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Biotic context and soil properties modulate native plant responses to enhanced rainfall

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- **Background and Aims** The environmental and biotic context within which plants grow have a great potential to modify responses to climatic changes, yet few studies have addressed both the direct effects of climate and the modulating roles played by variation in the biotic (e.g. competitors) and abiotic (e.g. soils) environment.
- **Methods** In a grassland with highly heterogeneous soils and community composition, small seedlings of two native plants, *Lasthenia californica* and *Calycadenia pauciflora*, were transplanted into factorially watered and fertilized plots. Measurements were made to test how the effect of climatic variability (mimicked by the watering treatment) on the survival, growth and seed production of these species was modulated by above-ground competition and by edaphic variables.
- **Key Results** Increased competition outweighed the direct positive impacts of enhanced rainfall on most fitness measures for both species, resulting in no net effect of enhanced rainfall. Both species benefitted from enhanced rainfall when the absence of competitors was accompanied by high soil water retention capacity. Fertilization did not amplify the watering effects; rather, plants benefitted from enhanced rainfall or competitor removal only in ambient nutrient conditions with high soil water retention capacity.
- **Conclusions** The findings show that the direct effects of climatic variability on plant fitness may be reversed or neutralized by competition and, in addition, may be strongly modulated by soil variation. Specifically, coarse soil texture was identified as a factor that may limit plant responsiveness to altered water availability. These results highlight the importance of considering the abiotic as well as biotic context when making future climate change forecasts.

Key words: Biotic context, California annual natives, *Calycadenia pauciflora*, climate change, competition, direct and indirect effects, enhanced rainfall, floral herbivory, grassland, *Lasthenia californica*, multiple global changes, plant–climate interactions, soil properties.

INTRODUCTION

It is becoming widely acknowledged that plant responses to environmental changes depend on biotic context (Tylianakis *et al.*, 2008; Van der Putten *et al.*, 2010; Zarnetske *et al.*, 2012; Parmesan *et al.*, 2013; Post, 2013; Grassein *et al.*, 2014). Interspecific interactions may buffer against, amplify or even reverse global change effects on individual organisms (Suttle *et al.*, 2007; Tylianakis *et al.*, 2008), and understanding these effects may help resolve unexplained variation in studies of species range shifts and community changes (Chen *et al.*, 2011; Moritz and Agudo, 2013). Some empirical studies suggest, for example, that natural enemies (Post and Pedersen, 2008; Kaarlejärvi *et al.*, 2013; Lu *et al.*, 2013) and resident competitors (Liancourt *et al.*, 2013; Eskelinen and Harrison, 2014; Goldstein and Suding, 2014) can considerably alter the impacts of global environmental changes on individual plants and communities, exhibiting potential to stabilize ecosystem dynamics and function under global change (Post, 2013). However, there is still very little experimental evidence of such complex interactions, and a more comprehensive understanding of biotic modulation of climate change effects is urgently needed

(Zarnetske *et al.*, 2012; HilleRisLambers *et al.*, 2013; Parmesan *et al.*, 2013; Post, 2013).

Plant interspecific interactions are one of the strongest biotic forces shaping plant population and community dynamics (Tilman, 1988; Crawley, 1997), and exhibit great potential to modify direct plant responses to global changes (Tylianakis *et al.*, 2008). If global change factors that add essential resources for plant growth (e.g. increased rainfall, nutrient enrichment) benefit the surrounding competitors more than the focal plant, then these global change factors can indirectly hamper the success of the focal plant via increased intensity of competition, even if the direct impacts on the focal plant were positive. At present, it remains unclear why some studies of the interplay among competition and climate change find the direct effects of climate to outweigh the indirect effects mediated by the biotic environment (e.g. Thomsen *et al.*, 2006; Levine *et al.*, 2010), while others find the reverse (e.g. Suttle *et al.*, 2007; Liancourt *et al.*, 2013). One little-explored aspect of this question potentially providing clues to uncover these disparate findings is how the abiotic environment influences the biotic modulation of climate change effects. For example, if plant

growth is limited by multiple resources (Harpole *et al.*, 2007; Eskelinen and Harrison, 2014), interactions among rainfall and competition could hinge on soil nutrient availability. Likewise, soil characteristics such as water-holding capacity, related to soil texture, could have a major impact on how altered rainfall patterns affect competitive intensity since it determines the capacity of the soil to retain additional water and how much plants actually benefit from ameliorated conditions (Knapp *et al.*, 2008). In addition to affecting competition, edaphic factors can also modulate other biotic pressures on plants, such as seed predation (Brown and Vellend, 2014; von Euler *et al.*, 2014) and insect herbivory (Lau *et al.*, 2008). In sum, the three-way interactions among local abiotic factors, biotic context and climate have considerable potential to help explain the complexity and contingency of global change outcomes, yet there are very few studies experimentally testing such interactions.

We experimentally investigated how above-ground competition interacts with climatic (rainfall) and edaphic (nutrients and soil water retention capacity) variables to control native plant performance in three different grassland types varying in soil fertility and species composition in California. Shifts in water balance, due to either altered rainfall patterns, temperature or solar radiation and cloudiness, can have major impacts on plant performance and community dynamics (e.g. Suttle *et al.*, 2007; Levine *et al.*, 2010; Wu *et al.*, 2011; Yang *et al.*, 2011; Hoepfner and Dukes, 2012; Liancourt *et al.*, 2013; Eskelinen and Harrison, 2014; Prevéy and Seastedt, 2014), and these impacts are likely to play an especially important role in arid and semi-arid systems where water is already strongly limiting to plant growth. In semi-arid grasslands of California, major shifts in climatic water balance are expected to occur due to climate change (National Assessment Synthesis Team, 2000; Cayan *et al.*, 2012). Although the exact effects are not known, changes in climatic conditions are anticipated to exert major influences on the endemic-rich flora of California (Damschen *et al.*, 2012), including considerable reductions in native species range sizes (Loarie *et al.*, 2008). In addition, native species in Californian grasslands have been suggested to suffer from exotic-driven extinction debt even many decades after the invasions started (Gilbert and Levine, 2013), and that, together with the new threats posed by climate change, makes it especially important to understand the interacting factors that affect native species performance.

Net effects of a climatic event on a focal species in the presence of competition can be decomposed into direct effects on the focal species and indirect effects mediated by the change in the abundance of other species. We investigated these different components of climate change effects and asked the following question. How do soil properties (i.e. soil nutrients and water-holding capacity) modulate (1) the direct effects of rainfall enhancement on our two focal native species (i.e. how rainfall affects plant success in the absence of competition); (2) the indirect effects of rainfall on the focal species (i.e. how rainfall affects the intensity of competition); and (3) the net effects of rainfall on the focal species (i.e. how rainfall affects focal plant success in the presence of competition)?

We predicted that (1) the direct effect of enhanced rainfall on target plant success would be more positive in productive conditions (i.e. in fertilized plots and/or in fertile habitats with greater soil water-holding capacity) where responses to water

are less limited by nutrients. Furthermore, we predicted that (2) the indirect effect of enhanced rainfall via intensified competition would be stronger (i.e. competition would become more intense) in productive conditions. Finally, we predicted that (3) the net effects of rainfall would be positive in infertile conditions (i.e. in unfertilized plots and in infertile habitats) where strong competitors are less abundant and indirect effects less strong, and negative in fertile conditions where competitors well adapted to take advantage of enhanced resources are abundant and indirect effects are stronger.

MATERIALS AND METHODS

Study system and grassland types

Our study was carried out at the Donald and Sylvia McLaughlin University of California Natural Reserve (38°851'N, 123°830'W) in Napa County, the North Coast Range of California, USA. This area is defined by Mediterranean climate with a rainy, cool growing season starting in the autumn (around October) when heavy rains trigger germination. Summers are dry and hot, and most annual plants senesce and set seeds by the late spring (May–June). Our experimental years were within one standard deviation of the 25 year mean annual rainfall (2009–2010, 79.5 cm; 2010–2011, 84.6 cm; 2011–2012, 53.8; 25 year mean \pm s.d., 69.7 \pm 23.3 cm; each value is for 1 September–31 August).

Our experimental site of approx. 1000 \times 500 m is a complex of grasslands on soils varying in nutrients, texture and water-holding capacity (Eskelinen and Harrison, 2014). The most infertile soil type of our system, harsh serpentine, is found on rocky hilltops and is characterized by very low N levels and soil water retention capacity. It supports low-productivity vegetation dominated by short-statured native annuals (Harrison, 1999; Harrison *et al.*, 2006). Deeper and finer textured serpentine soils on slopes and valley bottoms (lush serpentine) have higher water retention and N (Eskelinen and Harrison, 2014), and support lush vegetation consisting of a mixture of native and exotic plants (Harrison, 1999; Harrison *et al.*, 2006). Non-serpentine soils, derived from sedimentary rocks, are dominated by exotic grasses and forbs, and represent the most productive grassland type in our system, with high soil water-holding capacity and greater N and Ca concentrations than either harsh or lush serpentine grasslands (Eskelinen and Harrison, 2014). These grassland types are interspersed over relatively short distances (10–100 m), making it possible to replicate treatments on soils with different soil water retention capacity and fertility levels.

Experimental design

In March 2010, we selected nine transects that passed through patches of the three grassland types (harsh, lush and non-serpentine), and established 132 plots of 2 \times 2 m along these transects. There were 10–12 replicate plots per treatment combination, the slightly unequal number resulting from accidentally losing a few plots during the first year. The plots were randomly assigned to two levels of water addition (enhanced rainfall and ambient rainfall) and two levels of nutrient addition (fertilization and ambient nutrient conditions).

To investigate the impact of enhanced rainfall, we established an irrigation tubing system that used the nine transects as lines for bringing nearby harvested rainwater along to the rainfall addition plots. The water was delivered to sprinkler heads (Mini Rotor Drip Emitters, Olson Irrigation, Santee, CA, USA), placed 50 cm above the soil in the centre of each 2×2 m plot and watering a 3 m radius. Each year, we began watering when rains decreased or ceased after 15 March, and none was forecast. We added 2.5 cm of water over a 12 h period at night once a week for eight consecutive weeks in each year (2010–2012). This amount mimicked a moderate storm event, and the total precipitation increase per year was roughly 18 % over mean annual rainfall (see Suttle *et al.*, 2007 for a similar treatment level). In general, we based our watering treatment on previous work in Californian grasslands, which found water addition has strong effects in spring when rainfall has largely ceased and soils are drying rapidly, but little effect during the rainy winter (Suttle *et al.*, 2007; see also Dukes *et al.*, 2005, 2011). Some climate models have projected wetter springs for northern California (National Assessment Synthesis Team, 2000), although most recent models predict slightly to moderately drier springs (Cayan *et al.*, 2012).

To assess how the watering effect would be moderated by relaxing nutrient limitation as broadly as possible, we applied a slow-release granular NPK (10-10-10) fertilizer with micronutrients (Lilly Miller Ultra Green; Lilly Miller Brands, Walnut Creek, CA, USA). The fertilizer was supplied in three equal applications in November, early February and late March, a total of 10 g N m^{-2} , 10 g P m^{-2} and $10 \text{ g K m}^{-2} \text{ year}^{-1}$. The first fertilization was in November 2010 and the last in March 2012. We based our nutrient levels on the NutNet protocol (see <http://www.nutnet.umn.edu/nutrients>).

To examine the intensity of above-ground competition, we applied a competitor removal treatment nested within the main 2×2 m plots. We initiated this treatment in autumn 2011, after 2 years of precipitation addition and one full season of fertilizing, in order to account for already increased biomass of the surrounding vegetation. We selected two paired 25×50 cm sub-plots and randomly assigned one to the competitor removal treatment. Just before transplanting *Calycadenia* and *Lasthenia* seedlings, all above-ground biomass (both litter and live biomass) was hand-clipped and removed from the competitor removal sub-plots. We maintained the competitor removal treatment by repeatedly clipping all emerging biomass around the target transplants at least once a month throughout the experiment.

Study species

We chose two focal plants, *Lasthenia californica* and *Calycadenia pauciflora* (Asteraceae), both Californian endemic annuals that germinate after the autumn rains; *Lasthenia* flowers in spring (March–April) and *Calycadenia* in summer (July–August). *Lasthenia* is widespread but usually most abundant on serpentine soils (Kruckeberg, 1984; Rajakaruna and Bohm, 1999), while *Calycadenia* is endemic to rocky serpentine soils (Safford *et al.*, 2005). The seeds of *Lasthenia* were collected in May 2010 and the seeds of *Calycadenia* in September–October 2010, both from several locations close to our experimental site. Both species were collected from serpentine, where they are exclusively (or nearly so) found.

Transplants

Seeds of *Lasthenia* and *Calycadenia* were planted into potting soil (Modified UC Mix) in plug trays with 2×2 cm cells in November 2011, germinated in a greenhouse, and grown in outside conditions until transplanted to the experimental plots in December. Before transplanting, we thinned the seedlings to five individuals per plug tray cell for *Lasthenia* and to three individuals per cell for *Calycadenia* to take into account potential seedling losses due to transplanting. Seedlings were approx. 15 mm tall at the time of transplanting. Each sub-plot with the competitor removal treatment or not received seedlings and their pot soil within one cell, and was watered immediately after planting. Transplants of the two species were placed 20 cm apart in each sub-plot. Transplanting was done very gently into wet soils in cool weather, and ample time was allowed to establish before applying the experimental treatments. As December 2011 and early January 2012 were exceptionally dry, we watered all transplants in all plots once a week for 5 weeks to ensure establishment. After that the transplants were not watered unless assigned to the precipitation increase treatment.

We surveyed *Lasthenia* every day and *Calycadenia* every 4 d after the first signs of seed head maturation, and collected biomass when seeds had started ripening but not yet dropped. *Lasthenia* transplants were collected between 3 and 21 May 2012, and *Calycadenia* from 13 August to 4 November 2012. Reproductive and vegetative biomass were collected separately, dried at $+60 \text{ }^\circ\text{C}$ for 72 h, and weighed. We also recorded all signs of herbivory. We found that floral herbivory by beetles was conspicuous on *Lasthenia* flower heads as all or a large proportion of flowers in flower heads of many individuals were completely eaten. There were a number of different beetle species (see Supplementary Data Table S1 for a complete list), with *Bruchidius cisti* (Chrysomelidae) being one of the most abundant encountered in the flowers. To account for herbivory effects on *Lasthenia* reproduction, we therefore separately collected flower heads from which the flowers had been eaten. Other types of herbivory and herbivory on *Calycadenia* flowers were insignificant. We pooled the biomass of the surviving transplants in each sub-plot that started out from an equal number of seedlings (five for *Lasthenia* and three for *Calycadenia*), so that our measure of biomass integrates across seedling survival and plant growth.

Environmental variables

To examine the role of potentially important environmental variables mediating plant responses to competition and global change treatments, we collected pre-treatment soil samples (composites of three sub-samples) in early April 2010, just before the first treatment application from the main 2×2 m plots. The soils were analysed for moisture retention capacity (under a constant 0.3 ATM pressure potential), $\text{NH}_4\text{-N}$ and C:N ratio at UC Davis Analytical Laboratory. We chose these variables because they are important in characterizing our nutrient and water-limited habitats (Eskelinen and Harrison, 2014) and are potentially important in mediating plant responsiveness to precipitation. We also assessed the effectiveness of our resource addition treatments on soil nutrient and moisture levels in 2012, and have reported these results in Eskelinen and Harrison (2014).

Statistical analyses

To test whether soil properties modulate the direct and net effects of watering on the growth and reproductive performance of *Calycadenia* and *Lasthenia*, we applied linear mixed effects (LME) models (Pinheiro and Bates, 2000), where competitor removal, watering, fertilization, habitat, soil variables and their interactions were used as explanatory variables. After preliminary analyses, we focused on soil water retention capacity, since it was the only significant soil variable interacting with rainfall addition (which is the main focus of our study). Soil water retention capacity was a linear covariate whereas other variables (i.e. experimental treatments) were treated as fixed factors in the follow-up analyses. We separately analysed the total biomass (stem/leaf and seed head biomass) and seed head biomass for both species and the percentage of eaten flower heads for *Lasthenia* (response variables). The nested design of the experiment was included in the models as nested random effects, where the competitor removal treatment (sub-plot) was nested within the other treatments (plot) which were nested within the lines that brought water to the watering treatment plots. We separately analysed all response variables.

To examine how the treatments and soil water retention capacity affected plant survival, we applied generalized linear mixed effects models (GLMMs) with binomial error structure. Predictor variables were as above, except that we excluded habitat to improve the model fit and stability of the parameter estimates. We simplified the GLMMs to include only significant explanatory variables and used the Akaike information criterion (AIC) as our criterion for either retaining or deleting the explanatory variables.

We calculated log response ratio (logRR; Goldberg *et al.*, 1999) of the total biomass to investigate the intensity of above-ground competition in relation to watering, fertilization, habitat and soil water retention capacity. The logRR was calculated as a natural logarithm of total biomass in the competitor removal sub-plots divided by total biomass in the control sub-plots (no competitor removal). Positive values of logRR indicate positive impact of competitor removal, i.e. above-ground competition suppresses biomass production of the target species, with greater values indicating increased intensity of competition. In contrast, negative values indicate a negative impact of competitor removal, i.e. neighbouring plants facilitate biomass production of the target species. We added a constant ($x + 0.01$) to every value to account for those cases when one of the transplants had died. We then used LME models to investigate the biomass responses, similar to those above except without sub-plot as a nesting random variable.

The heteroscedasticity of variances and normality of errors were checked using model diagnostic plots (Crawley, 2007). We used the package ‘nlme’ for LME model analyses and the package ‘lme4’ for GLMM analyses, all in R statistical software (R Development Core Team, 2014).

RESULTS

Calycadenia

Approximately 50 % of *Calycadenia* individuals survived, and most surviving individuals (82 %) produced flowers and seeds.

Survival in general was high, also in the two more fertile habitats (Supplementary Data Fig. S1). We detected some signs of herbivory on leaves (14 %) but no floral herbivory. In general, we found complex interactions among watering, competition and fertilization, and these depended on soil water retention capacity (Table 1).

Hypothesis 1. We found that soil properties modulated the direct effects of rainfall addition on the growth and reproductive success of *Calycadenia*, partly as we predicted. In the absence of competitors, watering increased the total and seed head biomasses of *Calycadenia*, but only in ambient nutrient conditions (contrary to our prediction), and the effect was greater when soil water retention capacity was high (according to our prediction, Fig. 1; Supplementary Data Figs S2 and S3). The survival of *Calycadenia* acted differently, with a negligible direct impact of watering, and no interaction with soil water retention capacity (Supplementary Data Table S2, Fig. S1).

Hypothesis 2. Corresponding to the biomass responses, watering enhanced the intensity of competition (measured as logRR), but only when soil water retention capacity was high (according to our prediction) and in ambient nutrient conditions (contrary to our prediction, significant watering \times water retention capacity and watering \times water retention capacity \times fertilization interactions, $F_{1,96} = 3.6$, $P = 0.0598$ and $F_{1,96} = 6.6$, $P = 0.0108$, respectively, Fig. 2; Supplementary Data Table S3).

Hypothesis 3. In the presence of competitors, addition of water did not affect the total and seed head biomasses of *Calycadenia*, nor were there interactions among treatments and soil water retention capacity (Table 1; Fig. 1; Supplementary Data Figs S2 and S3), emphasizing the importance of competition in cancelling the positive effects of watering even in the most infertile conditions. However, it is noteworthy that soil water retention capacity modified the impacts of competition and fertilization on *Calycadenia* survival, with decreased survival under competition and fertilization when soil water-holding capacity was high (significant fertilization \times water retention capacity and competition \times water retention capacity interactions, $z = 2.0$, $P = 0.0498$ and $z = 2.7$, $P = 0.0064$, respectively, Fig. 3A; Supplementary Data Table S2, Fig. S1). Survival was highest in ambient nutrient conditions and in the absence of competitors when soil water-holding capacity was high (Fig. 3A; Fig. S1).

Lasthenia

Sixty-one per cent of *Lasthenia* individuals survived, with 93 % of survivors producing flowers, and survival in general was equally high at all habitats (Supplementary Data Fig. S1). In contrast to *Calycadenia*, *Lasthenia* flower heads experienced severe herbivory (63 % of the surviving individuals), and the extent of floral herbivory depended on the treatments (see below). In general, *Lasthenia* exhibited fewer responses to interactions among treatments, and soil water retention capacity did not play as significant a role as for *Calycadenia*.

Hypothesis 1. In the absence of competitors, watering significantly positively affected the growth of *Lasthenia* (i.e. total biomass), but only in lush and non-serpentine habitats (Table 1;

TABLE 1. Results of linear mixed effects (LME) models testing the effects of competition, watering, fertilization, habitat and their interactions on the vegetative and reproductive biomass of *Calycadenia* and *Lasthenia*

	<i>Calycadenia</i>				<i>Lasthenia</i>			
	Total biomass		Seed head biomass		Total biomass		Seed head biomass	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Habitat (H)	3.0 _(2,108)	0.0561	5.1 _(2,108)	0.0078	3.2 _(2,108)	0.0437	1.4 _(2,108)	0.2481
Watering (W)	3.3 _(1,108)	0.0731	2.5 _(1,108)	0.1152	2.5 _(1,108)	0.1166	<0.1 _(1,108)	0.8644
Fertilization (F)	25.0 _(1,108)	<0.0001	35.0 _(1,108)	<0.0001	3.5 _(1,108)	0.0630	0.3 _(1,108)	0.5912
Competition (C)	45.6 _(1,92)	<0.0001	37.7 _(1,92)	<0.0001	14.0 _(1,92)	0.0003	18.5 _(1,92)	<0.0001
Water retention capacity (WRC)	7.1 _(1,92)	0.0092	6.9 _(1,92)	0.0101	7.4 _(1,92)	0.0077	6.2 _(1,92)	0.0145
H × F	5.0 _(2,108)	0.0083	2.7 _(2,108)	0.0726	6.9 _(2,108)	0.0015	7.7 _(2,108)	0.0007
H × C	3.1 _(2,92)	0.0500	2.5 _(2,92)	0.0902	ns	ns	ns	ns
W × C	3.2 _(1,92)	0.0749	ns	ns	ns	ns	ns	ns
F × C	ns	ns	4.0 _(1,92)	0.0479	6.2 _(1,92)	0.0143	5.5 _(1,92)	0.0209
C × WRC	9.0 _(1,92)	0.0035	9.1 _(1,92)	0.0033	ns	ns	ns	ns
W × WRC	ns	ns	ns	ns	3.2 _(1,92)	0.0786	5.9 _(1,92)	0.0173
H × W × C	ns	ns	ns	ns	3.0 _(2,92)	0.0557	ns	ns
H × F × C	3.2 _(2,92)	0.0444	2.7 _(2,92)	0.0730	ns	ns	ns	ns
W × F × WRC	9.1 _(1,92)	0.0034	11.0 _(1,92)	0.0013	ns	ns	ns	ns
W × C × WRC	5.3 _(1,92)	0.0239	7.0 _(1,92)	0.0095	ns	ns	ns	ns
W × F × C × WRC	10.7 _(1,92)	0.0015	12.9 _(1,92)	0.0005	ns	ns	ns	ns

All main effects but only significant ($P \leq 0.05$) and marginally ($P \leq 0.07$, in italics) significant interactions are reported.

Lasthenia biomasses were log (+0.001) transformed and *Calycadenia* biomasses were square-root transformed for the analyses.

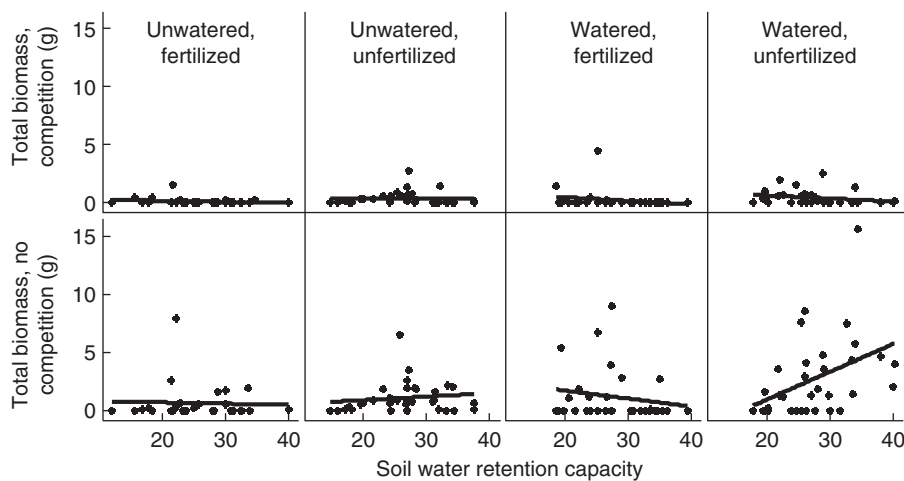


FIG. 1. The relationship among (A) the total biomass and soil water retention capacity (%), and (B) reproductive biomass (i.e. seed head biomass) and soil water retention capacity (%) of *Calycadenia* under different combinations of competition, watering and fertilization. The lines represent fitted lines between the response and predictor variables under different treatment combinations.

Fig. 4), matching our prediction of a greater positive direct effect of rainfall addition in more fertile habitats. However, there were no interactions among watering, fertilization and soil water-holding capacity (Table 1), indicating that soil nutrients or water retention capacity did not modulate the direct watering responses on *Lasthenia* growth and that something else related to the habitats was responsible for the greater watering effects in the two more fertile habitats.

Hypothesis 2. Our results using logRR corresponded to those of total biomass responses: watering alone increased the relative intensity of competition but only in the two more fertile habitats, in lush and non-serpentine (significant habitat × watering interaction, $F_{2,96} = 3.0$, $P = 0.0553$, Fig. 5; Supplementary

Data Table S3), and this interaction was independent of fertilization and soil water retention capacity.

Hypothesis 3. There were no significant net effects of watering on vegetative growth (Table 1; Fig. 4), emphasizing the importance of competition in offsetting the growth response of *Lasthenia* to water addition even in the most infertile conditions. When we separately analysed seed head biomass, we found that, statistically, independently of competition, watering increased reproductive performance when soil water-holding capacity was high (Table 1; Supplementary Data Fig. S4), indicating that the impact of watering on reproductive performance was contingent on soil properties. Although competition was not significant in this interaction, there was a strong direct

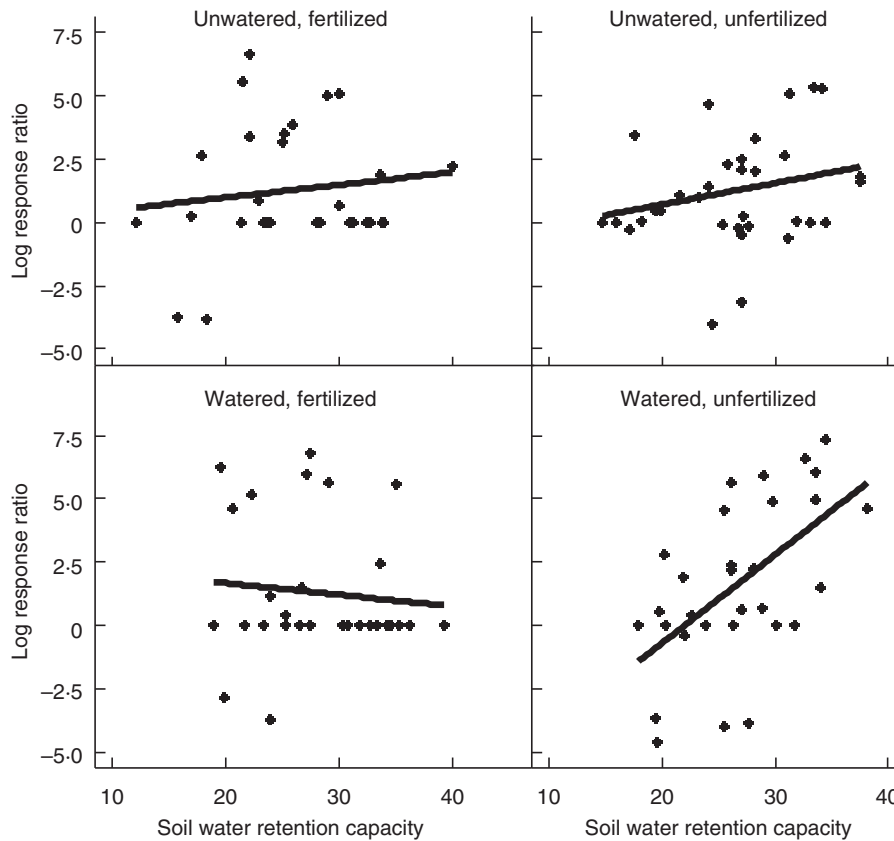


Fig. 2. The relationship among the neighbour removal impact (log response ratio) on *Calycadenia* biomass and soil water retention capacity (%) under different combinations of watering and fertilization. The lines represent fitted lines between the response and predictor variables under different treatment combinations.

negative effect of competition on seed head biomass, and the impact of watering in the presence of competitors was negligible (Table 1; Fig. S5), showing that competition did offset the reproductive response as well. Interestingly, this negligible net effect of watering on reproduction was accompanied by a finding that watering enhanced the percentage of *Lasthenia* flower heads eaten in the two more fertile habitats [significant habitat \times watering interaction ($F_{2,112} = 3.7$, $P = 0.0272$), Supplementary Data Fig. S5] and more in the competitor removal plots [significant main effect of biomass removal ($F_{1,120} = 4.6$, $P = 0.0339$), Fig. S5]. However, in contrast to vegetative and reproductive biomasses, watering had a net positive impact on *Lasthenia* survival (independent of competitor removal treatment), and both soil nutrients and water retention capacity modulated this impact: the survival was increased by watering in ambient nutrient conditions and when soil water-holding capacity was high (significant watering \times fertilization \times water retention capacity interaction, $z = 2.2$, $P = 0.0305$, Fig. 3B; Supplementary Data Fig. S1; Table S2).

DISCUSSION

Strikingly, we found that the direct benefits of an enhanced water supply were in most cases cancelled out by the indirect negative effect of increased competition. This stands in contrast to some studies finding that the direct effects of altered climate are stronger than the indirect effects (Thomsen *et al.*, 2006;

Adler *et al.*, 2009; Levine *et al.*, 2010). For *Calycadenia*, these impacts were surprisingly similar over different fitness components, including plant survival, growth and seed production, which suggests that these effects are likely to manifest themselves in population dynamics over longer time periods. For both species, in agreement with our first and second hypotheses, the direct and indirect effects were strongest in the most productive conditions, relating to soil nutrients and/or to soil water-holding capacity. In contrast to our predictions and previous studies (Hooper and Johnson, 1999; Harpole *et al.*, 2007; Eskelinen and Harrison, 2014), nutrient addition did not amplify the watering effects for either *Calycadenia* or *Lasthenia*, which implies little role for multiple resource limitation. Using experimental nutrient amendment and replicating our treatments along a natural gradient of grassland productivity, we were able to break productivity down into its different components and show that while soil nutrients played some role, the most important factor affecting plant responsiveness to enhanced rainfall was the ability of soil to retain water. These results highlight the critical role of soil properties in modulating both the intensity of competition and the direct effects of changed rainfall patterns.

Competition offsets the direct positive impacts of enhanced rainfall

Watering in the absence of competitors increased the performance of both study species, indicating that environmental

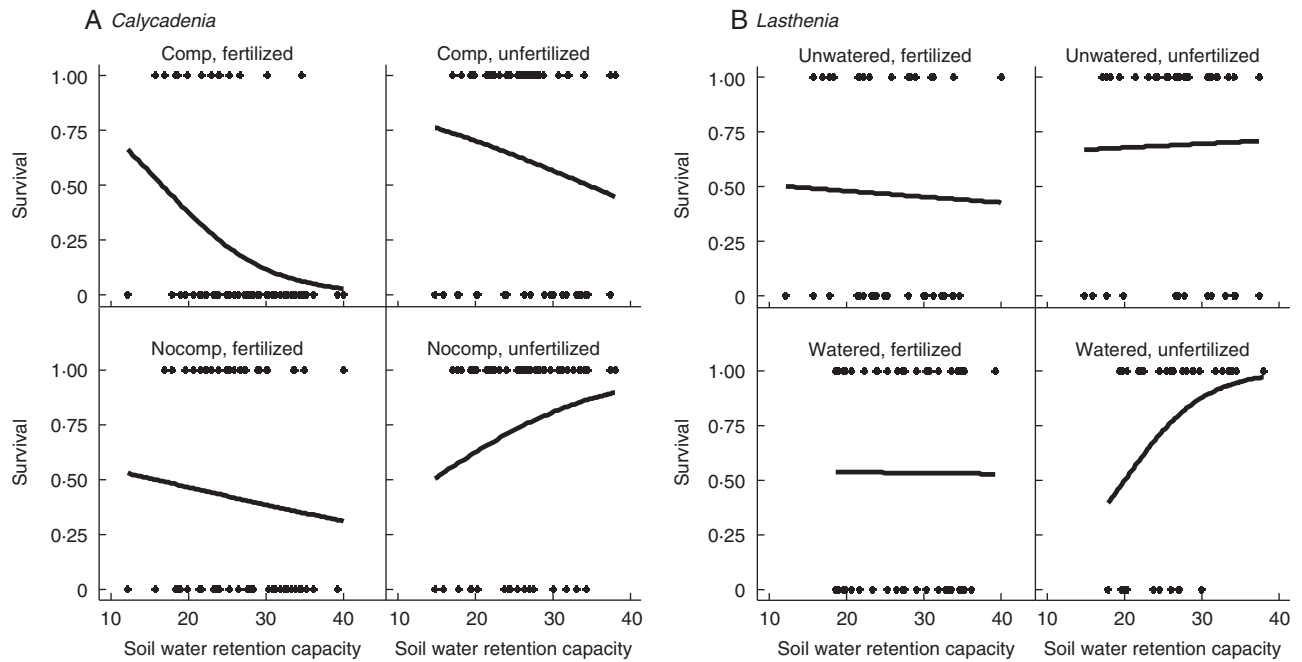


FIG. 3. (A) The survival of *Calycadenia* as a function of soil water-holding capacity (%) under different combinations of competition and fertilization. Watering is not included because it did not have a significant effects in the generalized linear mixed effects model (GLMM; see the Results). comp, competition; nocomp, no competition. (B) The survival of *Lasthenia* as a function of soil water-holding capacity (%) under different combinations of watering and fertilization. Competition is not included because it did not have significant effects in the model (GLMM; see the Results). In both figures, the lines represent fitted lines from the models where interactions among competition, watering, fertilization and soil water retention capacity were used as explanatory variables, and survival of each species in each subplot was used as a response variable (each species was assigned 1 if it survived and 0 if it did not). The models were simplified using the AIC, and only significant relationships are shown.

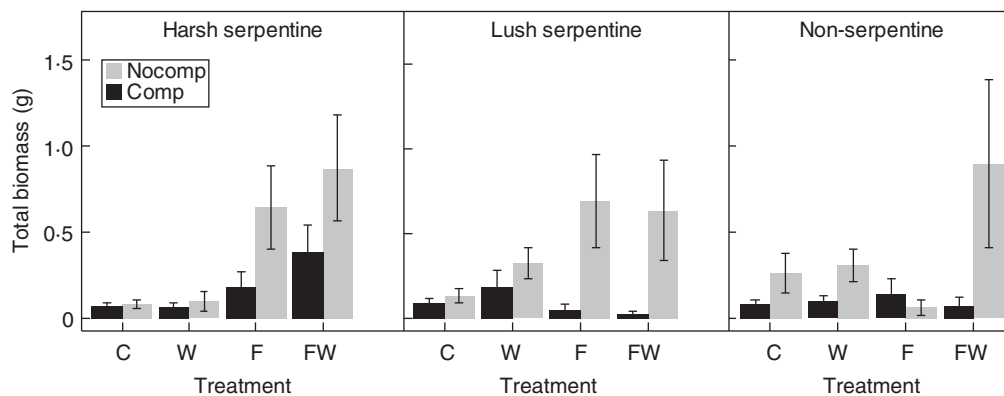


FIG. 4. The impact of watering, fertilization and competitor removal on the total biomass of *Lasthenia* in harsh, lush and non-serpentine habitats. C, control; W, watering; F, fertilization; FW, fertilization and watering. nocomp, no competition; comp, competition.

severity in terms of limited water availability is an important constraint over the fitness of our native focal plants. The direct impacts of watering were stronger on *Calycadenia*, which is understandable given its late flowering phenology and the spring timing of our watering treatment. [Prevéy and Seastedt \(2014\)](#) also found that enhanced rainfall favoured late-flowering natives in a grassland community. However, in our study, the benefits of watering were in many cases completely offset by the presence of competitors, which underscores the considerable importance of biotic context in modifying the net impacts of climate change. At our study system, late-flowering species are often exotic grasses and forbs (although there is a group of

native late-flowering forbs as well), that can strongly benefit from increased late-season rainfall ([Suttle et al. 2007](#)) and may exhibit strong competitive effect on natives. Besides our study, we are aware of only one other climate change study directly testing the intensity of competition and showing that plant competition under increased rainfall alone (without alleviation of nutrient limitation) can constrain plant fitness, and that study was carried out in Mongolian steppe (see [Liancourt et al., 2013](#)). Results from experiments such as ours and those from [Liancourt et al. \(2013\)](#) are an important step in understanding how plant competitive interactions may buffer against climate change-induced range shifts at least in some ecosystems

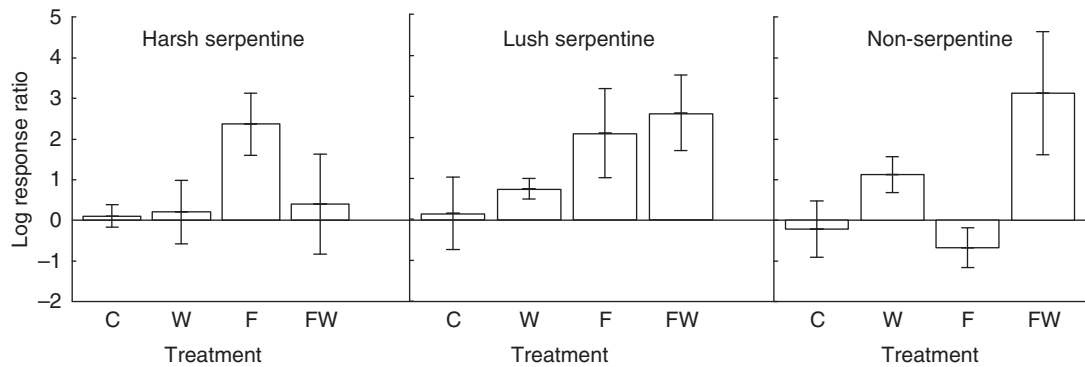


Fig. 5. The impact of competitor removal on *Lasthenia* biomass (log response ratio) with respect to different combinations of watering and fertilization in harsh, lush and non-serpentine habitats. C, control; W, watering; F, fertilization; FW; fertilization and watering.

(HilleRisLambers *et al.*, 2013), and highlight the importance of considering biotic context when making future climate change forecasts.

Soil properties drive plant responsiveness to competition and enhanced rainfall

One of the strongest and most novel results from our experiment was that soil properties modulated the direct and indirect (i.e. effects via modified intensity of competition) effects of enhanced rainfall on most fitness parameters of both focal plants. Especially for *Calycadenia* (but also for the survival of *Lasthenia*), one single variable, soil water retention capacity, played the strongest role in modulating the effects of enhanced rainfall and competition. Soil water retention capacity has been suggested to play an important role in organizing plant communities and determining plant responsiveness to precipitation patterns (Noy-Meir, 1973; Sala *et al.*, 1988; Weltzin *et al.*, 2003; Knapp *et al.*, 2008), yet it has been given surprisingly little attention in the climate change literature (but see Harrison *et al.*, 2015). In our study, sandy and rocky soils with lower soil water-holding capacity exhibited greater rates of soil moisture change between the weekly waterings (Eskelinen and Harrison, 2014), most probably as a result of rapid infiltration of water to the deeper soil layers, with important ramifications to our focal plants which were not able to benefit from added water. Soils with greater water-holding capacity remained moist for longer after each watering, resulting in greater growth of both our focal plants and their neighbours, and net zero effects of rainfall enhancement on the focal plants. Our findings underscore that soil texture (and the water-holding capacity that it generates) is an important abiotic filter that mediates shifts in soil water balance, and that regulates plant responses to altered rainfall regimes.

Adding soil nutrients did not amplify the impact of watering on plant success even in the absence of competitors; especially for *Calycadenia*, in fact, rainfall addition improved fitness only in ambient nutrient conditions with high soil water retention capacity. These results are in contrast to our own previous findings (Eskelinen and Harrison, 2014) as well as those of others (e.g. Harpole *et al.*, 2007) where nutrients and water have shown synergistic effects. These disparate outcomes may

reflect the fact that our study species here are endemic natives that have adapted to relatively low-productivity conditions, while our previous work was done using strongly invasive exotics (Eskelinen and Harrison, 2014). Natives adapted to low-productivity conditions generally exhibit less response to nutrient enrichment than exotics (Huenneke *et al.*, 1990; Seabloom *et al.*, 2003a,b; Going *et al.*, 2009; Polce *et al.*, 2011; Vallano *et al.*, 2012). Co-limitation by water and nutrients may therefore prove unimportant for at least some native plants, and natives and exotics may react fundamentally differently to multiple global changes (see also Sorte *et al.*, 2013; Eskelinen and Harrison, 2015). When predicting the simultaneous impacts of multiple global changes, such as nutrient enrichment and precipitation increase, it is therefore important to take into account plant adaptation to nutrient-poor vs. nutrient-rich conditions.

Of our two study species, *Lasthenia* flowers earlier in the growing season when water is still amply available and is adapted to less harsh edaphic conditions than *Calycadenia*. Accordingly, *Lasthenia* showed a less consistent effect of soil water-holding capacity than *Calycadenia* and the direct watering effects on its growth were greater in the two more fertile habitats (in ambient nutrient conditions). This result indicates that some habitat-specific factors other than water retention capacity or nutrients amplified the impact of watering in the two more productive habitats. Several soil and plant community variables, including plant and microbial community composition and function, mycorrhizal networks and soil fauna, vary among the habitats (Eskelinen and Harrison, 2015; K. Gravuer, A. Eskelinen and S. Harrison, unpubl. res.) and may contribute to these results.

Interactions among rainfall addition and herbivory

Interestingly, watering increased herbivory on *Lasthenia* flowers in the two more fertile habitats where *Lasthenia* does not normally grow, which suggests that flower-eating insect herbivores could constrain *Lasthenia* fitness under increased rainfall in these habitats (Louda and Potvin, 1995; Maron and Crone, 2006). This impact of watering on the intensity of herbivory was also greater in the absence of competitors. Watering could, in general, increase the attractiveness of *Lasthenia*

flowers by changing their nutritional quality or lead to greater rates of herbivory simply because of a positive correlation between plant size/flower number and rates of herbivory. In our study, there was no effect of watering in *Lasthenia*'s home habitat, nor was there an effect of fertilization or correlation among percentage of eaten flower heads and plant size/flower number (A. Eskelinen, unpubl. data), making these explanations unlikely. Another possible explanation is that watering altered the insect food web structure either by increasing the abundance of flower-eating herbivores or by decreasing their natural enemies (Suttle *et al.*, 2007), and this was contingent on the initial insect community composition. Furthermore, the absence of neighbours may have amplified the watering effects by making our focal plants more visible to the herbivores, especially in the two more fertile habitats where *Lasthenia* is otherwise absent (but see Lau *et al.*, 2008). Many studies focus on examining how herbivores may limit exotic performance and spread to new areas under global changes (e.g. Heard and Sax, 2013; Lu *et al.*, 2013), but our results suggest that similar effects may shape the distributions of natives. More generally, our results suggest that changes in precipitation patterns may affect plants via unpredictable interactions among herbivores, soil edaphic conditions and plant competitive interactions.

Implications for native plant fate under climate change

Our findings imply that, besides propagule and dispersal limitation (Seabloom *et al.*, 2003a, b; Seabloom, 2011; Brandt and Seabloom, 2012), interplay among soil properties and competition with neighbouring plants restrict the distributions of our focal plants to relatively unproductive and infertile grassland sites with low water-holding capacity (i.e. coarse-textured soils) and less intense competition. Even though our focal plants benefited from enhanced rainfall, increased competition outweighed the direct effects of water amendment, suggesting that these natives may not encounter immediate direct benefits from increased rainfall, predicted by some earlier climate change forecasts (National Assessment Synthesis Team, 2000). A low responsiveness of coarse-textured soils in our grassland system to rainfall enhancement may also buffer against extreme climatic events (Knapp *et al.*, 2008), as bigger rainfall events are needed to allow soils to become moist for long enough to support increased plant growth. Earlier studies have suggested that infertile soils support plants with resource-conservative traits (Reich *et al.*, 1997; Reich, 2014), which results in low responsiveness to nutrient and water additions (Eskelinen *et al.*, 2012; Fernandez-Going *et al.*, 2012; Laliberte *et al.*, 2012; Eskelinen and Harrison, 2015). Our findings suggest that soil texture is an additional important driver that engenders greater resistance of these endemic-rich, infertile grasslands. This conclusion is in line with Grime *et al.* (2008) who suggested that, besides plant traits, heterogeneity in soil moisture conditions drove recalcitrance of a calcareous grassland in England to manipulations of precipitation and temperature. Coarse-textured soils may therefore prove important local refugia in an otherwise changing landscape, with important consequences for regional species persistence under changing climatic conditions (Williams *et al.*, 2008).

CONCLUSIONS

In conclusion, our findings suggest that soil properties and competition acting in concert may limit native plant responses to climate change in terms of enhanced rainfall. These findings highlight the importance of addressing complex interplay among climatic variables, biotic context and soil properties in order to provide realistic predictions for the impacts of changing precipitation regimes. These results also suggest that synergistic co-limitation by nutrients and water is not uniform among all plants, which has to be taken into account when making future global change forecasts. Plant traits related to the resource-conservative trait syndrome (such as nutrient use efficiency) and phenological differences (early vs. late flowering) are likely to be important predictors of the outcomes of multiple global changes.

SUPPLEMENTARY DATA

Supplementary data are available online at www.aob.oxford-journals.org and consist of the following. Table S1: list of beetle species found in *Lasthenia* flowers. Table S2: results of generalized linear mixed effects models testing the effects of competition, watering, fertilization, habitat and their interactions on the survival of *Calycadenia* and *Lasthenia*. Table S3: results of linear mixed effects models testing the effects of watering, fertilization, habitat and their interactions on log response ratio of total biomass of *Calycadenia* and *Lasthenia*. Figure S1: impact of watering, fertilization and competitor removal on *Calycadenia* and *Lasthenia* survival in harsh, lush and non-serpentine habitats. Figure S2: reproductive biomass of *Calycadenia* as a function of soil water retention capacity under different combinations of competition, watering and fertilization. Figure S3: impact of watering, fertilization and competitor removal on the total biomass of *Calycadenia* in harsh, lush and non-serpentine habitats. Figure S4: impact of watering, fertilization and competitor removal on the percentage of eaten flower heads, the total biomass and the seed head biomass of *Lasthenia* in harsh, lush and non-serpentine habitats. Figure S5: reproductive biomass of *Lasthenia* as a function of soil water retention capacity under different combinations of watering and fertilization.

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