above average precipitation years (average, bold dotted line, calculated from 1995 to 2015; the two thin dotted lines correspond to the 95% confidence intervals). The curved blue arrow represents the potential for precipitation to affect the studied ecosystem through direct, indirect and modifying effects. 'Local conditions' represents differences in soil properties, plant composition and historical land-use. '+' and '−' indicate expected positive or negative effects. Among invertebrates of the Carrizo Plain, we included ants, beetles and orthopterans as the most likely to interact with other species in the community through herbivory, competition (with the two rodent species) or predation (as preys of squirrels and lizards; Hawbecker 1947; Parker & Pianka 1975). 'Krats' and 'Squirrels' stands for the density of giant kangaroo rat and San Joaquin antelope squirrel, each species dominating the nocturnal and diurnal rodent communities respectively. Similarly, the common side-blotched lizard was the only abundant reptile recorded, with other species being rare. [Colour figure can be viewed at wileyonlinelibrary.com]

2 years of above average precipitation (29·5–39·7 cm, 2010–2011) and 1 year did not differ from the average (16·9 cm, 2012). Thus, our study spanned a broad natural gradient of annual water availabilities, with a fivefold difference between the minimum and maximum rainfall amounts (Fig. 1). During the study period, growing-season temperature averaged 11·8 °C (range: 11·2–12·5 °C).

In 2007, we used stratified randomization to establish 30 plots across a 112-km^2 study area located within the core distribution of the giant kangaroo rat (Prugh & Brashares 2012). Each plot was 140 m × 140 m (2 ha). Plots were located in two sites of the CPNM ('Center Well' and 'Swain', 20 and 10 plots in each site respectively) that were 6·9 km apart. Vegetation in both sites lacked shrub cover and was dominated by native and exotic annual forbs such as *Lasthenia* spp. and *Erodium circutarium*.

The grass cover was dominated by several exotic annual grass species (e.g. *Schismus arabicus* or *Bromus madritensis* ssp. *rubens*). Although mostly similar, plant composition slightly varied annually between sites. The two sites differed in terms of soil properties, with Swain soils being sandier and with lower nutrient content, and Center Well soils having higher clay content (Gurney, Prugh & Brashares 2015). Finally, the two sites may differ in historical land-use, as agricultural activities (e.g. grazing, ploughing) occurred in the 20th century in parts of the CPNM area. We accounted for potential effects of local conditions (soil properties, plant composition, legacies of historical land-use) on the Carrizo Plain ecological community in our analyses (see 'Statistical analyses'). During our study, cattle grazing occurred in part of the CPNM and 10 of our plots were grazed. However, because cattle grazing only took place during 4 years and no grazing effects

were detected (Appendix S2, Supporting Information), this factor was not included in our analyses.

STUDY SYSTEM AND EXPECTATIONS

The ecological community of the CPNM was used to assess how precipitation affects species from multiple trophic levels and their interactions (Fig. 1). We expected precipitation to positively affect plant productivity and modify the effects of local conditions on plants (Sala *et al.* 1988; Yahdjian, Gherardi & Sala 2011). Plant productivity may benefit ants, beetles and orthopterans which fed mostly on plant materials (Appendix S1). However, each group may respond differently to micro-habitat characteristics resulting from changes in plant productivity. Two species of rodents, the giant kangaroo rat (hereafter 'kangaroo rats') and the San Joaquin antelope squirrel (*Ammospermophilus nelsoni*, hereafter 'squirrels') dominate the nocturnal and diurnal rodent communities respectively. As kangaroo rats mainly eat seeds and occasionally feed on greens or invertebrates during the breeding season (Tracy & Walsberg 2002), detrimental effects on arthropods may be expected (via competition, and to a lesser extent predation). However, previous studies have found that kangaroo rats had facilitative effects on these three groups through their burrowing activity (Edelman 2012; Prugh & Brashares 2012). We therefore expected a positive effect of kangaroo rats on lizards and squirrels that use burrows for shelter. Squirrels eat mainly greens and invertebrates, and they may negatively affect lizards through competition for food (invertebrates) or direct predation (Hawbecker 1947).

Precipitation may directly alter (positively or negatively) reproduction, survival, physiology or behaviour of the fauna of this ecological community. Moisture influences the development of invertebrates (Hagstrum & Milliken 1988) and the survival of lizard embryos (Warner & Andrews 2002). Water deprivation can affect the physiology, behaviour and survival of desert-adapted rodents (Boice & Witter 1970; Takei *et al.* 2012). However, giant kangaroo rats prefer low precipitation areas [annual precipitation <30 cm (Bean *et al.* 2014)], possibly because excess water could flood burrows.

We limited our analyses to species that were interacting locally on our study plots. Other vertebrates found in our study area included passerine birds, birds of prey, pronghorn antelopes (*Antilocapra americana*), lagomorphs (*Lepus californicus, Sylvilagus audubonii*), San Joaquin kit foxes (*Vulpes macrotis mutica*), and other rarely seen mammalian carnivores such as badgers (*Taxidea taxus*), coyotes (*Canis latrans*) and long-tailed weasels (*Mustela frenata*). Pronghorns and lagomorphs were rarely seen on our study plots. All of these species were highly mobile compared to our 2-ha study plots and it is thus likely their effects would be of similar type and strength across our 30 plots. While they may affect the species considered in our analyses (Fig. 1) at the scale of our study area, local differences in their potential influence on interactions among species included in our analyses should be weak and thus not change our results.

BIOLOGICAL SURVEYS

From 2007 to 2013, we surveyed each of our 30 plots to estimate plant productivity, abundance of ants (order Hymenoptera, family Formicidae), beetles (order Coleoptera), orthopterans (order Orthoptera) and lizards (order Reptilia, suborder Lacertilia), and density of giant kangaroo rats and San Joaquin antelope squirrels. Details of each survey may be found in Prugh & Brashares (2012). Here, we briefly describe data collection and computation to obtain abundance estimates. All analyses were performed in program *R* version 3.2.2 (R Core Team 2015). As a measure of plant productivity, plant biomass was measured at its peak in April by clipping vegetation in eight quadrats of 1/16 m^2 on each of the 30 plots and averaging weights of the dried samples. We collected invertebrates using four pitfall traps set in June for 2 weeks on each plot, and we used the average number of ant, beetle or orthopteran individuals captured as estimates of abundance. Lizards were counted along seven transects on each plot, with three visits in June each year. Abundance was estimated by summing transect counts within visits and averaging the sums across visits. Abundance was estimated for the common side-blotched lizard (*Uta stansburiana*, hereafter 'lizards') only as other reptiles were rarely seen. We conducted capture–mark–recapture surveys to estimate densities (number per ha) of kangaroo rats and squirrels in August and May, respectively, using package *RMark* (Laake 2013). These two rodent species were by far the most common species on our study area and other nocturnal or diurnal rodents were seldom captured or seen. Plant and animal productivity were measured in different units (biomass and abundance of individuals respectively), because of the conservation interest of *individual* as the reproductive unit of most animal populations. Although the estimated strength of the relationships between plant biomass and animal abundance or biomass could differ, their sign and response to precipitation should be similar because abundance and biomass are positively correlated.

STATISTICAL ANALYSES

To evaluate the hypothesized pathways by which precipitation could affect the ecological community, we first used mixed-effects modelling as a preliminary step to inform and support our structural equation modelling approach. This technique is particularly useful when evaluating dynamics of complex communities, because each variable in a structural equation model (SEM) may simultaneously function as a predictor and a dependent variable, and the direct and indirect effects of hypothesized drivers can be partitioned across the ecological community.

Mixed-effects modelling

We fit separate linear mixed-effects models with the R package *nlme* (Pinheiro *et al.* 2016) to each of the biological components of our system (plant biomass, abundance of ants, beetles, orthopterans and lizards, and density of kangaroo rats and squirrels) with predictor variables (precipitation, local conditions or biological components) included as fixed effects (Appendix S3, Fig. 1). We evaluated the effect of varying local conditions by including a binary variable taking the value 0 for plots located in the Center Well site and 1 for plots located in the Swain site. To explore whether the effect of a predictor variable on the response variable was modified by precipitation, we included a 'precipitation × predictor' interaction term for each predictor-response pair. We included plot identity (categorical variable with 30 levels) as a random effect on the intercept for all models to account for our repeated measures design (seven measures per plot). When necessary, variables were transformed to ensure

normality of model residuals (Appendix S3). For each model, we graphically assessed the variance of the residuals for signs of heterogeneity. When heterogeneity was suspected, we fit the models with different variance structures (using predictor variables or year as covariates) and selected the structure that yielded the best results according to Akaike's information criterion (Zuur *et al.* 2009). The sample size of each model was 210, as we used data from 30 plots surveyed for 7 years.

We performed marginal *F*-tests with univariate analysis of deviance (Pinheiro & Bates 2000) to investigate the effects of explanatory variables in each model. To balance our sample size with SEM model complexity (Grace, Scheiner & Schoolmaster 2015; Lefcheck 2016), we simplified each model by removing two-way interactions lacking support ($P > 0.05$) in this preliminary analysis. All single effects were kept in each model and included in the SEM for further evaluation of their role in the ecological community.

Structural equation models

Following results from the preliminary mixed-effects modelling analysis, we conducted piecewise structural equation modelling to join the multiple linear mixed-effects models into a single SEM (Shipley 2009). Piecewise SEM allows for the inclusion of random effects and variance structures from each linear mixed-effects model in the global SEM evaluation. We used the R package *piecewiseSEM* (Lefcheck 2016) to combine the linear mixed-effects models described above into a SEM evaluating hypothesized associations among components of our study system. To model potential reciprocal influences, we included correlations among the abundance of ants, beetles and orthopterans. Shipley's test of d-separation (Shipley 2009) was used to assess the overall fit of the SEM and whether paths were missing from the model. Following recommendations from Grace, Scheiner & Schoolmaster (2015), we added paths that were suggested by Shipley's test because a biologically plausible connection between variables existed in each case based on our knowledge of the system. To obtain a parsimonious model and fulfil the requirement that the ratio of sample size (in our case, 210) to the number of estimated paths is greater than five (Grace, Scheiner & Schoolmaster 2015), we removed non-significant two-way interactions and used AIC comparison to prune the SEM of non-significant paths. The magnitude of an indirect effect from A to C through B in a SEM is obtained by multiplying the direct path coefficients of A on B and B on C. We thus obtained the indirect plant-mediated effects of precipitation on each faunal group by summing all indirect effects from precipitation through plant biomass.

To better interpret the significant modifying effects of precipitation on interaction paths (i.e. two-way interactions between precipitation and predictor variables), we examined the relationship between annual growing-season precipitation and SEM path coefficients each year retrieved from a multi-group SEM with year as the grouping variable using the program Amos 22.0.0 (Arbuckle 2006). Precipitation was removed in the multi-group SEM because all plots received the same rainfall within each year. Using bootstrapping procedure (2000 bootstrap samples), we estimated the 95% bias-corrected confidence intervals (BCI) for the standardized coefficient of each path. Next, we tested for an effect of precipitation on the standardized coefficient of each path using separate linear models and *F*-tests with Type-III univariate analysis of variance using the R package *car* (Fox & Weisberg 2011). Models were weighted using 1/range(BCI) to account for differences in precision among the estimated standardized path coefficients.

Results

In total, our surveys on 30 plots during a 7-year period recorded 28 428 captures of 6963 individual kangaroo rats, 3814 captures of 1037 individual squirrels, 2377 lizard sightings, and captures of 108 680 ants, 60 722 beetles and 14 452 orthopterans in pitfall traps. Our final SEM adequately fit the data (*Fisher's C* = 19.55, $P = 0.812$); a $P > 0.05$ indicates no significant lack-of-fit between model and data). Compared to the hypothesized initial SEM (*Fisher's C* = 241.21, $P < 0.001$), 11 path additions were required and revealed the importance of local conditions for the faunal community (Fig. 2). Three non-significant modifying effects of precipitation were deleted ('Precip × Plant biomass' from the Krats, Beetles and Squirrels models) and one main effect that was not supported by the data was removed (the effect of precipitation on ants).

Precipitation had significant direct effects on six of the seven biotic components in the community. As expected, there was a strong positive effect of precipitation on plant biomass (standardized path coefficient, 0.57). Precipitation also had significant direct effects on higher trophic levels (Fig. 2), with positive effects on orthopterans (0.45), kangaroo rats (0.47) and squirrels (0.33), and negative effects on beetles (−0.04) and lizards (−0.45). Comparison of the direct and indirect, plant-mediated effects of precipitation indicated that direct effects were substantially stronger than indirect effects on all faunal groups except ants and beetles (Table 1).

Of the 25 interaction pathways among the components of our final SEM, there were eight biotic interactions that differed significantly from zero and six significant effects of local conditions (Fig. 2, Appendix S4). Five significant biotic interactions did not vary with precipitation, including positive effects of plant biomass and kangaroo rat density on ant abundance, negative effects of plant biomass and kangaroo rat density on beetle abundance, and positive effect of beetle abundance on lizard abundance. The effect of local conditions on ant abundance did not vary with precipitation, in contrast with other local conditions effects.

Precipitation significantly modified the effects of: (i) ant abundance on squirrel density (while ants main effect was not significant), (ii) beetle abundance on squirrel density, (iii) kangaroo rat density on orthopteran abundance, and (iv) kangaroo rat density on lizard abundance (Figs 2 and 3). Exploratory analyses had identified modifying effects of precipitation on the effect of plant biomass on beetles, kangaroo rats and squirrels (Appendix S3), but these effects were not supported in the final SEM. Overall, a third of interactions among higher trophic levels (four out of 12) varied with precipitation, whereas none of the plant–animal interactions did ($n = 6$). Additionally, precipitation modified the effect of local conditions on plant biomass, beetle abundance, kangaroo rat density, squirrel density and lizard abundance (Figs 2 and 4).

Fig. 2. Precipitation effects on the ecological community estimated by the structural equation model. 'Local conditions' and 'Precipitation' are independent variables while pictures are dependent variables which R^2 values are located on top right corners. Single-headed paths represent direct effects. Black and red arrows represent significant ($P < 0.05$) positive and negative paths among variables, respectively, with their standardized coefficients provided along arrows (also indicated by their width; Appendix S4). Blue squares on arrows indicate paths that varied with precipitation (i.e. corresponding to significant two-way interactions between precipitation and a predictor variable on a response variable). Grey dotted arrows represent non-significant paths (sign is not shown). Correlated errors among the abundance of ants, beetles and orthopterans are not shown for clarity. [Colour figure can be viewed at wileyonlinelibrary.com]
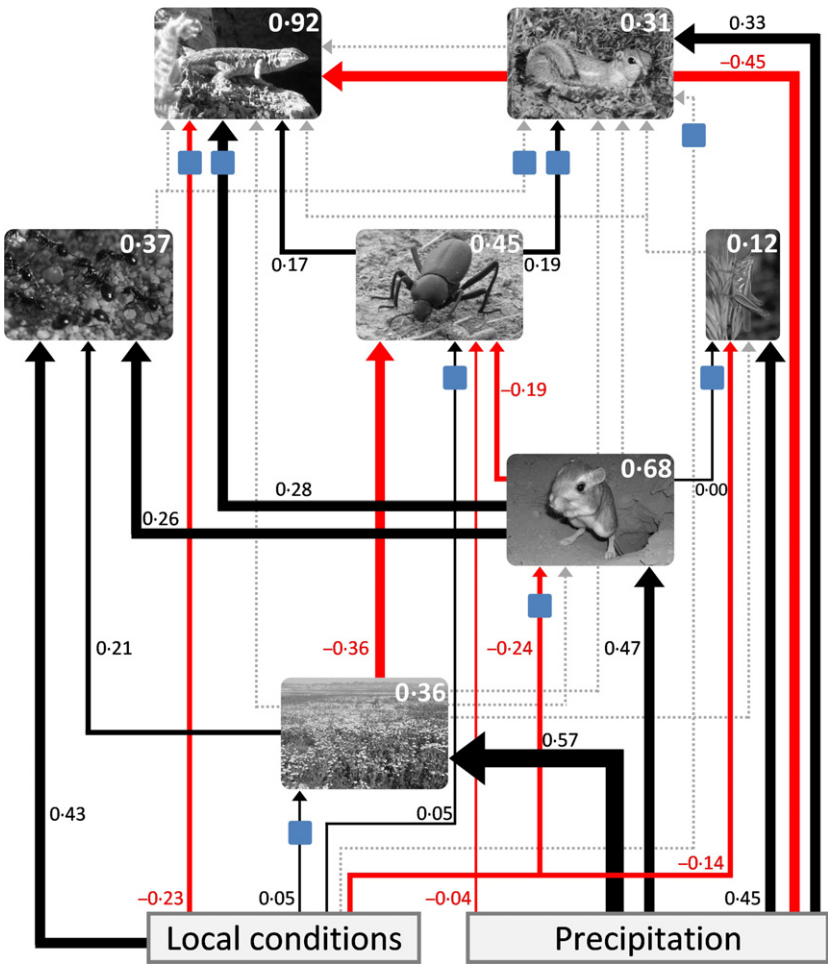
To understand how precipitation modified interactions in the community, we constructed a multi-group SEM with year as the grouping factor, and we examined the relationships between annual growing-season precipitation levels and interaction strengths (i.e. standardized path coefficients) over the 7-year study period. Several strong relationships were found, with increases in precipitation causing positive interactions to become negative or neutral, and vice versa (Fig. 3). We did not detect any cases in which precipitation appeared to increase the strength of a positive or a negative interaction. With increasing precipitation, the relationship between ants and squirrels switched from negative to positive (Fig. 3a), whereas the opposite pattern was found between beetles and squirrels (Fig. 3b). With higher precipitation, the effect of kangaroo rats on orthopterans tended to change from neutral to positive (Fig. 3c). Finally, the strong positive effect of kangaroo rats on lizards weakened to neutral with increasing precipitation (Fig. 3d). Two out of four relationships tested were not significant (Fig. 3). Although these discrepancies suggest caution, results from these regressions had low statistical power due to the small number of observations ($n = 7$ years).

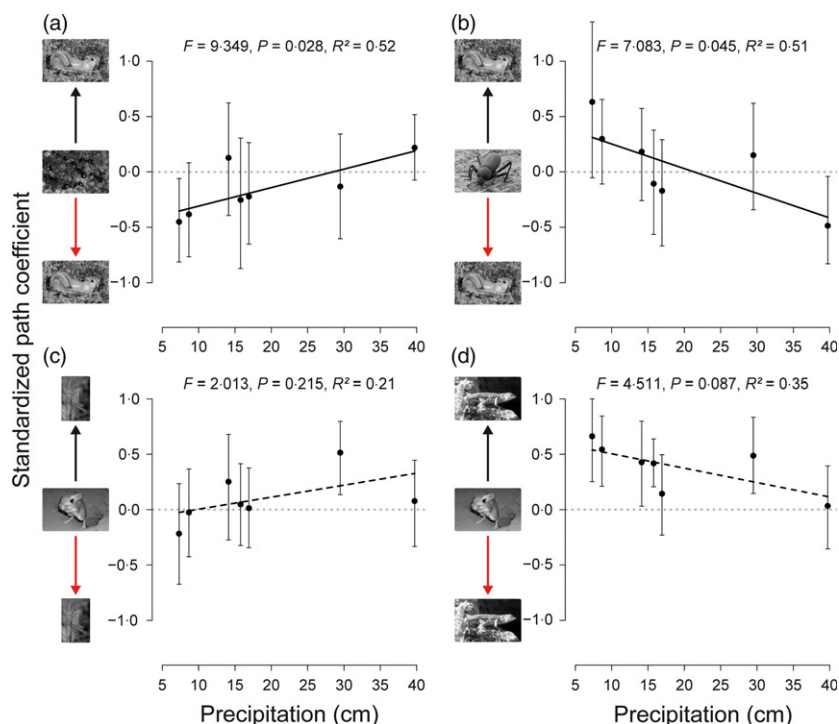Precipitation modified the effect of local conditions on five of six biotic components, indicating that spatial

Table 1. Direct and indirect standardized effects of precipitation on the ecological community

Response	Precipitation effect (standardized estimates)	
	Direct	Indirect, plant mediated
Plant biomass	0·57	–
Kangaroo rat density	0·47	0·04
Ant abundance	–	0·13
Beetle abundance	−0·04	−0·21
Orthopteran abundance	0·45	0·01
Squirrel density	0·33	−0·03
Lizard abundance	−0·45	0·03

differences in abundance reversed (plant and beetles; Fig. 4a and b), weakened (kangaroo rats and lizards; Fig. 4c and e), or arose (squirrels; Fig. 4d) as precipitation changed. Three of the five regressions were not significant, again possibly due to low statistical power.

Discussion

We jointly monitored multiple trophic levels in a semi-arid grassland ecosystem for 7 years, and our results
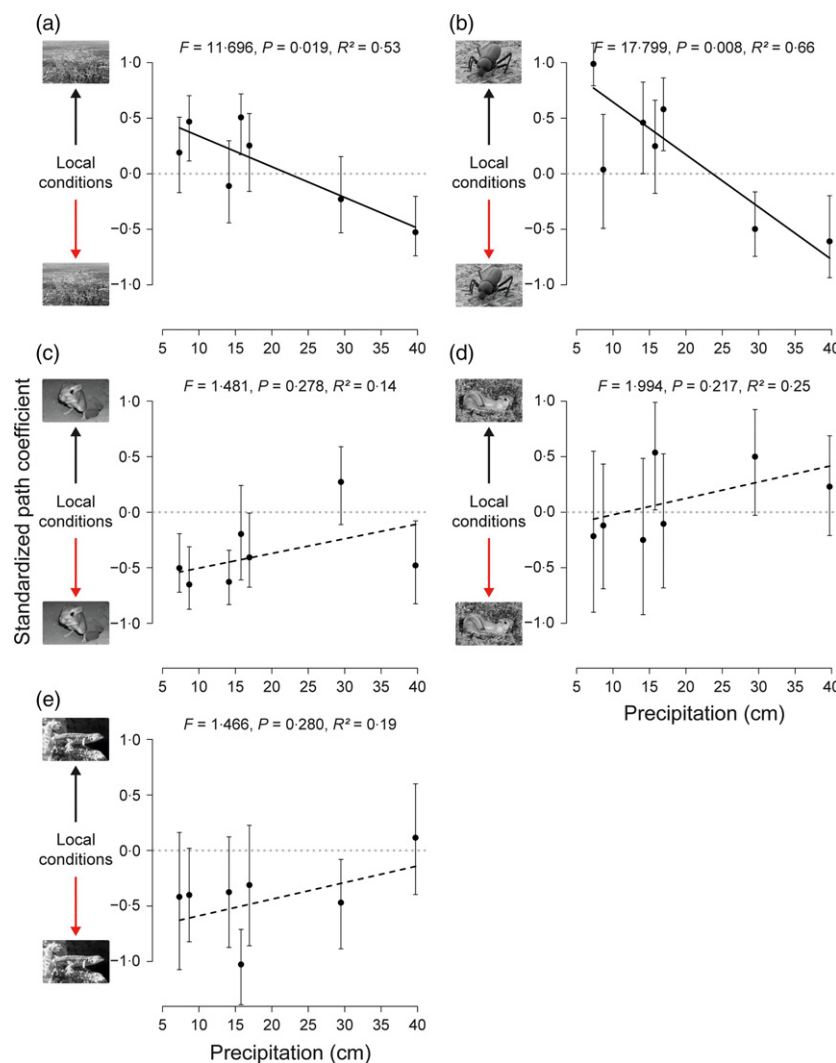
Fig. 3. Biotic interactions modified by precipitation. Panels show the effect of precipitation on the standardized path coefficient of interactions between (a) ant abundance and San Joaquin antelope squirrel density, (b) beetle abundance and San Joaquin antelope squirrel density, (c) giant kangaroo rat density and orthopteran abundance, and (d) giant kangaroo rat density and common side-blotched lizard abundance. The four biotic interactions were found to be significantly modified by precipitation in the SEM analysis (Fig. 2). In each panel, black dots are standardized coefficients estimated with the multi-group analysis in Amos 22.0.0 (Arbuckle 2006) and bars indicate the 95% bias-corrected confidence intervals. Black lines are estimates from weighted linear regressions; solid or dashed regression lines correspond, respectively, to significant or non-significant effects of precipitation on the path coefficients. F, P and R^2 values are provided at the top of each panel. [Colour figure can be viewed at wileyonlinelibrary.com]

highlight pervasive effects of precipitation on the ecological community. Precipitation had strong direct effects not only on plant productivity but also on higher trophic levels. Additionally, precipitation modified several biotic interactions as well as effects of local conditions on the abundance of organisms, illustrating the multiple pathways for precipitation to influence the dynamics of a grassland ecological community.

A variety of biotic interactions within this semi-arid grassland affect community dynamics, including facilitative, consumptive and competitive interactions. Most notably, we found a positive effect of kangaroo rats on ants, grasshoppers and lizards, supporting emerging research highlighting the importance of facilitation in structuring communities, particularly in stressful systems (Bruno, Stachowicz & Bertness 2003). This facilitation was most likely due to the creation of extensive burrow systems which are used by other species as refuges from heat and predators. However, the negative effect of kangaroo rats on beetles may have been due to competition, because most beetles in our system were granivorous (Appendix S1). Although previous findings in the area indicated that ground squirrels benefited from kangaroo rat burrows in some years (Prugh & Brashares 2012), our analysis over a longer time period did not find strong positive or negative interactions.

Competition for food may have cancelled out the benefits of providing burrow refuges for squirrels, and the opposite diel activity patterns of these rodents may have reduced direct interference.

Precipitation directly affected both plant biomass and animal abundances. As expected, the effect on plant productivity was strongly positive. Also in agreement with our expectation, the effects of precipitation on ants and beetles were indirect rather than direct. However, in contrast with our expectation that precipitation would affect higher trophic levels primarily through plant-mediated effects, precipitation had stronger direct than indirect effects on four of the six faunal groups. Although native fauna in dryland ecosystems often have specialized adaptations to conserve water, these results emphasize that water availability may be an important driver of population dynamics for many invertebrates and vertebrates, in agreement with recent work (Allen *et al.* 2013). We found a strong direct effect of precipitation on orthopterans, which may experience high water loss because of their relatively high body mass (average weight per capita in our data: 0·22 g; 0·005 g for ants and 0·16 g for beetles) or reliance on flight (Cloudsley-Thompson 1991; Addo-Bediako, Chown & Gaston 2001). The negative effect of precipitation on side-blotched lizards suggests that high

Fig. 4. Effects of local conditions modified by precipitation. Panels show the effect of precipitation on the standardized path coefficient of the effect of local conditions on (a) plant biomass, (b) beetle abundance, (c) giant kangaroo rat density, (d) San Joaquin antelope squirrel density and (e) common side-blotched lizard abundance. A positive effect of 'Local conditions' indicates that the response variable was higher in Swain (sandier soils with lower nutrient content, longer time since last grazed or cultivated) than in Center Well plots. These local conditions effects were found to be significantly modified by precipitation in the SEM analysis (Fig. 2). In each panel, black dots are standardized coefficients estimated with the multi-group analysis in Amos 22.0.0 (Arbuckle 2006) and bars indicate the 95% bias-corrected confidence intervals. Black lines are estimates from weighted linear regressions; solid or dashed regression lines correspond, respectively, to significant or non-significant effects of precipitation on the path coefficients. F, P and R^2 values are provided at the top of each panel. [Colour figure can be viewed at wileyonlinelibrary.com]

moisture conditions may be directly detrimental to this small-bodied species by shifting conditions away from optimal environmental parameters for nesting and hatching success (Warner & Andrews 2002). However, larger lizard species may be more sensitive to plant-mediated effects of precipitation, because the resultant dense vegetation can impede their movements and predator evasion (Germano, Rathbun & Saslaw 2001).

Most importantly, we found that a major effect of precipitation was to modify biotic interactions in our study system. Our results suggest that interactions among higher trophic levels may be particularly sensitive to precipitation given that no plant–animal interactions were modified. Our study shows that not only the strength but the sign of biotic interactions may change over time with precipitation, supporting Poisot, Stouffer & Gravel's (2015) caution against the common assumption that species interactions are "an immutable 'property' of a species pair." For example, ants' and beetles' interactions with squirrels shifted in opposite directions with fluctuations in precipitation. We suggest this pattern arose from opposite indirect effects of precipitation on the abundance of ants

(positive) and beetles (negative), leading to squirrels opportunistically adapting their diet according to prey availability (Best *et al.* 1990), relying on beetles in drier years and ants in wetter years. Our results also revealed that the expected facilitative effect of kangaroo rats on lizards weakened with increased precipitation, which may indicate that the lizards' use of kangaroo rat burrows for shelter may be hampered at high kangaroo rat densities, illustrating a shift from commensalism to neutralism. Overall, we detected that almost a quarter of the interactions in the ecological community fluctuated with precipitation. These interactions shifted in sign or alternated between neutral and positive as precipitation increased. Although environmental stochasticity is often viewed as a mechanism reducing stability at the population level (Foley 1994), our results suggest it may instead promote stability at the community level by buffering the strength of biotic interactions (Berlow 1999; O'Gorman & Emmerson 2009). By weakening the average strength of species interactions over time, stochastic fluctuations in abiotic factors may thus be an important mechanism facilitating species coexistence.

Mean precipitation levels are predicted to decrease, whereas variability is predicted to increase in many areas world-wide (IPCC 2014). Our results indicate that changes in mean precipitation levels could lead to stronger and less variable interactions over time, potentially contributing to ecosystem instability and state-shifts. However, climatic variability could counteract this effect and increase ecosystem stability. Two mechanisms involving variable outcomes of competition among species, the storage effect and relative nonlinearity, may complementarily promote species coexistence in fluctuating environments (Yuan & Chesson 2015). Here, we show that fluctuations in an abiotic factor may modify the outcome of trophic and facilitative interactions across an ecological community. Variability in species interactions (i.e. non-monotonicity, Zhang *et al.* 2015) may thus be an important yet previously overlooked mechanism that can promote ecosystem stability in response to climate variability. Models predicting the effects of future precipitation regimes on ecosystems thus need to account for the role of biotic interactions in ecosystem responses (Lavergne *et al.* 2010). McCluney *et al.* (2012) proposed a model considering how plant–herbivore and predator–prey interactions might shift with changes in the mean and the variability in precipitation. In our study, we differentiated invertebrates into ants, beetles and orthopterans and found they had different roles in our ecological community. Our findings therefore suggest that models of community dynamics may need to differentiate among groups of organisms within trophic guilds, stressing the need to examine traits that may be relevant for anticipating interaction responses to climate fluctuations.

While our two study sites were close to each other and similar in many respects (e.g. vegetation, topography), their differences ('local conditions') had strong effects on higher trophic levels. Ants in particular benefited more from local conditions in the Swain site than from plant productivity, in agreement with a study from Boulton, Davies & Ward (2005) finding that ant abundance was higher in sandier soils and depended more on soil than plant attributes. However, preliminary models including soil properties in place of site identity did not adequately fit the data, indicating other site-specific differences such as land-use history may have also been important. The Swain site has received less cattle grazing and may not have been cultivated as recently as the Center Well site, but precise histories of these areas are unfortunately lacking. Additionally, variations in precipitation yielded shifts in spatial differences in populations of beetles, kangaroo rats, squirrels and lizards, suggesting that fluctuations in climate can modify habitat suitability on a local scale. Different soil types and history of cultivation and grazing could affect soil compaction and thus water infiltration rate and soil moisture (Hamza & Anderson 2005). Soil moisture in turn affects numerous properties such as plant productivity and composition, burrowing ability or invertebrate and lizard development. Thus, local-scale variation in soil conditions can have surprisingly pervasive effects on community dynamics.

We acknowledge that our observational approach bids caution in interpreting causality from our SEM. It was not feasible to manipulate rainfall at a scale relevant to the vertebrate fauna included in our analyses (2 ha) and we thus cannot rule out confounding effects from covarying factors such as temperature. However, although averages of daily mean temperature during the growing season were negatively correlated with precipitation among years ($r = -0.78$, $P = 0.04$, $n = 7$), temperature varied little during our study (range: 11·2–12·5 °C). Conversely, the large fluctuations in growing-season precipitation were expected to strongly affect plant biomass as rainfall is the most limiting abiotic factor of vegetation in arid areas (Noy-Meir 1973; Knapp, Briggs & Koelliker 2001). Results from our SEM are in strong agreement with this expectation – plant biomass was greatly enhanced by precipitation – and with work showing that nutrient limitation occurs once water limitations are alleviated (Fig. 4a shows that local conditions with sandier soils and lower nutrient content had lower plant productivity at high precipitation level; Yahdjian, Gherardi & Sala 2011), further supporting a precipitation effect. Thus, our study measured how an ecological community responded to natural variation in its most limiting factor, thereby improving our understanding of how climate change might impact the dynamics of ecological communities. Future studies with more extensive data sets could examine multiple abiotic drivers.

Similarly, an ideal SEM would investigate the possibility that population responses to changes in their resources may be delayed, that is, display a time-lag. Inclusion of time-lags would have made our SEM substantially more complex and would thus have required a larger sample size. If lag effects are strong, failure to account for them could result in failing to detect an important interaction. For example, the lack of a significant effect of plant biomass on orthopteran abundance in our SEM counter-intuitively suggested that orthopterans did not respond to variation in their primary food resource. However, complementary analyses revealed that orthopterans responded to plant biomass with a 1-year lag, and so did the relationship between ants and lizards (Appendix S5). Other interactions in the community may occur both without and with a time-lag, but we found no indication that the dynamics of the biotic components were exclusively lagged. Overall, modelling potential lag effects in this community-level study would have brought limited further insights at a high statistical cost, as most R^2 values and the overall statistics associated with our final SEM indicated an adequate description of our system.

Understanding how climate change impacts natural systems is a major ongoing challenge for ecologists (Lavergne *et al.* 2010; Bellard *et al.* 2012). Decades of research have documented how changes in mean conditions may result in plant and animal species' shifts in range, phenology or abundance (Parmesan & Yohe 2003),

with effects scaling up to the level of species assemblages (Princé & Zuckerberg 2015). Our ecosystem-wide approach highlights that inter-annual variation in a climatic factor can drive changes in biotic interactions, thus suggesting potential for more complex impacts of climate change than those solely predicted from single-species analyses. Our findings emphasize the need to consider precipitation as an important climatic variable affecting the functioning and stability of ecological communities.

Authors' contributions

N.D. and L.R.P. defined the objectives of the study. N.D. analysed the data. N.D., L.R.P. and J.S.B. wrote the manuscript. J.S.B. and L.R.P. started the Carrizo Plain Ecosystem research project and collected data.

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Data accessibility

The data and associated script running our analyses are available from the Dryad Digital Repository http://dx.doi.org/10.5061/dryad.pb4p1 (Deguines, Brashares & Prugh 2016).

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Supporting Information

Details of electronic Supporting Information are provided below.

Appendix S1. Taxonomic and feeding group information of sampled arthropods.

Appendix S2. Examination of grazing effects in the Carrizo Plain ecological community.

Appendix S3. Results of the preliminary mixed-effects modelling analysis.

Appendix S4. Raw and standardized path coefficients and unresolved correlations in the final SEM.

Appendix S5. Investigation of potential lag effects in the Carrizo Plain ecological community.