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Do competitors modulate rare plant response to precipitation change?

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Abstract. Ecologists increasingly suspect that climate change will directly impact species physiology, demography, and phenology, but also indirectly affect these measures via changes to the surrounding community. Unfortunately, few studies examine both the direct and indirect pathways of impact. Doing so is important because altered competitive pressures can reduce or magnify the direct responses of a focal species to climate change. Here, we examine the effects of changing rainfall on three rare annual plant species in the presence and absence of competition on the California Channel Islands. We used rain-out shelters and hand watering to exclude and augment early, late, and season-long rainfall, spanning the wide range of precipitation change forecast for the region. In the absence of competition, droughts reduced the population growth rates of two of three focal annuals, while increased rainfall was only sometimes beneficial. As compared to the focal species, the dominant competitors were more sensitive to the precipitation treatments, benefiting from increased season-long precipitation and harmed by droughts. Importantly, the response of two of three competitors to the precipitation treatments tended to be positively correlated with those of the focal annuals. Although this leads to the expectation that increased competition will counter the direct benefits of favorable conditions, such indirect effects of precipitation change proved weak to nonexistent in our experiment. Competitors had little influence on the precipitation response of two focal species, due to their low sensitivity to competition and highly variable precipitation responses. Competition did affect how our third focal species responded to precipitation change, but this effect only approached significance, and whether it truly resulted from competitor response to precipitation change was unclear. Our work suggests that even when competitors respond to climate change, these responses may have little effect on the focal species. Ultimately, the strength of the indirect effect depends on how strongly climate change alters competition, and how sensitive focal species are to changes in competition.

Key words: annual plant population; Bromus diandrus; *California Channel Islands; climate change; competition;* Gilia tenuiflora *ssp*. hoffmannii; Lasthenia californica; Malacothrix indecora; Phacelia insularis *var*. insularis; *precipitation*.

Introduction

The impacts of climate change on plant species arise via two primary pathways. Altered climatic conditions can directly affect species' physiological functioning, phenology, and demographic rates (Fig. 1, arrow A; de Valpine and Harte 2001, Root et al. 2003, Weltzin et al. 2003, Zavaleta et al. 2003, Thomas et al. 2004, Cleland et al. 2007). Climate change can also indirectly affect focal species via its influence on the surrounding community of competitors, predators, mutualists, and pathogens (Fig. 1, pathway through arrows B and C; Ives 1995, Davis et al. 1998, Walther et al. 2002, Schmitz et al. 2003, Visser and Both 2005, Buckley and Roughgarden 2006, Suttle et al. 2007, Adler and HilleRisLambers 2008, Tylianakis et al. 2008). Unfortunately, we are only beginning to understand how climate change alters species interactions (Dormann et al. 2004, Klanderud 2005, Tylianakis et al. 2008), and this adds considerable uncertainty to ecological forecasts (Schmitz et al. 2003).

For example, "bioclimatic models" use climate variables associated with species' current ranges to project their future distributions under climate change scenarios (Pearson and Dawson 2003). The accuracy of this approach, with no explicit consideration of competitors, at least partly depends on the role of competition in setting range limits and how that role might change in the future (Davis et al. 1998, Pearson and Dawson 2003, Schmitz et al. 2003). Will species face different competitors in their current or new habitats? Will their current competitors become more or less abundant? Answering these questions is particularly important as recent work suggests that changes to competitor communities can reverse species' direct responses to climate change (Suttle et al. 2007).

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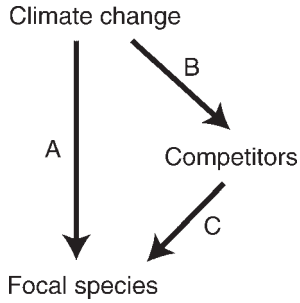

FIG. 1. Climate change can affect focal species through direct effects on physiology, demography, and phenology (arrow A), and indirectly via impacts on competitors (arrow B) that negatively influence the focal species (arrow C).

The indirect effect of climate change (Fig. 1, pathway through arrows B and C), mediated by the surrounding community of competitors, can either counter or augment species' direct responses to altered climate conditions (Fig. 1, arrow A). As explained by Ives (1995), which of these outcomes emerges depends on species differences in their direct physiological or demographic response to environmental change (Fig. 1, arrow A vs. B). When a focal species and its surrounding competitors are similarly favored or harmed by climate change, a change in competitive pressures could oppose the direct physiological effects of changing climate. For example, a focal species harmed by future environmental conditions may indirectly benefit from decreased competition by similarly responding neighbors. By contrast, when climate change has opposing effects on competitors, changes to the surrounding community can magnify the direct effects. A focal species harmed by climate change will be even further harmed if its competitors benefit from new conditions. Last, even if climate change impacts the community surrounding a focal species, this need not translate into strong indirect effects. Focal species may simply be insensitive to the increase or decrease in competition induced by a changing climate.

Although ecologists increasingly expect that plant species' responses to climate change will depend on the response of the surrounding community (Ives 1995, Davis et al. 1998, Walther et al. 2002, Schmitz et al. 2003, Buckley and Roughgarden 2006, Adler and HilleRisLambers 2008, Tylianakis et al. 2008), few global change experiments have directly quantified the influence of surrounding competitors on the response of focal species (Dormann et al. 2004, Klanderud 2005). Here, we examine the effects of experimentally altered precipitation regimes on three rare annual plant species in the presence and absence of competitors on the California Channel Islands.

Rare island plants provide ideal test cases to examine the interaction between competition and climate in controlling future abundances for several reasons. First, these species are particularly threatened by climate change because their narrow geographic ranges are unlikely to overlap the more favorable habitats of the future (Walther et al. 2002, Thomas et al. 2004, Loarie et al. 2008). Isolation and restricted dispersal will prevent rare island plants from reaching more favorable habitats, and thus their persistence often depends on how they respond to climate change in their current locations. Because rare plants are already environmentally constrained, they may be a precursor of climate change impacts. Second, these species are often locally sparse and surrounded by competitors. Thus, how rare plants respond to climate change is likely tied to the response of their competitors. Third, because our focal species are annuals, with short and relatively simple life cycles, we can examine the impact of climate change on population growth rate, the key predictor of species persistence.

Changing precipitation is expected to be a major driver of climate change impacts on plant communities in California (Pope et al. 2000, Bell et al. 2004, Hayhoe et al. 2004, Salinger 2005, Cayan et al. 2006, Dukes and Shaw 2007). Both the quantity and timing of precipitation are leading controls over plant composition, productivity, and phenology in the region (Heady 1958, Pitt and Heady 1978, Young et al. 1981, Zavaleta et al. 2003, Hobbs et al. 2007). The mediterranean climate is expected to hold over this century, so winters should remain cool and wet, and summers warm and dry (Cayan et al. 2006, Dukes and Shaw 2007). Total annual precipitation forecasts at the state level are variable, ranging from a 157 mm decrease to a 38 mm increase (Pope et al. 2000, Bell et al. 2004, Hayhoe et al. 2004, Salinger 2005, Cayan et al. 2006, Dukes and Shaw 2007), with additional uncertainty about when the rain will fall. Because of the lack of concordance among projections for California's future climate, we examined the response of three rare and endangered annual plant species, each existing in a different competitive environment, to a range of possible rainfall scenarios. By manipulating early, late, and season-long precipitation, we could ask which changes to the rainfall regime would be most damaging or beneficial to the focal species.

By examining the response of the rare annuals to rainfall in the presence and absence of surrounding competitors, we evaluated how altered precipitation directly (Fig. 1, arrow A) and indirectly influences the focal species (Fig. 1, pathways through arrows B and C). To quantify the direct effect, we examined rare annual response in the absence of competition. To quantify the indirect effect, we asked: How does altered precipitation influence the competitive environment (Fig. 1, arrow B)? And how sensitive are the focal species to the variation in competition driven by precipitation change (Fig. 1, Arrow C)? To predict whether the indirect effect should counter or augment species direct responses to altered climate conditions, we quantified the similarity in responses of the focal species and their competitors to precipitation change (Fig. 1, arrow A vs. B).

Methods

Study system

We conducted our study on Santa Rosa Island, roughly 40 km off the coast of Santa Barbara, California, USA. Nearly all precipitation falls between October and April (Fig. 2A), and averages 32 cm per year. Annual precipitation is considerably variable, exhibiting sixfold variation since the island's weather station was deployed in 1991 (Levine et al. 2008). The current study extended over two growing seasons: fall 2003 to spring 2004, a year with somewhat below-average precipitation (26 cm); and fall 2004 to spring 2005, an El Niño year with significantly more rain than average (51 cm). Hereafter, we will refer to rainfall years by the year of the spring.

Our study examined the response of three rare and endangered annual plants, *Gilia tenuiflora* ssp. *hoffmannii*, *Malacothrix indecora*, and *Phacelia insularis* var. *insularis* (hereafter *Gilia*, *Malacothrix*, and *Phacelia*) to precipitation manipulations. All three focal species are endemic to the northern Channel Islands, and federally listed as endangered. All germinate with the first major rains of the fall or winter (>2.5 cm), develop a taproot, and are small statured. With low germination rates and high annual survival of buried seed (Levine et al. 2008), all three annuals develop a seed bank. Flowering peaks in early March, mid April, and early June for *Phacelia*, *Gilia*, and *Malacothrix*, respectively. Past observational work (Levine et al. 2008) shows that populations of all three annuals fluctuate through time in a manner partially correlated with precipitation.

We hypothesized that the effects of changing precipitation on the focal annuals would depend on the response of their competitors. *Gilia* is found on stabilized dune soils, with a mix of annual and perennial plants. *Bromus diandrus*, a European annual grass, is the most common of *Gilia*'s competitors. It and other competing species only sum to about 60% absolute cover (Levine et al. 2008), likely due to the shifting sands of their habitat. *Malacothrix* is found in somewhat denser vegetation on the sandy, eroding terraces of the north side of the island. The competitor community is dominated by the native annual *Lasthenia californica* and two native perennial grasses. *Phacelia* is found in the most vegetated landscape of the three focal annuals. It occurs on stabilized dune headlands in small clearings within an otherwise dense cover of *Bromus diandrus*.

In our experiments, we examined the response of our focal species to altered precipitation in the presence and absence of the entire competitor community. Additionally, to examine the response of the competitors to precipitation change, we focused attention on the most abundant annual competitor at each site, because changes in that species' abundance were most likely to affect the focal species. *Bromus* and *Lasthenia* were the most abundant annual competitors in the *Phacelia* and *Malacothrix* habitats, respectively. *Bromus* was also the most abundant competitor in the *Gilia* habitat, though it and other competitors were relatively sparse.

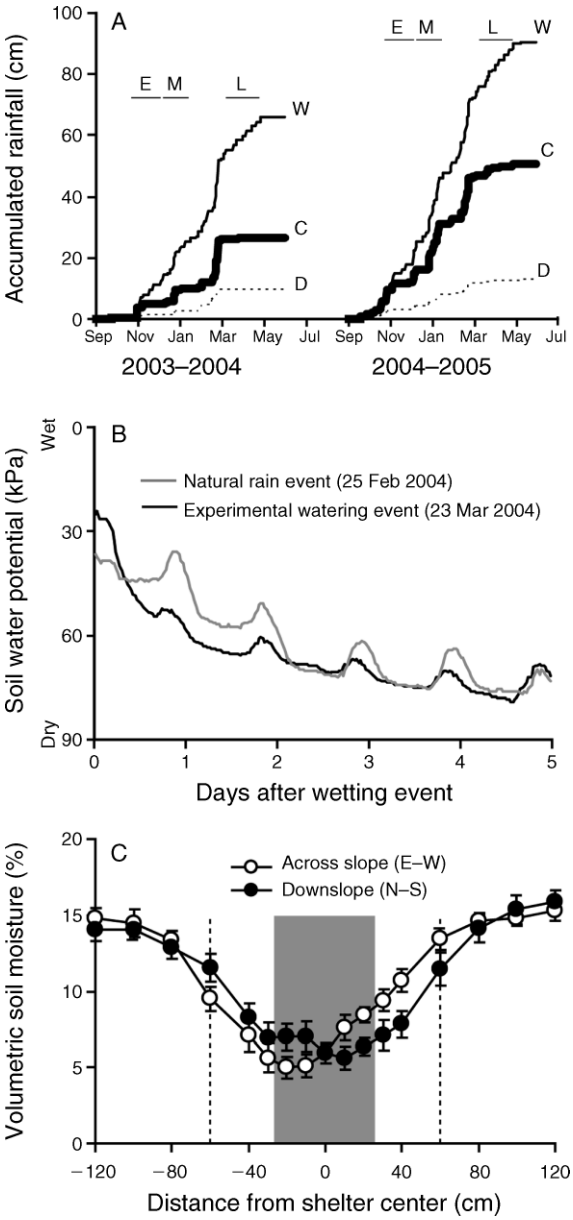

FIG. 2. (A) Water received by plots in control (C), drought (D), and watered (W) treatments in the two growing seasons of this study. The bars labeled E, M, and L above the accumulation lines indicate the time period over which the early-, mid-, and late-season climate manipulations were imposed. (B) Soil water potential following natural and experimentally imposed rain events of similar magnitude at the *Phacelia insularis* var. *insularis* site in spring 2004. (C) Soil moisture as a function of location under eight replicate drought shelters at the *Phacelia* site in spring. The shaded region indicates the area under the shelter in which we examined our focal species and their competitors. The dashed lines indicate the edge of the shelter. Points show means ± SE.

Precipitation manipulations

We conducted our precipitation manipulations at three field sites, each adjacent to a population of one of our focal annuals. Our goal in selecting these sites was to match the physical conditions of the habitat of each species without disturbing existing populations or including a preexisting seed bank.

At the *Gilia* and *Malacothrix* sites, we located 64 60 × 60 cm plots at 2.5-m intervals along transects. Eight plots were randomly assigned to each of the rainfall treatments: (1) early drought, (2) mid-season drought, (3) late drought, (4) season-long drought, (5) early water addition, (6) late water addition, (7) season-long water addition, and (8) control. Early treatments (1 and 5) were imposed from first rainfall until mid-December. We imposed the mid-season drought from mid-December through mid-January. Late treatments (3 and 6) were imposed from March through April. While early- and late-season manipulations potentially alter the length of the growing season, mid-season droughts may disrupt the growing season after germination (Pitt and Heady 1978). Due to limited *Phacelia* seed, we used six rather than eight replicate plots and excluded the mid-season drought for this species.

We used fixed rain-out shelters to decrease precipitation over the period designated in treatments 1–4. We based our design on Yahdjian and Sala (2002), and constructed the shelters to be 1.25 m on a side. The shelter frame was constructed of welded aluminum square tubing with 30 and 50 cm legs at the low and high ends, respectively, yielding a roughly 10% slope when placed on level ground. Using the same materials as Bates et al. (2006), we attached clear (95% transmittance) polycarbonate gutters cut from corrugated roofing (Dynaglas; Palram Americas, Kutztown, Pennsylvania, USA) to the top of the frame, and spaced the individual gutters to intercept 75% of incoming rainfall. In 2004, such interception would have lead to an extremely dry season-long drought treatment. We thus added an additional 3 cm of water spread over two bouts, more closely matching the 2002 drought (12 cm). In 2005, a wetter year, this supplementation was not necessary.

Shelters were oriented so their incline faced the direction of prevailing winds during storm events, and permanently fixed over the 60 × 60 cm plots assigned to drought treatments. This left a 35-cm buffer between the edge of the shelter and the edge of our plot (including a 5-cm plot buffer in which no measurements were made). As is common with this method (Lucas et al. 2008), the rainout shelters insulated the plots to some extent, reducing daily maximum temperatures at the soil surface. However, the windy conditions on Santa Rosa Island, combined with the gaps between the gutters minimized this artifact.

To simulate increased rainfall in treatments 5–7, we hand-watered 1.5 cm every 4–10 days (averaging once per week) over the seasonal period designated by the treatment. Specifically, we used a watering can to distribute the water over a 70 × 70 cm area. By rotating among the replicate plots, we spread watering over three or more hours. We logged soil water potential through time with Watermark sensors (Spectrum technologies, Plainfield, Illinois, USA) in shelter, water addition, and control treatments, and took spatial measurements of volumetric soil moisture with time domain reflectometry (TDR).

Plot design

Each 60 × 60 cm plot was split into four subplots. Two subplots were used to examine the precipitation response of the focal species in the presence and absence of competitors, while a third was used to asses the response of its principal competitor. The fourth subplot was unmanipulated. In early fall 2003, we seeded the central 15 × 15 cm area within two of the subplots with seed of the focal species for the site. In summer 2004, the location of all of the plots and their accompanying climate manipulations were shifted along the transect to be non-overlapping. This ensured that seed did not carry over between the 2004 and 2005 experiments. The amount of seed added to each subplot varied across year and species. Although we aimed for 100 seeds per subplot, we were limited by seed production the prior spring. Therefore, in the 2004 and 2005 experiments, we sowed the subplots with 20 and 40 seeds respectively of *Phacelia*; 100 and 50 seeds respectively of *Malacothrix*, and 100 and 200 seeds respectively of *Gilia*. Germination rates and plant size were low enough in all years that interaction among the seeded individuals was minimal.

For each plot, we cleared competing vegetation from one of the two subplots planted with the focal species. We clipped the competitors at ground level early in the season, which usually killed the annuals. Clipped plots were also cleared of all perennial vegetation and litter prior to seed sowing. Regrowth was minimal, and clipping was repeated when necessary, except for *Gilia* plots in 2005 when high rainfall reduced site access after the early-season clipping. Although competitive effects on *Gilia* were underestimated in 2005, similar effects were found in 2004. Because we could not work within the focal populations directly, the experimental sites for *Malacothrix* and *Phacelia* contained denser background vegetation than their habitat. We thus thinned the uncleared subplots at these sites by about half so they would better match the natural habitat.

In each year, we used a third subplot to evaluate how the dominant competitor of each focal species responded to precipitation manipulation. In the *Phacelia* experiment, we harvested the biomass of *Bromus diandrus* in a 100-cm^2 area of an unseeded subplot. The biomass was then dried and weighed. In the *Malacothrix* experiment, we measured the percent cover in 2004 and biomass in 2005 of *Lasthenia californica* within an unseeded subplot. Naturally occurring *Bromus* is sufficiently sparse at the *Gilia* site that it was not always present

in our subplots. Thus, in the *Gilia* experiment, we harvested the biomass of *Bromus diandrus* from 20 seeds sown in each year into an otherwise unmanipulated subplot.

Estimating population growth rates of the focal species

We parameterized an annual plant population model to estimate per capita population growth rates under the experimentally imposed precipitation regimes. Mathematical models describing the dynamics of annual plant populations are well-developed (Watkinson 1980, Pacala 1986, Levine and Rees 2004) and provide a reasonable approximation of the annual life cycle. Per capita population growth from one year to the next (λ), including both above and belowground processes, can be described as follows:

$$\lambda = s(1 - g) + gV \quad (1)$$

where g is the fraction of germinating seeds, s is the annual survival of ungerminated seeds in the soil, and V is the number of viable seeds produced per germinant. Our projected growth rates are modeled with the assumptions of a closed population and seed vital rates that are independent of age. As long as these assumptions are not differently violated among treatments (and we have no reason to believe they would be), the relative value of the growth rates across treatments should remain informative for assessing species response to precipitation change.

We measured germination fractions (g) and the seeds produced per germinant (V) in each subplot in the experiment. Seed bank survival fractions (s) for *Gilia*, *Malacothrix*, and *Phacelia* were 75%, 57%, and 57%, respectively (from Levine et al. 2008), and assumed to be independent of the treatments. In each plot, we measured germination by placing a toothpick near each plant observed in multiple censuses beginning after the first major rains. To estimate the germination rate, the number of germinants was divided by the total number of seeds added, discounted by their viability (98%, 84%, and 90% for *Gilia*, *Malacothrix*, and *Phacelia*, respectively, from Levine et al. 2008). In the spring we measured the total number of flowers produced by the focal species in each subplot. This number was divided by the number of germinants to yield flowers or heads per germinant. To yield the seeds per germinant, this latter number was multiplied by the number of seeds per flower (23.3, 28.3, or 8.0 for *Gilia*, *Malacothrix*, and *Phacelia*, respectively, as determined in Levine et al. 2008).

Statistical analyses

We statistically evaluated the main and interactive effects of precipitation and competing vegetation on the germination, flowers produced per germinant, and per capita population growth rate of our three focal annuals in each year with a split plot analysis of variance. The effects of precipitation were tested against the whole plot error term, while the effects of vegetation and the precipitation × vegetation interaction term were tested against the plot × vegetation interaction term. Of particular interest was the precipitation × vegetation interaction term, because it quantifies the degree to which the effect of surrounding vegetation changes with the precipitation manipulation, including the indirect effect in Fig. 1. We tested the effect of precipitation on the competitor species with a one way ANOVA. To meet the assumptions of ANOVA, germination data were arcsine root transformed, population growth rates were inverse transformed, and flowers per germinant and *Bromus* biomass were log transformed. Because there was no measurable rain in 2004 over the late drought period, this treatment and the controls received the same season-long rainfall that year. To compensate for low replication ($n = 6$) and low germination in the *Phacelia* experiment, we pooled data from the control and late drought treatment for 2004.

Results

Efficacy of climate manipulations

Season-long water addition more than doubled the water received by plots in 2004 (Fig. 2A). The proportional increase in 2005 was somewhat less because of more ambient rainfall that year. Because we added the water by hand over a several hour period, experimental watering led to somewhat higher initial water availability than a natural storm of the same magnitude and season (Fig. 2B). Still these differences are within the natural variation of storm events, and soil water potential was comparable two and a half days after the natural and experimental events (Fig. 2B). The drought treatments effectively reduced soil moisture within the plots, and the area used for experimentation within the shelter experienced only marginal edge effects (Fig. 2C).

Species responses to climate and competition

The precipitation treatment significantly influenced the population growth rate of *Gilia*, but only in 2004 (Fig. 3A, B, Table 1). In this year, *Gilia* had its lowest population growth rate in the season-long drought treatment (Fig. 3A), driven by low germination and flowers produced per germinant (Table 1, Appendix: Fig. A1), though precipitation effects on the latter were not significant. Population growth rate in the mid-season drought treatment was almost as low as in the season-long drought, suggesting that mid-season droughts have the greatest influence on *Gilia* demographics. Outside of these drought treatments, *Gilia* proved insensitive to the climate manipulations, and this result was repeated in 2005 (Fig. 3B). Consistent with the relatively low vegetative cover in the *Gilia* habitat (Levine et al. 2008), competition from surrounding vegetation had no significant effect on *Gilia* per capita growth rate in either year (Fig. 3A, B, Table 1).

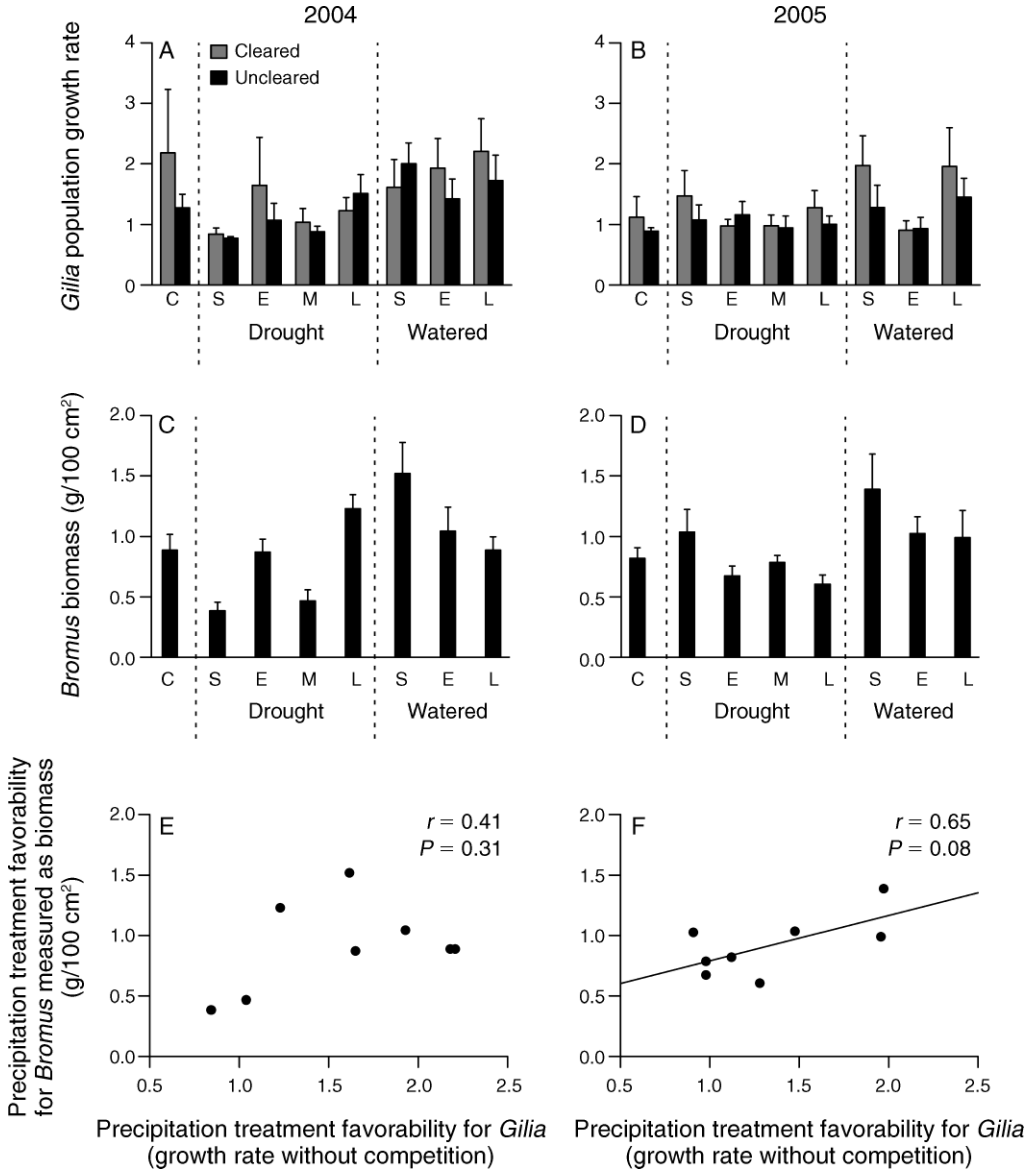

FIG. 3. (A, B) *Gilia tenuiflora* ssp. *hoffmannii* per capita population growth rate as a function of precipitation and competition treatments in 2004 and 2005. The precipitation treatments are control (C), drought, and watered, imposed season-long (S), early season (E), mid-season (M), or late season (L). (C, D) *Bromus diandrus* biomass response to precipitation manipulations at the *Gilia* site in 2004 and 2005. (E, F) Correlation between the favorability of precipitation treatments for *Gilia* and its *Bromus* competitor (measured as biomass) in 2004 and 2005. Bars in panels (A)–(D) show means + SE.

In contrast to *Gilia*, its *Bromus* competitor was sensitive to the precipitation manipulations in both 2004 (Fig. 3C, $F_{7,55} = 7.56$, $P = 0.001$) and 2005 (Fig. 3D, $F_{7,54} = 2.30$, $P = 0.040$). Relative to controls, season-long water addition led to 75% increases in *Bromus* biomass in both years. Meanwhile, drought manipulations reduced its biomass in 2004. Of all the partial year drought treatments that year, those in mid-season had the greatest influence on *Bromus*.

Largely due to *Gilia*'s rather low sensitivity to precipitation, we found only weak ($P = 0.31$ and 0.08) positive correlations between the favorability of the precipitation treatment for *Gilia* (measured as population growth rate) and *Bromus* (measured as biomass; Fig. 3E, F). Combined with *Gilia*'s insensitivity to the sparse competition in all precipitation environments, indirect effects of precipitation on *Gilia* via surrounding competitors were weak to non-existent. This result was supported by a non-significant precipitation × vegetation interaction in Table 1.

Like *Gilia*, *Malacothrix* was somewhat insensitive to the precipitation treatment in 2004 (Fig. 4A, B). In contrast to our expectations, 2005 population growth rates tended to be higher in early and season-long

TABLE 1. Split-plot ANOVA results for the main and interactive effects of precipitation and vegetation removal on demographic rates of the three focal species.

Source of variation	Germination			Flowers per germinant			Population growth rate		
	df	*F*	*P*	df	*F*	*P*	df	*F*	*P*
2004									
Gilia tenuiflora									
Precipitation	7	2.33	0.037	7	0.97	0.471	7	2.63	0.020
Whole-plot error	56			33			56		
Vegetation	1	0.93	0.340	1	0.12	0.729	1	0.01	0.925
Precipitation × vegetation	7	1.15	0.342	7	0.58	0.770	7	0.99	0.451
Plot × vegetation error	56			33			56		
Malacothrix indecora									
Precipitation	7	6.24	0.001	7	0.32	0.942	7	0.44	0.876
Whole-plot error	56			43			56		
Vegetation	1	1.51	0.224	1	14.76	0.001	1	31.98	0.001
Precipitation × vegetation	7	1.43	0.211	7	0.30	0.948	7	0.84	0.559
Plot × vegetation error	56			43			56		
Phacelia insularis									
Precipitation	5	3.52	0.011	5	1.66	0.184	5	2.01	0.101
Whole-plot error	36			23†			36		
Vegetation	1	34.87	0.001	1	5.37	0.030	1	17.65	0.001
Precipitation × vegetation	5	5.99	0.001	4	0.63	0.645	5	2.21	0.075
Plot × vegetation error	36			23†			36		
2005									
Gilia tenuiflora									
Precipitation	7	0.52	0.818	7	0.65	0.710	7	0.92	0.497
Whole-plot error	56			12			56		
Vegetation	1	0.51	0.478	1	0.77	0.397	1	1.62	0.208
Precipitation × vegetation	7	0.73	0.647	7	0.27	0.954	7	0.63	0.727
Plot × vegetation error	56			12			56		
Malacothrix indecora									
Precipitation	7	3.21	0.006	7	4.84	0.001	7	4.07	0.001
Whole-plot error	56			31			56		
Vegetation	1	9.18	0.004	1	4.95	0.033	1	0.23	0.633
Precipitation × vegetation	7	1.65	0.140	7	4.96	0.001	7	1.63	0.147
Plot × vegetation error	56			31			56		

† The error term and *F* statistics for the analysis of *Phacelia* flowers per germinant were calculated assuming a fully randomized design due to low sample size.

drought treatments than controls (Fig. 4B, Table 1), driven by greater seeds produced per germinant (Appendix: Fig. A2). Excluding early rain may have ameliorated the impact of damping off (fungal attack), a phenomenon that we observed to be particularly intense in 2005. High seedling mortality was also related to wooly bear (*Pyrrhactia isabella*) herbivory. Consistent with the high vegetative cover in its habitat, *Malacothrix* population growth was strongly limited by competition in 2004 (Fig. 4A, Table 1). The much weaker 2005 effect likely relates to the heavy but patchy germinant mortality, which minimized the opportunity for competition to reduce growth, and contributed to high among plot variability, reducing statistical power.

The most abundant *Malacothrix* competitor, *Lasthenia* was sensitive to precipitation in both 2004 (Fig. 4C, $F_{7,56} = 3.90$, $P = 0.002$) and 2005 (Fig. 4D, $F_{7,56} = 2.88$, $P = 0.012$). It performed about one third as well in season-long drought vs. control treatments in both years, and increased 50% in season-long watered plots in 2004 (Fig. 4C, D). However, given the insensitivity of *Malacothrix* population growth to precipitation there was no correlation between the favorability of precipitation treatments for it and *Lasthenia* (Fig. 4E, F). Moreover, due to large among plot variation, we found a nonsignificant precipitation × vegetation interaction (Table 1). Statistically, the surrounding community failed to differentially reduce *Malacothrix* population growth rates in different climate treatments.

Phacelia responded most strongly of all focal species to the precipitation regime (Fig. 5A). In 2005, germination was found in only two *Phacelia* subplots experiment-wide, and thus we only present results from 2004. Although the precipitation × vegetation effect on *Phacelia* population growth missed significance ($P = 0.075$, Table 1), growth was very low in uncleared plots, and highly responsive to precipitation in cleared plots. In the absence of competition, *Phacelia*'s per capita population growth rate was almost 10-fold less in season-long drought, and almost three-fold greater in season-long watered treatments, than in control treatments. These changes in per capita growth rate were due largely to precipitation impacts on the flower production per germinant (Appendix: Fig. A3B),

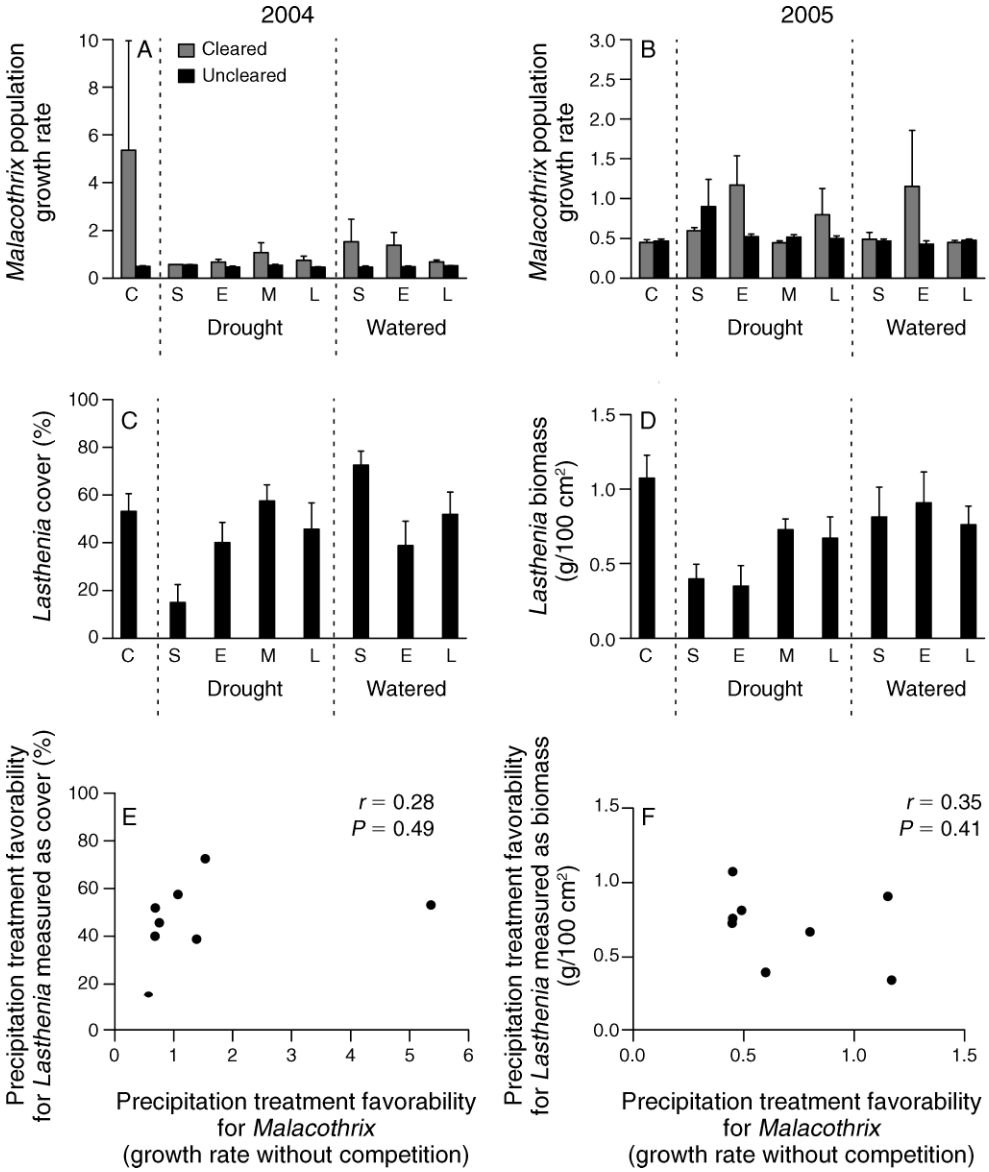

FIG. 4. (A, B) *Malacothrix indecora* per capita population growth rate as a function of precipitation and competition treatments in 2004 and 2005. The precipitation treatments are control (C), drought, and watered, imposed season-long (S), early season (E), mid-season (M), or late season (L). (C) Cover response in 2004 and (D) biomass response in 2005 of *Lasthenia californica* to precipitation manipulations at the *Malacothrix* site. (E, F) Correlation between the favorability of precipitation treatments for *Malacothrix* and its *Lasthenia* competitor in 2004 and 2005. Bars in panels (A)–(D) show means + SE.

though the high per capita growth rate in the early drought treatment related to high germination (Appendix: Fig. A3A; explained in *Discussion*). With exotic grass competition, *Phacelia* had very low population growth rates (Fig. 5A), supported by a significant main effect of competing vegetation on per capita growth rates (Table 1).

Bromus biomass varied considerably with the precipitation regime at the *Phacelia* site (Fig. 5B, $F_{6,35} = 3.64$, $P = 0.007$). Relative to controls, wetter conditions yielded higher biomass, and droughts less biomass. We found a strong positive correlation between climate treatment favorability for *Phacelia* and its *Bromus* competitor (Fig. 5C), indicating that increased *Bromus* might offset the benefits of more favorable conditions. Possibly due to this indirect effect, the precipitation × vegetation interaction approached significance ($P = 0.075$, Table 1).

DISCUSSION

Although numerous studies have now examined how community composition changes with experimental manipulations of climate, the degree to which individual species responses are determined by the response of their

surrounding community is poorly understood (Davis et al. 1998, Walther et al. 2002, Schmitz et al. 2003, Visser and Both 2005, Buckley and Roughgarden 2006, Suttle et al. 2007, Adler and HilleRisLambers 2008, Tylianakis et al. 2008). We found that two focal species and their competitors tended to respond similarly to precipitation change, leading to the expectation that changes in competitor abundance might offset these focal species' direct precipitation response. For example, wetter years that directly benefit *Phacelia* might indirectly harm the species by increasing *Bromus* competition.

In contrast to expectations, however, results from factorial manipulations of precipitation and vegetation showed little evidence for indirect effects of precipitation change via competitors. Competitors had no influence on the precipitation response of *Gilia* and *Malacothrix*, due to their low sensitivity to competition and highly variable precipitation responses. Competition did affect how *Phacelia* responded to precipitation change, but the precipitation × vegetation interaction only approached significance ($P = 0.075$), and as we explain below, whether it truly resulted from competitor response to precipitation change was unclear. For our system, we thus conclude that competitors tend not to modulate the response of rare plants to precipitation change.

Direct and indirect effects of precipitation change

All three focal annuals of our study had their competitive environment significantly altered by precipitation change. The *Bromus* competitors surrounding *Gilia* and *Phacelia* showed four-fold differences in biomass between the most and least favorable precipitation treatments. The *Lasthenia* competing with *Malacothrix* showed a similar response to precipitation, matching earlier work in mainland California (Hobbs et al. 2007). Importantly, in all but one instance, the relative favorability of precipitation treatments for a focal species and its principal competitor were positively correlated (Fig. 3E, F, Fig. 5C), though the correlation only reached significance for *Phacelia*/*Bromus* in 2004. That focal species and their competitors respond in the same direction should not be surprising considering that water generally limits growth in California habitats (Zavaleta et al. 2003, Hobbs et al. 2007, Suttle et al. 2007). Dormann et al. (2004) and Klanderud (2005) found a similar result for the direct effects of increased temperature on various plants in arctic and alpine areas.

In systems where competitors respond similarly to climate change, one might expect more favorable climate conditions to be countered by increased competition. Yet, for *Gilia* and *Malacothrix*, we found no evidence that precipitation affected the influence of competition on their population growth rate. Given that both of these species' principal competitors responded strongly to precipitation change, why did these species not show indirect effects? For *Gilia*, this result is consistent with the sparse vegetation in its habitat and its general insensitivity to surrounding competitors (highly nonsignificant main effects of vegetation in Table 1). None of the rainfall treatments exerted a large enough change in competitor abundance to influence *Gilia*'s population growth rate (arrow C in Fig. 1 was very weak). Like *Gilia*, *Malacothrix* population growth showed no significant precipitation × vegetation interaction (Table

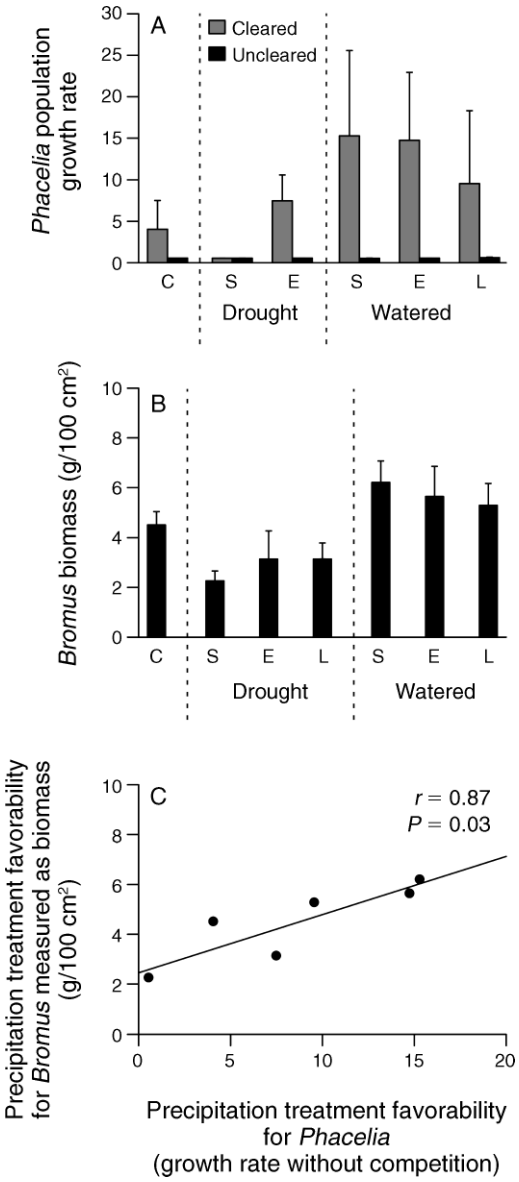

FIG. 5. (A) *Phacelia insularis* var. *insularis* per capita population growth rate as a function of precipitation and competition treatments in 2004. The precipitation treatments are control (C), drought, and watered, imposed season-long (S), early season (E), or late season (L). Data from control and late-season drought treatments were pooled for *Phacelia* demographics (see *Methods: Statistical analysis*). (B) Biomass response of *Bromus diandrus* to precipitation manipulations at the *Phacelia* site in 2004. (C) Correlation between the favorability of precipitation treatments for *Phacelia* and its *Bromus* competitor in 2004. Bars in panels (A) and (B) show means + SE.

1), but here, the lack of significance was more a function of large unexplained variation than insensitivity to competition.

We did find that *Bromus* competition regulated the response of *Phacelia* to precipitation change. Though the precipitation × vegetation interaction only approached significance ($P = 0.075$), *Phacelia* responded strongly to the precipitation manipulations in the absence of competition, and showed no response in the presence of surrounding vegetation (Fig. 5A). While this result suggests that competition changed the response of *Phacelia* to precipitation, whether this interaction reflects an indirect effect of precipitation change mediated via changes in *Bromus* competition is unclear. In other words, is the failure of *Phacelia* to respond to wetter treatments a direct function of increased *Bromus* competition in those treatments (Fig. 5B)? Or instead, is *Phacelia* simply intolerant of *Bromus* competition, making the latter's response to rainfall irrelevant? Experimentally resolving this issue would require holding *Bromus* competition constant while changing rainfall for *Phacelia*, an unfortunately difficult manipulation.

California climate change implications

Forecasts for California precipitation change over this century range from a 157 mm decrease to a 38 mm increase in total annual rainfall, with additional uncertainty surrounding when the rain will fall (Dukes and Shaw 2007). Because our rainfall treatments cover the full range of possible precipitation scenarios forecast for the region, our experiments allow us to predict the types of changes with the greatest potential to influence the rare and endangered plant species.

In general, all of our species suffered from drought conditions at some life stage in 2004, and to a lesser extent in 2005, whereas the effects of additional rainfall were less consistent. Two of three focal species experienced little benefit from wetter treatments in both the 2005 El Niño year and the below average rainfall year of 2004. Although somewhat surprising given expectations of water limitation, these experimental results are generally consistent with the response of the focal species to natural variation in rainfall (Levine et al. 2008) and results from other systems in the state. Zavaleta et al. (2003) found only weak effects of increased season-long precipitation on forbs in a California grassland. Meanwhile, Suttle (2007) found that water addition tended to favor annual grasses over forbs, particularly when water was applied late in the year.

Our results also suggest that changes to the timing of the rainfall may rival season-long changes in their impact on plant populations. In 2004, the mid-season drought treatment largely excluded the only major (>2.5 cm) storm that occurred between germination in November and later rain in February, significantly reducing *Gilia* population growth and the biomass of its *Bromus* competitor (Fig. 3A, C). Meanwhile, *Phacelia*'s high population growth rate with early-season drought (Fig. 5A) resulted from a six-fold increase in germination in early drought vs. other treatments (Appendix: Fig. A3). Because the early drought treatment largely excluded rainfall through mid-December, it shifted the first major storm from late October to a 2°C cooler event in late December. In long term monitoring, years with cool first rains tend to have larger emergent *Phacelia* populations (Levine et al. 2008).

Conclusions and future directions

Recent studies have suggested that climate change projections that do not explicitly account for indirect effects via the surrounding community may poorly predict the fate of individual species (Davis et al. 1998, Walther et al. 2002, Schmitz et al. 2003, Visser and Both 2005, Buckley and Roughgarden 2006, Suttle et al. 2007, Adler and HilleRisLambers 2008, Tylianakis et al. 2008). Our work suggests that even if competition operates in a system, and competitors respond to climate change, whether the indirect effect proves important depends on how strongly climate change affects competition, and how sensitive the focal species are to changes in competitor abundance. In our system, precipitation change did not sufficiently alter the competitive environment of the three focal species to drive clear indirect effects.

Our results examined one type of surrounding community response to climate change, that of competitors already present in the habitat. This response is likely to dominate in the short term and on island systems like our own. Over longer time scales, climate change also brings new species to ecological systems (Root et al. 2003, Thomas et al. 2004), species with even greater potential to modulate the response of focal species. Given that we are already beginning to see the arrival of climate change migrants, experiments like those conducted here, but focused on recently arrived competitors are now feasible and justified. Such experiments may form the next generation of studies examining how surrounding competitors modulate ecological responses to climate change.

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APPENDIX

Figures showing additional demographic responses to precipitation and vegetation manipulations for the three focal species of the study (*Ecological Archives* E091-012-A1).