

Outside the envelope: rare events disrupt the relationship between climate factors and species interactions

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Abstract. The order in which species arrive during community assembly can be an important driver of community composition and function. However, the strength of these priority effects can be variable, in part because of strong site and year effects. To understand how priority effects vary in importance with abiotic conditions, we initiated identical community assembly experiments in which we varied the timing of arrival of native and exotic grass species in each of 4 yr across three grassland sites in northern California. This uniquely replicated experiment tested the power of priority to determine initial community structure in a restoration context across a natural range of conditions. There were large and significant differences in both total seeded cover and the strength of priority across sites and years of initiation, confirming the suspicion that most ecological experiments may lack spatial and temporal generality. On the other hand, much of the variation in strength of priority could be related to climate. Strikingly, however, the model fit across the three sites and the first 3 yr of the study (the first nine experiments) was radically altered when we included the fourth year, which was characterized by an unusual weather pattern with higher temporal variability in rainfall (a rainfall pattern predicted to increase with climate change). This year produced relatively low strength of priority, supporting the suggestion that highly variable climates may be associated with lower strength of priority effects. Experiments that examine community assembly over a range of naturally occurring abiotic conditions enhance our ability to predict when priority effects will be important, allowing us to explore shifting patterns of community assembly in the face of climate change and optimize restoration strategies based on environmental conditions.

Key words: climate change; climate variability; community assembly; no-analog climates; priority effects; restoration; site effects; year effects.

INTRODUCTION

Priority effects are strong drivers of community structure and function, often conferring a substantial advantage to species that arrive early (Connell and Slayter 1977, Chase 2003, Fukami 2015). Priority effects can shape the dynamics between native and exotic species (Dickson et al. 2012, Wilsey et al. 2015, Stuble and Souza 2016) and during community assembly can impact community composition far into the future (Plückers et al. 2013, Vaughn and Young 2015, Werner et al. 2016). However, the importance of priority effects in shaping communities varies across studies (Young et al., *in press*). These effects are often contingent on environmental conditions during community assembly (Kardol et al. 2013, Tucker and Fukami 2014); in particular, site and year effects (Vaughn and Young 2010). Despite their apparent importance in driving community structure, such contingencies in community assembly processes are rarely explored outside of highly

controlled laboratory or greenhouse conditions (Young et al., *in press*).

In nature, it can be difficult to know the order in which species arrived in a community. However, we can manipulate community assembly under a range of abiotic conditions in the field to begin to understand when and where priority effects may have strong effects on community structure. Understanding such contingencies in the strength of priority effects may be particularly important as climate change begins to alter the abiotic conditions under which communities assemble.

Climatic conditions that are projected for the future, such as warmer temperatures and fewer, but more extreme rain events (Easterling et al. 2000, Allan and Soden 2008, IPCC 2014), may already occur occasionally, perhaps offering glimpses into the effects of future climate change. These shifting climatic conditions likely have large implications for plant communities by shaping seedling establishment and therefore the long-term makeup of communities (Serra-Diaz et al. 2016). Climate manipulations are one approach to beginning to tease apart the importance of likely shifts in climate on biotic communities (Suttle et al. 2007, Kardol et al. 2010, Pelini et al. 2011, Young et al. 2015). These ambitious manipulative experiments typically isolate a single

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(though sometimes several) climate variable (e.g., rainfall, temperature) and manipulate it in one to several specific ways (Kreyling and Beier 2013). Such manipulative experiments are typically initiated in a single year at a single site and followed for up to several years. An alternative route to understanding the nuanced responses of community assembly to climate may be to replicate experiments across space and time to examine how natural variation in climate affects experimental outcomes (De Boeck et al. 2015).

Seeking to understand the role of priority effects in driving community composition as well as the importance of climate in modifying priority effects, we initiated identical manipulations of community assembly in which we varied order of arrival of native and exotic grasses across three sites throughout northern California in each of four consecutive years. Exotic annual grasses dominate these California grasslands at present, and restoration practitioners often (temporarily) suppress these exotic grasses when restoring natives to an area in order to allow the native species a chance to establish. We sowed study plots with native grasses alone as well as with and without temporal priority over exotic grasses. We documented native and exotic grass cover after one growing season as a function of these priority treatments and of year effects and site effects. We also examined how environmental context (year effects and site effects) impacted the magnitude of priority effects.

METHODS

Study sites

In 2011, 2012, 2013, and 2014 we established a series of experimental plots to study priority effects, site effects, and year effects in the context of grassland restoration. The entire experiment is replicated over three grassland sites in north-central California. The sites were: the UC Davis Agricultural Experiment Station in Davis, California; the McLaughlin Natural Reserve near Lower Lake, California; and Hopland Research and Extension Center in Hopland, California. The Mediterranean grassland habitat at all three sites is characterized by hot dry summers and cool wet winters. All study sites have similar flat topography and clay loam soils, but differ moderately in elevation, climate (temperature and rainfall), and neighborhood weed pressure (see Young et al. 2015 for site details, and Appendix S1: Fig. S1). All three sites had been used for crop agriculture in the past, but had been fallow for several years before the experiment, and were dominated by exotic annual weeds before site preparation.

Conditions at all three of our sites were drier and mostly warmer than the historical average in all 4 yr of study (see Appendix S1: Fig. S1). However, the 2014–2015 growing season was significantly anomalous, with rainfall falling in a few large rain events, driving significant differences in variance of daily rainfall across sites

and years (Fig. 1; year: $F_{3,6} = 5.25$; $P = 0.04$; site: $F_{2,6} = 5.97$; $P = 0.04$). This greater rainfall variability is one of the predictions for climate change: a shift toward less frequent, but more intense precipitation events (Easterling et al. 2000, Allan and Soden 2008, Kruk et al. 2015) and increasing periods without rain (Kruk et al. 2015). Such conditions have been predicted to alter the structure and function of ecosystems (Knapp et al. 2002, 2008, Fay et al. 2011), in part through altered interspecific interactions (Goldstein and Suding 2014).

Experimental design

In March–September of each of the initiation years, we collected seed of local provenance at each of the three sites (where possible) from four native perennial grasses and four exotic annual grasses (Table 1). We based species mixes and seeding rates of native grasses on recommendations consistent with grassland restoration practices in the region (Hedgerow Farms, *personal communication*). Exotic grasses were chosen based on local dominance, and seeding rates were sufficient to achieve complete cover in the absence of competition with natives. Germination rates were tested prior to sowing each year to ensure live sowing rates were consistent across sites, years, and species. For a few of these 96 provenances (4 yr \times 3 sites \times 8 species) for which local reproductive populations could not be located, we purchased seed from local native seed providers. Purchased seed were derived from populations originating from the same county as the site when available. We made some adjustments at the species level to match local sites: for the annual *Avena* species, we collected and sowed

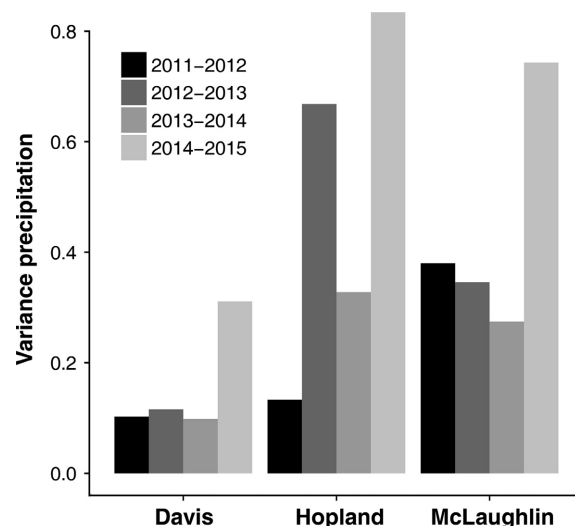


FIG. 1. Variance of daily precipitation showing the relatively high variability in daily rainfall for the 2014–2015 growing year. Bars indicate the variance associated with daily precipitation (i.e., how variable rainfall was from day-to-day) at each site for each growing year (July–June).

TABLE 1. Seeding rates of sown grasses.

Species	Seeding rate (live seed/m ²)
Native grasses	
<i>Bromus carinatus</i> Hook & Arn.	100
<i>Elymus glaucus</i> Buckley	100
<i>Hordeum brachyantherum</i> Nevski	100
<i>Stipa pulchra</i> (Hitche.) Barkworth	100
Exotic grasses	
<i>Avena barbata</i> Pott ex Link/ <i>fatua</i> L.†	100
<i>Bromus hordeaceus</i> L.	400
<i>Hordeum murinum</i> L.	100
<i>Vulpia myuros</i> (L.) C.C. Gmel./ <i>bromoides</i> (L.) Gray‡	400

† *Avena fatua* was sown at Davis while *Avena barbata* was sown at Hopland and McLaughlin.

‡ *Vulpia myuros* was sown at Davis and McLaughlin while *V. bromoides* was sown at Hopland.

A. fatua in Davis and the very similar *A. barbata* at McLaughlin and Hopland; for the annual *Vulpia* species, we collected and sowed *V. myuros* at Davis and McLaughlin, and the similar species *V. bromoides* at Hopland. We used locally sourced seed primarily to avoid translocating new genetic stock of exotic species.

At each site, we established five replicates of each of the following three planting treatments: (1) natives sown alone (N), (2) natives sown together with exotics (NE), (3) natives sown first and exotics sown 2 weeks after the next germinating rain (NtE). We used a randomized complete block design in which each site had five blocks per planting year, each block containing one replicate of each experimental treatment. Each experimental plot was 1.25 m on a side and was separated from adjacent plots by 1 m. Blocks were separated by 4 m.

Prior to planting, we tilled all sites to control weeds, both before and 1–2 weeks after the first germinating rains in the fall. Within 1 week of the second tilling, we completed the first sowing (within a 4-d period each year; dates ranged from 17 November to 6 December). We lightly raked each plot, sowed the seeds, and then raked again to increase seed-soil contact. To ensure that natives from the priority treatment's (NtE) first round of planting had an opportunity to establish before the exotic seeds were added, we waited for another germinating rain to occur after the phase one planting. In the NtE treatment, exotics were sown 2 weeks after the first rain following the sowing of native seed. In three of the 4 yr, a germinating rain occurred soon after the first planting, and in 2011, 2012, and 2013, the second set of seeds were added between 14 and 20 d following the first planting. In 2014, however, conditions were dry for 2 months following the first planting and the second round of planting was delayed until February, 74 d after the first planting.

Over the following weeks, we weeded plots of volunteer forbs to reduce competition with non-sown species. Because grasses are difficult to reliably identify at the seedling stage, we only weeded the obvious non-sown

grass species. The result was that all plots had some background of non-sown individuals, potentially diluting the priority effect.

We assessed results at a time when most grass species were flowering. For the Davis and Hopland sites, this was between 5 May and 6 June each year. The phenology of the grasses was delayed at the higher-elevation McLaughlin site, which was surveyed between 19 May and 14 June each year. The areal cover of each seeded species was visually estimated for each plot by T. Young. We collected information on temperature and precipitation from weather stations near each study site.

Statistical analysis

To understand variability in native establishment in the absence of experimentally sown competitors, we used ANOVA to examine native cover in plots in which only native grasses were sown (N) with site, year, and their interaction as explanatory variables. To determine the relationship between native cover and exotic cover when both groups were planted, we ran a linear mixed effects model exploring native cover in NE and NtE plots as a function of exotic cover (fixed effect), planting treatment (NE vs. NtE, fixed effect), site (random effect), and year (random effect) using the lme4 package in R (Bates et al. 2015). We determined significance of the fixed effect using a Likelihood Ratio Test. Data were log-transformed to improve normality.

To examine how planting treatment (planted with or without exotic grasses and with or without priority) affected native cover, we ran a fully factorial ANOVA considering the effects of site, planting year, and treatment. To examine differences in native cover across priority treatments for each planting year at each site, we conducted multiple comparisons using least squares means and determined significance based on the Tukey HSD adjustment for comparing a family of three estimates using the lsmeans package in R (Lenth 2016). We used Tukey's HSD to: (1) determine the benefit conferred by priority by comparing native cover in NtE and NE plots, (2) examine the cost of competition by comparing native cover in NE vs. N plots, and (3) examine whether native cover in priority plots differed from native cover in plots without exotics (NtE vs. N), to determine the extent to which priority might mitigate the effects of competition.

To determine the strength of 2-week priority in driving the cover of native grasses within our plots, we calculated Cohen's *d*:

$$\frac{\text{MNtE} - \text{MNE}}{\text{SD}_{\text{pooled}}}$$

where MNtE was the mean native cover within plots in which natives were given two-week priority over exotics, MNE was the mean native cover in plots in which native and exotic seeds were sown at the same time, and $\text{SD}_{\text{pooled}}$ was the pooled standard deviation. Mean

cover was averaged across blocks for each site-year combination.

To determine the environmental factors driving differences in the strength of priority among sites and years, we compared several models relating Cohen's d to environmental conditions based on P values. These models contained abiotic metrics we predicted would affect seedling establishment, including: (1) total precipitation during the growing season; (2) precipitation early in the growing season (November and December, combined); (3) precipitation in the 2 weeks following the first seeding event; (4) precipitation in the 2 weeks following the second seeding event; (5) number of rainy days during the growing season, and 6–10) mean monthly temperatures during the early growing season (November–March). We tested each of these environmental explanatory variables individually in models including site and planting year as random effects using the package lme4 in R (Bates et al. 2015). We determined significance of the fixed effect with a Likelihood Ratio Test. All statistics were run in R (R Development Core Team 2016).

RESULTS

Native cover differed significantly across sites, planting years, priority treatments, and their interactions (Table 2). When native species were seeded alone (N), native cover differed substantially across sites ($F_{2,47} = 23.00$, $P < 0.0001$) and planting years ($F_{3,35} = 44.04$, $P < 0.0001$), and there was a significant site by year interaction ($F_{6,35} = 14.76$, $P < 0.0001$; Fig. 2). Native cover in this treatment ranged from a low of just over 1% for the 2013 planting year at Davis, to a high of 89% for the 2011 planting year at Davis.

In the plots into which both native and exotic grasses were sown, there was a negative correlation between native grass cover and exotic grass cover (exotic cover: $\chi^2 = 55.19$, $P < 0.0001$; planting treatment: $\chi^2 = 98.33$, $P < 0.0001$; exotic cover \times planting treatment: $\chi^2 = 0.31$, $P = 0.58$; see Appendix S1: Fig. S2). The negative effects of exotic competition (N vs. NE) on native cover were observed across the three sites and four planting years (Fig. 2; see Appendix S1: Table S1). Providing natives with 2-week priority over exotic annuals,

however, can increase their success compared to when grown in direct competition (NtE vs. NE; Fig. 2; see Appendix S1: Table S1). In some cases this resulted in native cover that was nearly as high as that achieved when seeded without exotic species (NtE vs. N). However, the strength of this priority effect differed significantly across sites and years of initiation (Fig. 2; see Appendix S1: Table S1).

The strength of the experimental priority effect, as measured by Cohen's d , was strongly positively correlated with the number of rainy days in the growing season across the three sites and the first three planting years (2011, 2012, 2013; i.e., across nine of our twelve experimental replicates; Fig. 3a). Of the ten climatic factors considered, the number of rainy days was the predictor included in the best-fit general linear model of the strength of priority across sites in these first three years ($\chi^2 = 9.36$, $P < 0.01$, see Appendix S1: Table S2). This correlation was broadly consistent during the first 3 yr of study, apparent within each site (across years) and within each year (across sites).

The 2014–2015 growing season differed in the timing of rainfall, which primarily fell in a few large multi-day rain events that occurred in the first 2 months of the growing season (before 1st January), putting it in the top 20% of years with respect to a simple metric of this pattern: daily variance of rainfall (Fig. 1). When data from this growing season were included in the model (across all three sites), growing season precipitation (number of rainy days) essentially disappeared as a predictor of priority strength ($\chi^2 = 0.67$, $P = 0.41$). Instead, the best-fit model was one that included mean December temperature as the explanatory factor for the strength of priority ($\chi^2 = 3.31$, $P = 0.07$, Fig. 3b), though the overall fit was relatively poor.

DISCUSSION

Our unique experimental design, which replicated a priority experiment across four different years of initiation at each of three different sites, revealed a richly multi-layered contingency, with native grass cover significantly impacted by priority effects, but also by year effects, site effects, and their interaction. While we found evidence that 2-week priority had a generally positive effect on native grass cover (see also Young et al. 2015), the answer to the question—“How important are priority effects in driving initial plant community structure?”—differed strongly across sites and years. While our study provides strong evidence that the timing of arrival is an important driver of success and failure for both native and exotic species, it also provides further evidence that the outcomes of interspecific interactions are often driven by environmental contingencies (Chamberlain et al. 2014, Vannette and Fukami 2014). On the one hand, these ecological contingencies can be seen as compromising the generalizability of results from individual ecological experiments. On the other, the strong spatial and

TABLE 2. Full Factorial ANOVA results considering native cover as a function of planting treatment (N, NtE, NE), site, planting year, and their interactions.

Factor	df	F-value	P-value
Treatment	2, 143	100.50	<0.0001
Site	2, 143	34.57	<0.0001
Planting year	3, 143	66.46	<0.0001
Treatment \times site	4, 143	9.03	<0.0001
Treatment \times planting year	6, 143	18.37	<0.0001
Site \times planting year	6, 143	20.69	<0.0001
Treatment \times site \times planting year	12, 143	6.97	<0.0001

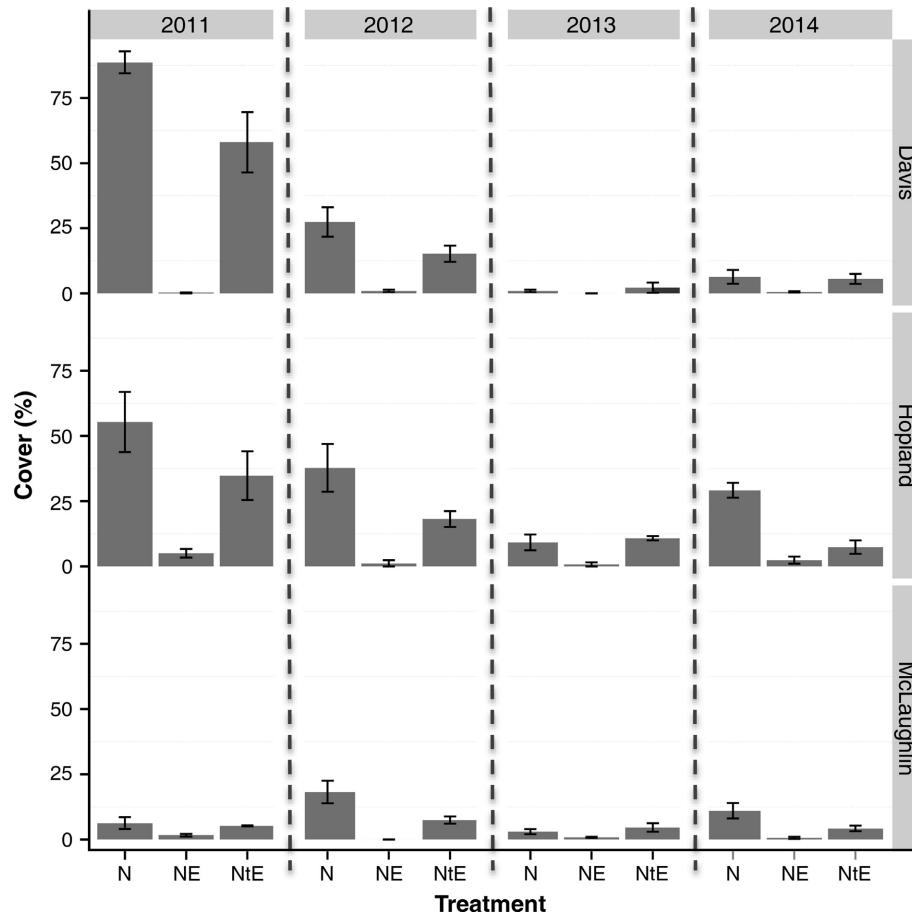


FIG. 2. Percent cover of native grasses for cohorts planted in 2011, 2012, 2013, and 2014 at Davis, Hopland, and McLaughlin.

temporal variation observed in such studies can also allow more powerful analyses of the climatic factors that are associated with various experimental outcomes, which can both inform more effective restoration practices and aid in our understanding of the effects of climate change.

The concept of harnessing spatial and temporal variation to better understand the impacts of climate change is not new. The potential impacts of climate change have been inferred from patterns across elevational or latitudinal gradients, including how biotic systems may respond to linear shifts in temperature (Ibáñez et al. 2013, Pelini et al. 2014). Likewise, historical datasets collected over many years can uncover likely responses of biotic systems to past climate change (Pitt and Heady 1978, Grabherr et al. 1994, Tingley et al. 2009, Resasco et al. 2014, Harrison et al. 2015). However, these studies often lack controlled conditions or experimental components, making it difficult to understand the shifting role of community assembly in driving community composition. Encouragingly, we found strong and significant correlations between strength of priority effects and climate (specifically, the number of rainy days) across multiple sites and (“normal”) years.

However, these projections were entirely unable to predict plant community dynamics during a year in which rain fell in a few large events, mostly early in the growing season. Despite the relatively high total rainfall, this year yielded relatively low plant cover and low strength of priority effects. Others have also found the past to be a poor predictor of relationships between vegetation and climate (Nippert et al. 2006). In our case, this less common rainfall pattern occurring in the fourth year of study may be representative of climatic conditions that will likely become more common in northern California, as rainfall events are predicted to become less frequent, but more extreme (Easterling et al. 2000, Allan and Soden 2008). The failure of the model generated across the first 3 yr (nine separate experiments) of this study to predict community dynamics within the 2014/15 year highlights the difficulties in predicting community dynamics and composition under likely future climate change scenarios.

A fundamental question is, “How can we make projections to conditions that are outside the envelope of current climate norms?” Our results suggest that such unusual rainfall patterns are already occurring in rarer

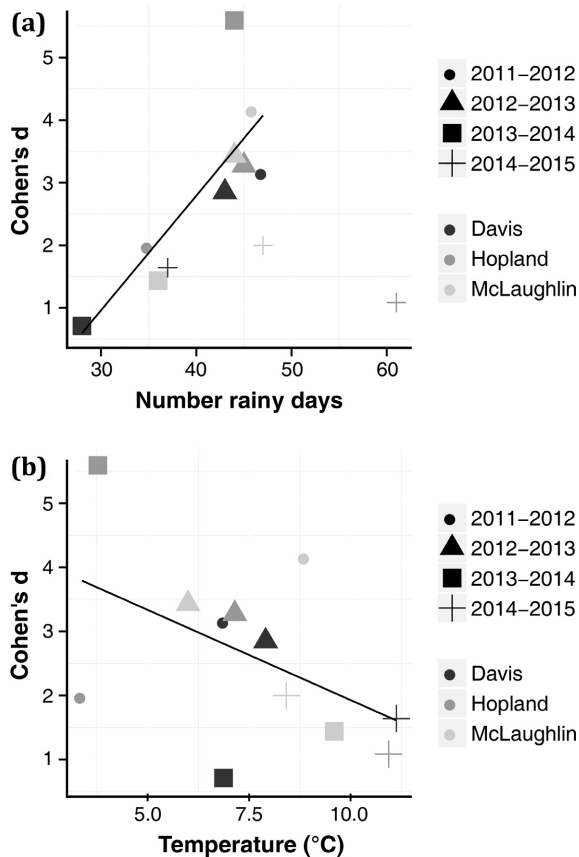


FIG. 3. Strength of priority (as measured by Cohen's *d*) as a function of (a) precipitation during the growing season ($P < 0.01$), with the 2014/2015 cohort excluded from the fitted line and (b) mean December temperature ($P = 0.07$), for all cohorts. A larger value for Cohen's *d* indicates stronger priority effects, meaning that native species attained greater cover when added earlier than exotics than when added at the same time, whereas a Cohen's *d* value of 0 would indicate that there was no difference in native cover between plots with and without native priority (NtE vs. NE).

years (and have done so in the past), and can provide windows into the future even for "non-analog" climates. Encouragingly, our results derived under field conditions are consistent with predictions from laboratory-based priority experiments suggesting that priority effects may be weak under highly variable abiotic conditions (Tucker and Fukami 2014, Fukami 2015).

While in this study we examined the impacts of priority effects after one growing season, a related field experiment in the same study system revealed that the signature of priority effects can be detected in community composition even 8 yr after planting (Werner et al. 2016), providing evidence that the impacts we see in this study will likely have persistent impacts on the plant community. Of course, our observation of the shifting strength of priority is most relevant in a restoration context in which suites of species are introduced in several stages, or non-desired species are suppressed while

desired species are establishing (Young et al., *in press*). Community dynamics become more complicated when considering natural community assembly. While shifting climatic conditions will alter the strength of priority effects, they will also simultaneously shift species' phenologies (Walther 2010, Walck et al. 2011, Polgar et al. 2014), likely altering the order and spacing of species' appearances. Our results are also driven to some extent by the amount of time between plantings. Experimental evidence suggests that longer durations between plantings generally increase priority effects (Kardol et al. 2013). As such, our relatively short interval between plantings likely yielded conservative estimates of the impacts of priority effects, and we expect stronger effects would be seen if the amount of time between plantings was increased.

California grasslands are already losing diversity as a result of recent climate change, driven in part by reduced rainfall during the growing season (Harrison et al. 2015), but community composition in these grasslands is strongly reliant on biotic, as well as abiotic, drivers (Suttle et al. 2007, Goldstein and Suding 2014). As such, species interactions provide an additional pathway by which climate change can lead to shifts in community composition (Suttle et al. 2007). Our results suggest the possibility of further reductions in native species in the future, with perennial grasses less able to compete with exotic species as rainfall events become fewer and advantages associated with priority during community assembly are diminished.

Our findings also have implications for restoration in the face of climate change. It has been shown that native grasses in California's invaded grassland systems are recruitment-limited and that established native grasses can successfully compete with exotic grasses, especially over longer time scales (Seabloom et al. 2003, Young and Veblen 2015, Young et al. 2015). Active planting of these species in invaded grasslands has been suggested as an effective means of reestablishing native communities (Seabloom et al. 2003, Corbin and D'Antonio 2004). Our study supports others that suggest that providing native grasses with even short-term priority over exotics (e.g., through seed priming or initial weed control) has the potential to further enhance restoration efforts in these ecosystems (Porensky et al. 2012, Vaughn and Young 2015, Young et al. 2015). However, our results also demonstrate that the success of this restoration strategy will be strongly variable across space and time, and may shift radically as the climate continues to change, potentially becoming less effective.

Climate-based contingencies will influence our ability to predict how restoration actions will drive conservation outcomes as the climate shifts. In our system, in "normal" years when rainfall is distributed relatively evenly throughout the growing season, using priority as a restoration strategy may be more useful during years where total rainfall is high relative to very dry years. However, extreme rainfall patterns in which much of the

rainfall occurs in a small number of large events may disrupt this rule, resulting in lower effectiveness of priority effects as a restoration strategy, even in relatively wet years. These strong context-dependent outcomes make it challenging to initiate appropriate conservation, restoration, and management strategies, but better understanding the nature of these contingencies will ultimately aid in the development of more nuanced and effective restoration strategies. Our direct test of site effects and year effects reveals that variation in conditions during experimental initiation produces profound differences in the results of community assembly manipulations, driving the importance of priority effects in shaping plant communities. Although disconcerting, this variability may give us a glimpse at the complex nature of ecological interactions under future climatic conditions, and, in the near-term, may aid in our development of management strategies for this and other imperiled ecosystems.

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