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# Climate change alters plant biogeography in Mediterranean prairies along the West Coast, USA

## Running Head: Prairie biogeography altered by climate change

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## **ABSTRACT**

Projected changes in climate are expected to have widespread effects on plant community composition and diversity in coming decades. However, multi-site, multi-factor climate manipulation studies that have examined whether observed responses are regionally consistent and whether multiple climate perturbations are interdependent are rare. Using such an experiment, we quantified how warming and increased precipitation intensity affects the relative dominance of plant functional groups and diversity across a broad climate gradient of Mediterranean prairies. We implemented a fully factorial climate manipulation of warming (+2.5-3.0°C) and increased wet-season precipitation (+20%) at three sites across a 520-km latitudinal gradient in the Pacific Northwest, USA. After seeding with a nearly identical mix of native species at all sites, we measured plant community composition (i.e., cover, richness and diversity), temperature, and soil moisture for three years. Warming and the resultant drying of soils altered plant community composition, decreased native diversity, and increased total cover, with warmed northern communities becoming more similar to communities further south. In particular, after two full years of warming, annual cover increased and forb cover decreased at all sites mirroring the natural biogeographic pattern. This suggests that the extant climate gradient of increasing heat and drought severity is responsible for a large part of the observed biogeographic pattern of increasing annual invasion in U.S. West Coast prairies as one moves further south. Additional precipitation during the rainy season did little to relieve drought stress and had minimal effects on plant community composition. Our results suggest that the projected increase in drought severity (i.e, hotter, drier summers) in Pacific Northwest prairies may lead to increased invasion by annuals and a loss of forbs, similar to what has been observed in central

and southern California, resulting in novel species assemblages and shifts in functional composition, which in turn may alter ecosystem functions.

## INTRODUCTION

Projected changes in climate are likely to exacerbate the already alarming rates of biodiversity loss (Bellard *et al.*, 2012), with the potential to surpass habitat loss as the largest threat to biodiversity in the coming century (Pereira *et al.*, 2010). Moreover, climate change will likely act synergistically with other global threats, such as biological invasions, to further alter community composition (Bradley *et al.*, 2010, Walther *et al.*, 2009). Changes in species composition and diversity may in turn have widespread effects on ecosystem function (Hooper *et al.*, 2012, Hooper *et al.*, 2005). Numerous studies have examined the responses of plant communities to simulated global change, including various combinations of elevated CO<sub>2</sub>, warming, altered precipitation regimes, and fertilization (e.g., Hoepfner & Dukes, 2012, Wu *et al.*, 2012, Zavaleta *et al.*, 2003a), with many studies demonstrating changes in net primary productivity, community composition, and diversity (see meta-analysis by Wu *et al.*, 2011). However, the majority of these studies examined only a single site (but see notable exceptions reviewed by Fraser *et al.*, 2013). Given the idiosyncratic nature of many ecological interactions, regional extrapolation of results from single-site studies should be done cautiously. Studies that embed experimental manipulations within natural climate gradients are needed to discriminate local controls from regional climate change effects (Dunne *et al.*, 2004, Pfeifer-Meister *et al.*, 2013, Rustad, 2008). Moreover, consistent responses across natural climate gradients, within climate manipulations, and over multiple years provide strong support for the direction and magnitude of expected changes under future climate (Elmendorf *et al.*, 2015).

While climate change will impact all ecosystems, regions with Mediterranean climates are of particular concern as they are diversity hotspots with high levels of endemism (Myers *et al.*, 2000). These ecosystems are already significantly impacted by land-use change, habitat fragmentation, and invasive species, and as such, are expected to be particularly vulnerable to climate change (Klausmeyer & Shaw, 2009, Sala *et al.*, 2000). Prairies along the Pacific coast of the U.S. are no exception, with most remaining prairies being highly degraded, in large part due to a high abundance of invasive introduced species (D'Antonio *et al.*, 2007, Sinclair *et al.*,

2006), and as such are considered critically endangered ecosystems (Noss *et al.*, 1995). Furthermore, most climate change research on grassland systems has occurred in the Great Plains and Midwest regions of North America. Far fewer studies have investigated grasslands with a Mediterranean climate (e.g., Zavaleta *et al.*, 2003a). Given the asynchrony in precipitation and temperature in Mediterranean C3 grasslands, the response to climate change will likely be very different from that of the mid-continental region where the rainy season coincides with warmer months.

Despite the historical dominance of West Coast prairies by perennial bunchgrasses, invasion of introduced species has followed a biogeographic pattern with annual species tending to invade the hotter, dry prairies found in Southern California, and perennial species tending to dominate the moister prairies of Northern California, Oregon, and Washington (Clary, 2012, D'Antonio *et al.*, 2007, Everard *et al.*, 2010, Sinclair *et al.*, 2006). This pattern has been ascribed to shifts in competitive hierarchies between annual and perennial species due to changing moisture limitation along this gradient (Everard *et al.*, 2010, Richardson *et al.*, 2012). In support of this, Clary (2012) found a significant negative correlation between perennial grass cover and temperature and a positive correlation with warm-season precipitation in central California. Given these studies, the projection for prairies of this region to experience more severe summer drought (Mote & Salathé, 2010) has profound implications for future plant functional group composition (i.e., shift to annual dominance), patterns of invasion (Richardson *et al.*, 2012), diversity (Harrison *et al.*, 2015), and ecosystem processes such as albedo, evapotranspiration, and carbon cycling (Meir *et al.*, 2006, Reynolds *et al.*, 2015).

The interactive effects of temperature and precipitation may be particularly important because an increase in precipitation could ameliorate the increase in water stress associated with warming or a decrease could exacerbate the effect by further drying. This could be especially critical in Mediterranean systems, where water is limiting during the warm-season. Previous studies have found that the interactive effects of warming and precipitation on plant functional group composition and diversity were large (Hoepfner & Dukes, 2012), small (Grime *et al.*, 2008, Yang *et al.*, 2011, Zavaleta *et al.*, 2003a), or nonexistent (Wu *et al.*, 2012). However, studies that manipulate both temperature and precipitation are rare and to our knowledge, only one other experiment (Zavaleta *et al.*, 2003a) has been conducted in a Mediterranean climate (reviewed in Wu *et al.*, 2011). Despite this, recent observational studies in Mediterranean

climates have attributed the loss of species over the past 10-15 years to climate change (Harrison *et al.*, 2015, Pauli *et al.*, 2012), highlighting the need for experimental manipulations to determine the mechanisms.

In addition to the direct effects of climate on plant responses, indirect effects through altered species interactions (e.g., competition) can create feedbacks that compound or offset direct effects (Tylianakis *et al.*, 2008, Walther, 2010). For example, in response to increased spring precipitation in a California grassland, forbs decreased due to an increase in competition with introduced annual grasses, which in turn altered higher trophic levels (Suttle *et al.*, 2007). The synergistic effects of invasive species and climate change can have a particularly powerful negative impact on native biodiversity (Thuiller *et al.*, 2007), which has been attributed to invasives' wider environmental tolerances, shorter generation times, and high dispersal abilities (Bradley *et al.*, 2010, Dukes & Mooney, 1999).

We investigated the extent to which projected changes in climate may alter prairie plant diversity and community composition across a regional climate gradient by embedding a large manipulative warming and precipitation study within a 520 km Mediterranean climate gradient of increasing drought severity from north to south across Washington and Oregon, USA. Specifically we hypothesized that (1) plant diversity and richness would decrease with warmer and drier conditions (i.e., increased Mediterranean severity); (2) warming would favor introduced species; and (3) plant functional group composition of warmed plots would become more similar to that of communities further south, but added precipitation would reduce such trends by alleviating drought stress.

## **MATERIALS AND METHODS**

### **Study sites**

We selected three upland prairie study sites across a 520 km climate gradient located in the interior valleys of the western Pacific Northwest (Fig. S1). Our northern site, Tenalquot Prairie is a Nature Conservancy (TNC) preserve managed by the Center for Natural Lands Management located near Rainier, WA (46°53'47" N; 122°44'06" W). Our central site, Willow Creek (TNC preserve), is located near Eugene, OR (44°01'34"N; 123°10'56" W). Our southern site, the Deer Creek Center, is located in Selma, OR (42°16'41"N; 123°38'34" W) and is run by the Siskiyou Field Institute.

The climate of all sites is Mediterranean with increasing summer drought severity from north to south. The mean (12.3°C) and maximum (20.2°C) monthly temperatures (1981-2010) of the southern site are 1.8°C and 4.6°C warmer than the northern site (mean = 10.5°C, max = 15.6°C), respectively, with the central site intermediate (mean = 11.4°C, max = 17.3°C, PRISM Climate Group, Oregon State University, <http://prism.oregonstate.edu>). Long-term mean annual precipitation is 1434, 1134, and 1196 cm in the southern, central, and northern sites, respectively, but the southern site receives the greatest proportion of its precipitation from November through March and generally has less precipitation than the other sites in other months (Reynolds *et al.*, 2015). The 2010-11 and 2011-12 growing seasons (~mid-September- mid-June) both experienced La Niña conditions, causing lesser differences in temperature and somewhat different precipitation patterns among the sites (data shown in Reynolds *et al.*, 2015). However, the overall gradient of increasing Mediterranean drought severity from north to south held despite these conditions (Fig. S2).

Soils differ substantially among the sites, with the southern site (Loamy-skeletal, mixed, superactive, mesic Entic Ultic Haploxeroll) having the highest pH (~6.5) and nutrient availability (Pfeifer-Meister *et al.*, 2013, Reynolds *et al.*, 2015). The soil of the central site (Very-fine, smectitic, mesic Vertic Haploxeroll) has an intermediate pH (~5.8) and nutrient availability, but is more similar to the northern site (Medial-skeletal over sandy or sandy-skeletal, amorphic over isotic, mesic Typic Melanoxerand), which has the lowest nutrient availability and pH (~5.6).

Based on maps from General Land Office surveys, all sites were prairie or oak savanna around the time of Euro-American settlement circa 1850 (Central: Christy *et al.*, 2011, Southern: Hickman & Christy, 2012, Northern: <http://www.blm.gov/or/landrecords/>). However, prior to treatment implementation, all sites were dominated by introduced perennial grasses (Table S1), which is common for prairies of the Pacific Northwest. As one of the main goals of the study was to examine the effects of climate change on the range distributions of native prairie plant species (Pfeifer-Meister *et al.*, 2013) and given the rarity of high-quality prairies in the region, it was necessary to first restore the sites. We used a common seed mix and standard protocols that are typical for degraded prairies of the Pacific Northwest, giving all sites a common point of departure under the climate treatments. Moreover, this reduced the influence of local site conditions and history (e.g., seed bank, priority effects, dispersal, disturbance, etc.) in determining the initial plant community. Finally, given the extensive prairie restorations along

the West Coast (using many of the same species we seeded), our protocol made our results directly relevant to groups involved in the conservation of these imperiled ecosystems.

Extant vegetation was removed from each site in the spring of 2009 using a combination of hand raking and multiple herbicide applications (glyphosate), followed by seeding with a nearly identical mix of 32 native species in December 2009 (Table S2). Thirteen (starred species of Table S2) of the 32 species were range-restricted in the Pacific Northwest and the remaining 19 were common natives throughout the region. Seeds were wild collected or from first generation growout from the closest available source (for full details see Pfeifer-Meister *et al.*, 2013). During the establishment phase (summer 2010), the most aggressive introduced species were weeded (see starred species of Table S1), after which natural succession was allowed to occur.

## Experimental design

At each of the three sites, we increased plant canopy temperature 2.5-3.0°C and precipitation by 20% above ambient year round in a fully factorial design (3 sites  $\times$  4 treatments  $\times$  5 replicates = 60 7.1m<sup>2</sup> circular plots, Fig. S1). We increased plant canopy temperature in each heated plot by modulating infrared radiation from six overhead Kalglo 2000 watt heaters (angled at 45° to the surface) that were controlled by the average canopy temperature in the control plots. The heating technology is described in detail by Kimball (2005, 2008). An increase of 3°C was achieved for the 2010-11 growing season at each site (Oct 2010-August 2011), but due to budget constraints the heating treatment was reduced to 2.5°C for the 2011-12 growing season (September 2011-August 2012, Fig. S2). This increase is similar to both the average predicted warming of a multi-model ensemble of 3.0°C by the 2080s (Mote & Salathé, 2010) and within the range and differences among sites in annual mean and maximum monthly temperatures.

“Dummy” heaters were erected in the ambient warming treatments to control for shading effects.

Rainfall was collected on site using large polycarbonate sheets that drained into a 1900 liter cistern. Prior to the onset of the experiment (2009), 0.5-m trenches were dug around each plot and lined with aluminum metal flashing to minimize lateral flow of water and nutrients among plots. Using a gauged hose, we added the additional 20% precipitation within 2 weeks of when it fell, resulting in an increase in intense precipitation events during the wet season (~October through mid-May, Fig. S2) with little to no change during the summer drought season (~mid-May through September; see Fig. S2 for variability among sites). Though little change in

annual rainfall is predicted for the Pacific Northwest, most models predict an enhanced seasonal cycle with wetter autumns and winters, and drier conditions during the summer season (Mote & Salathé, 2010). The precipitation treatment was initiated in the spring of 2010 at all sites.

Canopy temperature (Apogee SI-121 infrared thermometer), soil temperature at 10 cm depth (107-L thermistor, Campbell Scientific Inc., Logan, Utah), and volumetric soil moisture content (0-30 cm depth, CS616-L Water Content Reflectometer, Campbell Scientific) were logged continuously (via AM16/32B Multiplexors connected to CR1000 datalogger, Campbell Scientific) in each plot for the duration of the experiment.

### **Plant community composition**

At peak growing season (May-June, determined individually by site and treatment), we measured plant cover by species using the point-intercept method (Elzinga *et al.*, 1998, Pfeifer-Meister *et al.*, 2012). In each plot, we established two 1 m<sup>2</sup> quadrats that we sampled in 2010 (pre-treatment), 2011 (year 1), and 2012 (year 2). In each quadrat, we dropped 25 equally spaced pins vertically from the plant canopy to the soil surface. Every plant touch was recorded by species, thus greater than 100% cover was possible when the canopy was layered. Any species present in the quadrat, but not hit by a pin, was given a cover of 0.4% (trace) for diversity calculations. In addition to sampling each of the experimental plots, we sampled 5 randomly located plots in the adjacent, unrestored prairies at each site in 2011 and 2012 to serve as baseline data (Table S1). In 2011, cover was likely underestimated in the southern heated plots due to a sudden onset of drought that caused plants in these plots to begin senescing prior to sampling. Species nomenclature follows the Oregon Flora Project database (<http://www.oregonflora.org>).

### **Statistical analyses**

We used a 3-way repeated measures ANOVA with site, heat, and precipitation as fixed between-subject effects and year as a within-subjects effect to examine plant cover (both absolute and relative to plot total) of functional groups, species richness, and Simpson's index of diversity ( $1 - D = 1 - (\sum_i^s p_i^2)$ , where  $p_i$  is the proportion of cover belonging to species  $i$  and  $s$  is the total number of species). Because treatments were not initiated in 2010, only data from 2011 and 2012 were included in the repeated measures ANOVA. We averaged data from the two quadrats for all analyses and used plot as our replicate unit ( $n=5$ ). Diversity metrics were calculated prior to quadrat averaging so that numbers reflect richness and diversity per m<sup>2</sup>.



Because year always significantly interacted with one or more of the main effects, we also ran individual ANOVAs within each year (where we also included the 2010 data). Finally, in cases where the sites interacted with climate treatments within a year, we further broke down ANOVAs by site. Tukey's pairwise comparisons were used to examine differences among sites. To correct for violations of normality, total cover was log transformed, metrics of relative cover (e.g., % annuals, % forbs, etc.) were arcsine square-root transformed, and diversity metrics were squared. ANOVAs were run using SPSS v. 21 (<http://www-01.ibm.com/software/analytics/spss/>). Means  $\pm$  1 standard error are presented in the results.

We performed non-metric multidimensional scaling (NMDS), an ordination method which does not assume linear relationships among variables (McCune & Grace, 2002), using the absolute species cover data (square-root transformed) to visualize differences in plant community composition among sites, years, and treatments. We also used the non-parametric analysis, ADONIS, on non-transformed data to test for significant differences among years, sites, and treatments. For the NMDS (function metaMDS) and ADONIS (functions vegdist and adonis) analyses, we used the Bray-Curtis distance matrix using the package vegan (Oksanen *et al.*, 2012) in R v. 2.15.2 (R Development Core Team, 2012).

## RESULTS

### Plant diversity

Species richness responded to interactions among year, site, warming and precipitation (Table S3), and Simpson's index of diversity (1-D) responded to an interaction among year and site ( $p = 0.010$ ) as well as site and warming ( $p < 0.001$ ). Species richness decreased over time at all sites, but the most dramatic affects were observed in the southern site, where species richness declined from an average of 32 species per  $m^2 \pm 0.5$  in 2010 to 11 species per  $m^2 \pm 0.5$  by 2012 across all treatments (Fig. 1a). This decrease in richness at the southern site was exacerbated by the heating treatment which decreased richness relative to ambient plots by  $\sim 11$  species per  $m^2$  in both 2011 and 2012 ( $p < 0.001$ , means ambient vs. warmed in 2011: 27 vs. 15; 2012: 17 vs. 6). Diversity at the southern site responded similarly with an initial Simpson's index of  $0.83 \pm 0.01$  in 2010 decreasing to  $0.63 \pm 0.02$  in ambient temperature plots and  $0.24 \pm 0.02$  in heated plots by 2012 (Fig. 1d). Unlike the southern site, Simpson's index of diversity in the central and northern sites increased slightly from 2010 to 2012 (increase of 0.06-0.11). No differences in Simpson's

index of diversity were observed at these two sites among the climate treatments, but species richness decreased in response to warming at the central site in 2011.

Native richness (Fig. 1b) and diversity (Fig. 1e) consistently decreased over time at all sites, and the warming treatment tended to further exacerbate this effect (native richness response to warming: Southern & Central ↓ 2011, Southern ↓ 2012; native diversity response to warming: Southern & Central ↓ 2011, all sites ↓ 2012). In general, the magnitude of change was less for introduced species richness (Fig. 1c) and diversity (Fig. 1f), and the effects of site, time and climate treatments were less consistent, with warming both increasing (central site 2012) and decreasing (southern site) introduced diversity.

The effect of enhanced precipitation on richness and diversity varied by year for total and native species richness ( $p \leq 0.016$ ), but was minor overall. Enhanced precipitation resulted in marginally significant decreases in overall species richness at the central site in 2011 ( $p = 0.061$ , -3 species per  $m^2$ ) and in overall and native species richness in the northern site in 2012 ( $p \leq 0.084$ , -2 species per  $m^2$ ).

#### **Plant cover**

Enhanced precipitation had no effect on plant cover, but the effects of warming and site on plant cover almost always varied by year (Table S3). Total cover tended to increase from north to south and over time (2010 < 2011 & 2012, Fig. 2a). In 2011, warming increased cover in the central and northern sites, and in 2012, warming increased cover at all sites (central site was only marginally significant,  $p = 0.074$ ). In all years, the proportion of annuals (relative to total cover) was highest in the south, intermediate at the central site, and lowest in the northern site (with perennial cover decreasing respectively, Fig. 2b, Fig. S3a). By 2012, the warming treatment amplified this natural climate gradient by increasing the relative proportion of annual cover by 10% across all sites ( $p < 0.001$ ). Although initially relative introduced cover was lowest in the southern site ( $35 \pm 2\%$ ), over time introduced species became the dominant component of the southern plots ( $92 \pm 3\%$  by 2012) despite the heavy initial seeding of native species (Fig. S3b). This dominance was even more pronounced in the warming treatment (98% introduced in warmed plots vs. 85% in ambient plots). The climate treatments did not affect the relative proportion of introduced and native species in the central and northern sites, and these sites retained a relatively equal proportion of these groups in 2011 and 2012 (introduced cover ~55%). The warming treatment increased graminoid dominance in the southern and central sites

in 2011 (marginally in southern site,  $p = 0.068$ ) and across all sites in 2012 with a mean increase of  $18 \pm 2\%$  (Fig. S3c). Forb abundance decreased accordingly. Initially, forbs were the dominant component of both the southern (88%) and northern (50%) sites, but only the northern site maintained forb dominance by the end of 2012 (68%), with the southern site (23%) becoming similar to the central site (30%).

### **Plant community composition**

The NMDS ordination revealed clear differentiation of the warming treatments, sites, and years (ellipses of Fig. 3) and explained 97.4% of the variation in our plant communities with two axes (final stress = 0.16). The x-axis primarily represented a regional gradient of space with plots in the southern site grouped on the left and plots of the northern site grouped on the right, with the central site plots intermediate. The y-axis primarily represented a gradient of succession from 2010 (lowest values) to 2012 (highest values). Warming tended to shift plots further to the left (i.e., southward) and up (i.e., accelerated succession). Though significant at all sites, this effect was most pronounced in the southern site. Plots further to the left (especially the southern site) were strongly associated with introduced species, particularly introduced annuals, while plots to the right were associated with ferns, small woody seedlings, and native perennials (vectors of Fig. 3 and Table S4). Native annuals loaded negatively on the y-axis, suggesting that over time they quickly were lost. Increases in introduced annual grasses were primarily responsible for the general shift upwards and to the left over time, while increases in native perennial grasses shifted plots upward but to the right. The ADONIS analysis revealed a significant year by site by warming interaction on the community matrix ( $P = 0.001$ , 999 permutations, Table S5). When this interaction was deconvolved, community composition of the warmed plots was always significantly different from the ambient temperature plots at all sites in both treatment years ( $P \leq 0.054$ , 999 permutations), though differences were strongest in the south ( $P < 0.001$ , Table S5). Precipitation had no effect ( $P \geq 0.212$ ).

### **DISCUSSION**

Predicting how communities will respond to climate change has emerged as one of the critical questions in ecology, particularly given that climate change may become the largest driver of species loss by the end of the century (Pereira *et al.*, 2010). To make robust predictions about climate impacts at regional scales, it is necessary to deconvolve regional trends from idiosyncratic site- and species-specific responses. We found consistent decreases in native plant

diversity, increases in total cover, and shifts in functional composition in response to warming across the regional climate gradient despite large differences in initial site conditions (e.g., current climate, seed banks, soil nutrients, etc.). Most pronounced was a consistent shift to greater dominance by annual plants and loss of forbs as the severity of Mediterranean climate was accentuated under our experimental manipulations, suggesting the potential for climate change to alter the biogeographic gradient whereby Pacific Northwest prairies may begin to resemble those in central and southern California with future climate change. This in turn could alter multiple ecosystem functions, including resistance to invasion, diversity, canopy phenology, forage quality, fire regimes, and nutrient, carbon, and water dynamics (Fridley *et al.*, 2007, Harrison *et al.*, 2015, Koteen *et al.*, 2011, Reynolds *et al.*, 2015, Richardson *et al.*, 2012, Zavaleta *et al.*, 2003b). Furthermore, this effect was greatest at the southern end of the gradient, with smaller effects further north as the experimental climate treatments interacted with the regional climate gradient, emphasizing the value of regional-scale experiments. Below, we address our original hypotheses and conclude with implications for conservation and management of these prairie ecosystems under future climate.

## **H1. Plant diversity**

Our first hypothesis, that a warmer and drier climate would decrease plant diversity and richness, and that this effect would be intensified with a greater severity of Mediterranean climate was generally supported. Heating dramatically decreased diversity and species richness in our southernmost site, and richness declined at all sites in at least one treatment year, with the strength and consistency of these effects diminishing further north (Table S3, Fig. 1). Trends in native richness and diversity were more consistent among sites, with all sites having reduced native diversity in response to warming by 2012. The precipitation treatment did little to relieve the severity of summer drought because, consistent with regional climate projections (Mote & Salathé, 2010), rainfall was primarily increased during the already wet season (Fig. S2). As a result, and contrary to our hypothesis, added precipitation decreased diversity when significant, although this effect was rare (Table S3). This indicates that the timing of precipitation may be more critical for these prairie systems than the total annual amount and that shifts toward less warm-season precipitation may exacerbate the effect of warming. Comparable decreases in diversity in response to warming have been observed in similar climates in both experimental (Lloret *et al.*, 2004, Prieto *et al.*, 2009) and observational studies (Harrison *et al.*, 2015).

However, in studies with even more severe summer drought, warming resulted in no or minimal changes in diversity while added precipitation drove diversity gains (Yang *et al.*, 2011, Zavaleta *et al.*, 2003a). In particular, the fact that Zavaleta *et al.* (2003a) observed no diversity response to warming in a California grassland further south than those in our climate gradient, suggests that there is a threshold whereby moisture stress becomes so severe that additional warming does little to further alter diversity. Their finding, in conjunction with ours, highlights the importance of soil moisture in mediating diversity responses to warming in Mediterranean and arid climates.

In a similar experiment to ours along a north-south gradient in Europe, Peñuelas *et al.* (2007) observed minimal impacts of drought or warming on plant species richness, with the only significant decrease detected in their southernmost site. However, warming levels were much lower (ca. 1°C) than in our experiment and all but the southern community were established and not undergoing rapid succession. The latter also may have contributed to the lack of response at the Jasper Ridge Biological Preserve near San Francisco, CA (Zavaleta *et al.*, 2003a). In our experiment, communities were undergoing rapid succession (see y-axis of Fig. 3). Despite using typical restoration practices, we found that current techniques were unsuccessful establishing diverse, species rich native communities under the warming treatments in our southern, central, and to a lesser extent, northern (only 2012) sites. Our findings suggest that communities at early successional stages coupled with rapid changes in climate may be more vulnerable to species loss than mature communities (e.g., Peñuelas *et al.*, 2007, Zavaleta *et al.*, 2003a). However, established plant communities may eventually experience similar losses of species richness following periodic disturbances (e.g., fire, grazing) that are characteristic of these ecosystems.

## **H2. Invasibility**

Our second hypothesis, that warming would favor introduced species, was somewhat supported. We only observed an increase in the relative cover of introduced species with warming in our southern site, which was consistent for the two treatment years (Fig. S3b, Table S3). In 2011, we also observed an increase in response to additional wet-season precipitation, but this effect was not consistent over time. We attribute the warming effect in our southern site primarily to the earlier emergence of introduced annual species in heated plots (personal observation, L. Pfeifer-Meister), even though the identity of the dominant annual changed each year (the forb *Trifolium subterraneum* L. in 2011 and the grass *Bromus hordeaceus* L. in 2012). These species formed a dense cover early in the growing season that excluded other species from

the plots, particularly native perennial species (< 2% relative cover in the warmed plots by 2012). We hypothesize that the earlier emergence of introduced annual species may have led to a priority effect that altered the successional trajectories of these warmed communities, an effect that has remained visible even three years after the warming was terminated (personal observation, L. Pfeifer-Meister). The native species may be more tightly coupled with other environmental cues (e.g., photoperiod) (Körner & Basler, 2010) or have lower phenotypic plasticity (Davidson *et al.*, 2011). Thus, the native species may be less able to exploit the increase in temperature with earlier germination, though this remains to be tested.

Interestingly, a recent meta-analysis suggests that invasion risk may be higher for sites becoming more climatically favorable (Sorte *et al.*, 2013). Conversely, sites becoming 'harsher' climatically may be more resistant to invasion. Our data do not support this hypothesis as we would have expected the highest levels of invasion in our northern site with the effect diminishing further south as drought severity became greater. However, as the authors recognized, only 5 of the 26 terrestrial studies included in the meta-analysis were sites that are relatively dry during the growing season (Sorte *et al.*, 2013). Consistent with our findings and the observed biogeographic pattern, a modeling study by Everard *et al.* (2010) suggested that reduced soil moisture can allow invasive annual grasses to competitively exclude native perennial bunchgrasses in a California grassland by more effectively competing for nitrogen, with co-existence occurring in wetter environments.

### **H3. Shifts in functional composition**

Our final hypothesis was partially supported. Community composition of warmed plots consistently became more similar to communities further south relative to the ambient temperature plots (Figs. 3, S3 & Table S5) despite the large differences in initial site conditions. However, added precipitation during the rainy season did not reduce such trends by alleviating drought stress as we initially hypothesized, because it was insufficient to counteract the effects of warming on the length and intensity of summer drought (Fig. S2). Moreover, the magnitude of these shifts in community composition appeared to be constrained by the regional climate gradient, with the greatest changes in the south (Figs. 2, 3, S3 & Tables S4, S5). The most notable changes in community composition were a loss of forb species and increases in introduced annual grasses in response to warming, with these effects dampening as one moved north. We suspect this reflects both the shorter periods of soil water deficit (Fig. S2) and slower

plant establishment and growth further north (absolute cover was lowest in the north and became progressively larger as one moved south and with warming, Fig. 2a), allowing perennial species sufficient time to establish the extensive root systems needed to survive the summer drought with less competition from introduced annuals. Previous research has shown that moisture availability mediates competitive hierarchies between annual and perennial grasses, thus influencing the success of native perennial species in these systems (Dyer & Rice, 1999, Pfeifer-Meister *et al.*, 2008). Moreover, Harrison and colleagues documented a loss of forb species (and diversity) over the past 15 years in non-restored Northern California grasslands, which they attributed to climatic drying (2015).

The timing, intensity, and duration of future precipitation coupled with increases in evapotranspiration from warming will likely be dominant drivers of annual vs. perennial dominance in these prairies (Clary, 2012, Cowling *et al.*, 2005). If current climate models are correct (Mote & Salathé, 2010), our data suggests that the increases in warm-season soil moisture deficits predicted for the Pacific Northwest will result in reductions of the perennial species that currently dominate these systems, with forbs being particularly vulnerable. This reduction in forbs at all sites in response to warming may pose substantial challenges for sustaining prairie diversity as the maintenance of forbs in the face of grass dominance is an ongoing challenge for conservation practitioners (Pfeifer-Meister *et al.*, 2012).

## Conclusions

Our results demonstrate that future climate change could have substantial effects on both native plant diversity and functional group composition in Mediterranean prairies. Importantly, our results were not idiosyncratic by site but rather followed a consistent pattern aligned with the regional climate gradient despite large differences in site characteristics. A key trend was that the effects were most dramatic on sites already experiencing more extreme Mediterranean climate and were ameliorated further north because of much shorter periods of soil water deficit. With more extreme summer drought severity, our results suggest prairies of this region may lose native diversity (especially forb species) and that annual species, particularly introduced annual grasses, will become increasingly important. Such shifts in functional composition could produce feedbacks that alter carbon, nutrient, and water cycling via changes in tissue chemistry, allocation of biomass, and phenology. We already have observed important effects of the switch

to an annual plant community on the seasonal dynamics of soil respiration in the southern site (Reynolds *et al.*, 2015).

While we observed greater differences in community composition across our latitudinal gradient than in response to warming within a site, the dual approaches of using a latitudinal gradient and experimental warming generally agreed in the direction of change, with warmed communities becoming more ‘south-like’. Using latitudinal gradients alone to infer responses of communities to climate change may overestimate the magnitude of responses to climate change on decadal scales (Elmendorf *et al.*, 2015). On the contrary, experimental warming has been shown to systematically underestimate climate impacts relative to historical observations (Wolkovich *et al.*, 2012). The agreement in direction of our coupled approach along with the historical pattern of invasion along the West Coast of the U.S. offers compelling evidence that Pacific Northwest prairies may face an increase in annual invaders. These prairies may be particularly susceptible to invasion following intense disturbances, whether wildfires, droughts, or ecological restoration.

The replacement of native perennial species by introduced annuals in California is purported to be one the “most dramatic ecological invasions worldwide” (Seabloom *et al.*, 2003), with an average loss of 40 Mg/ha in soil carbon attributed to this invasion (Koteen *et al.*, 2011). The possibility that such effects could propagate further northward under future climate will challenge conservation and restoration practitioners to navigate between the tendency to try and restore historical prairie communities, the potential for increased invasion by introduced species, and the need to reevaluate restoration targets for diversity and functional group composition in response to shifting plant biogeographies.

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## FIGURE LEGENDS

**Figure 1.** Species richness (a-c) and Simpson's index of diversity (1-D) per m<sup>2</sup> (d-f; mean  $\pm$  1 SE) in the ambient heat and heat treatments at the southern (S), central (C), and northern (N) experimental sites in 2010 (pre-treatment), 2011 (year 1), and 2012 (year 2).

**Figure 2.** Percent (a) absolute and (b) relative cover (mean  $\pm$  1 SE) in the ambient and heated treatments in the southern, central, and northern experimental sites in 2010 (pre-treatment), 2011 (year 1), and 2012 (year 2). Bars are further partitioned by functional group cover (N: native, I: Introduced, A: annual, P: perennial, G: graminoid, F: forb—see Figure S3 for coarse groups). Small letters indicate significant differences ( $p < 0.05$ ) among sites within years and asterisks indicate significant warming effects within years and sites (\*\*\* $p < 0.001$ , \*\* $p < 0.05$ , \* $p < 0.1$ ).

*Note that in 2011 absolute heated cover is likely underestimated in the Southern site as the dominant annual plants had begun to senesce prior to sampling.*

**Figure 3.** Nonmetric Multidimensional Scaling (NMDS) of plant cover in all climate treatments, sites, and years (stress = 0.16). Warming treatments began in 2011. Ellipses are included for visual differentiation of groups. Vectors are the average species loadings for each functional group (N: native, I: Introduced, A: annual, P: perennial, G: graminoid, F: forb; see Table S4 for individual species loadings). Note that the x-axis predominantly represents change over space and the y-axis predominantly represents change over time, with warming generally shifting communities left (further south) and up (enhanced succession).

## SUPPORTING INFORMATION

664 Table S1: Relative percent cover of extant vegetation prior to restoration and climate  
665 manipulations.

666 Table S2: Species and associated seeding densities used for restorations of the three sites.

667 Table S3: P-values for repeated measures, three-way, and two-way ANOVAs.

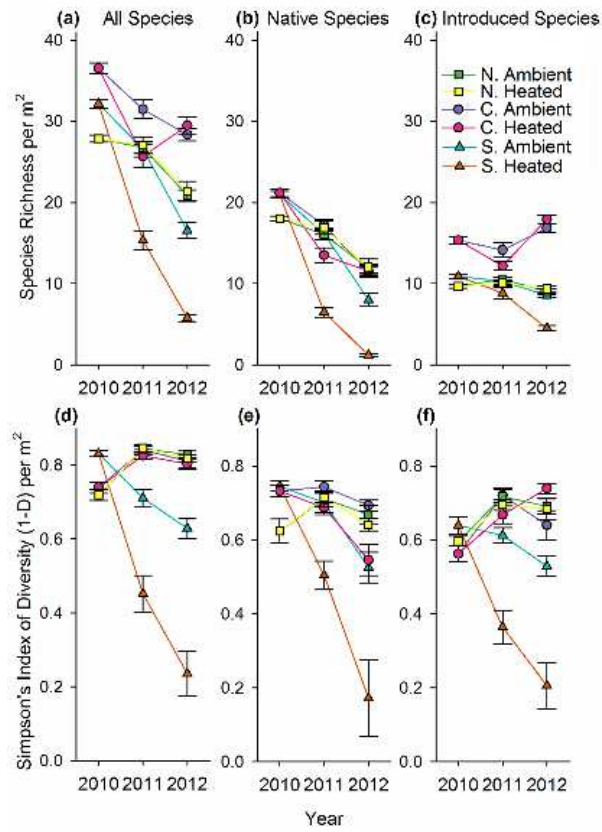
668 Table S4: Species axes loading from Non-metric multidimensional scaling (NMDS) analysis.

669 Table S5: F and P-values from PERMANOVA analyses (R-vegan function ADONIS) on the  
670 community matrix.

671 Figure S1: Map of sites and schematic of experimental design.

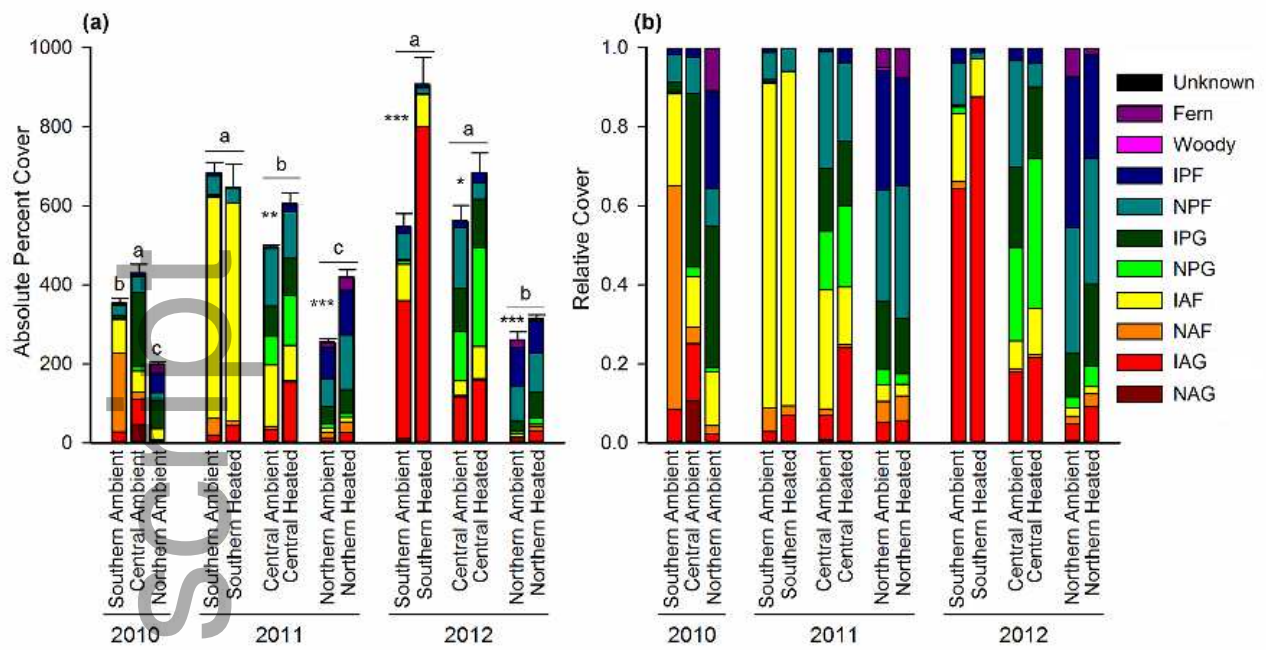
672 Figure S2: Mean soil temperature and matric potential in the climate treatments at the three sites.

673 Figure S3: Relative cover of annual vs perennial, native vs introduced, and graminoid vs forb  
674 functional groups in the climate treatments at the three sites.

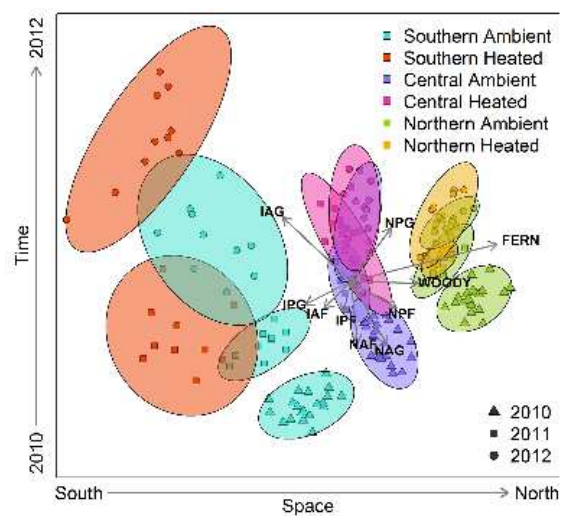


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