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RESEARCH ARTICLE

# Using priority effects to manipulate competitive relationships in restoration

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**Restoration success is often hampered by the failure of less dominant competitors to establish. An emerging literature on priority effects suggests the manipulation of community assembly as a useful technique to help overcome these difficulties by altering competitive relationships. We present data from a set of four priority experiments, carried out at each of three sites in restoration settings in California grasslands. These data, combined with patterns summarized from the literature, indicate that both short-term priority (1–3 weeks) and long-term priority (1 year) can profoundly shift interspecific relationships and benefit otherwise subordinate plant species, but that these effects are sometimes transitory, asymmetric, and contingent on environmental conditions and species composition. Restoration interventions that can produce priority effects include staggered planting times, weed control, seed pre-germination, plug planting, and spatial aggregation. Such interventions are likely to be at least initially effective, but their strength and persistence can differ considerably across systems in space and time. Further research may help identify the conditions that maximize the strength and persistence of priority effects in restoration settings.**

**Key words:** assembly, competitive hierarchy, contingency, dominance, grassland, site effects

### Implications for Practice

- A common impediment to successful restoration is the competitive exclusion of desired subordinate plant species, both exclusion of native species by exotics, and exclusion of some species by others within a native seed mix.
- Priority effects (planting or seeding of subordinate species earlier than competitive dominants) may offset this competitive exclusion.
- Even short-term temporal priority can profoundly shift competitive relationships in favor of earlier-planted species, but these effects differ considerably in strength and persistence across systems and even within systems across sites or planting years.
- Several restoration techniques may serve to implement these priority effects and improve restoration outcomes, including staggered planting times, initial weed control, seed pre-germination, plug planting, and spatial aggregation.

## Introduction

One of the emerging conceptual frameworks for restoration is assembly theory, either narrowly or broadly defined (Temperton et al. 2004; Young et al. 2005; Suding & Hobbs 2009), but applying these concepts to increase restoration success has lagged, perhaps in part because their direct utility to practitioners has been obscure. One of the central underlying concepts of assembly theory is that the order of arrival of species (temporal priority) can influence long-term community structure through niche preemption (Belyea & Lancaster 1999; Young et al. 2005). For example, it has been suggested that the earlier germination and faster initial growth rate of annuals gives them a competitive advantage over perennials, and short-term priority experiments suggest that this is indeed the case (Deering & Young 2006; Vaughn & Young 2015). Temporal priority may also function to increase initial densities of recruits that only later come to dominate in cover (Vaughn & Young 2015).

Although our emphasis here is on interspecific priority, this process also can occur within species. Initial size advantage can increase through time, perhaps because larger individuals get better access to limiting resources, essentially outcompeting smaller individuals (e.g. Ellison & Rabinowitz 1989; Rice & Dyer 2001; Harmon & Stamp 2002).

Restoration ecologists recently have begun to explore whether manipulating community assembly, and more specifically priority effects, could assist in restoration by shifting competitive relationships. There are two situations in particular where competition among plant species reduces restoration

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success. First, competition with non-native invasive species can be a strong impediment to restoration success (Wilson & Gerry 1995; Dyer & Rice 1997; Brown & Rice 2000; Stromberg et al. 2007), particularly in less stressful habitats (Zefferman et al. 2015). In some plant communities (California U.S. grasslands in particular), competition with invasives is the single greatest impediment to restoration (Stromberg et al. 2007). Second, within a restoration palette, a few strongly competitive native species often quickly come to dominate restoration plantings. For example, in tallgrass prairies, perennial grasses tend to dominate over co-planted forbs (Shirley 1994). In both cases, temporal priority may allow otherwise subordinate species to benefit from early arrival into the system, allowing them to establish more successfully and/or persist longer within the restored community.

Here, we report on the strength and longevity of priority effects as determined from several short-term (2-week) and long-term (1-year) priority experiments followed for 4 years after the initial plantings. This is the first study to examine priority across multiple study sites and multiple forms of priority. We also report a review of the literature on priority effect experiments in plant communities. We then explore the practical applications for this emerging restoration technique.

In particular, our experimental study was designed to test: (1) Can short-term and long-term priority seeding alter restoration outcomes in favor of the species seeded earlier? (2) Are priority effect symmetrical; that is, is the priority advantage of native grasses over native forbs similar in magnitude to the priority effects or native forbs over native grasses? (3) Does the strength of such priority effects vary at different sites or with time?

## Methods

We experimentally tested four priority treatments in restoration settings in California grasslands: (1) giving native perennial grasses a 2-week seeding advantage over exotic annual grasses, (2) giving native perennial grasses a 1-year seeding advantage over exotic annual grasses, (3) giving native perennial grasses a 1-year seeding advantage over native forbs, and (4) giving native forbs a 1-year seeding advantage over native perennial grasses. Each of these experiments was carried out at each of three similar sites in northern California. All 12 experimental combinations (four priority trials and three sites) were replicated five times.

### Study Sites

The experiments were carried out at three sites in north-central California on flat, relatively fertile clay loam soils, but that differ moderately in climate (temperature and rainfall; Table S1, Supporting Information). All three sites had been used for crop agriculture in the past, but had been fallow for several years before the experiments, and were dominated by exotic weeds before site preparation.

Site preparation for all experiments replicated standard restoration practices for California grasslands. There were one to two initial tillings at each of the three sites for weed control, and subsequent tilling or herbicide treatment of the sites one to two times per year between and around the perimeter of all seeded blocks, and mowing (Davis) or herbicide treatment (Hopland and McLaughlin) between individual plots within blocks. Plots scheduled for seeding were tilled or treated with glyphosate after the first germinating rains.

### Experimental Implementation and Data Collection

There were two experimental designs, each of which comprised two experiments sharing controls and blocked together. The first two experiments tested (1) short-term and (2) long-term priority of native perennial grasses over exotic annual grasses, compared with these two guilds planted at the same time. The third and fourth experiments tested (3) giving native grasses a 1-year advantage over native forbs, and (4) giving native forbs a 1-year advantage over native grasses, compared with seeding these two guilds at the same time. Species composition and seedling rates of all treatments (Table 1) were based on local restoration standards (J. Anderson, Hedgerow Farms personal communication January 2010). The seeding density for exotic grasses is at the low end for naturalized annual grassland reseeding rates in the field (e.g. Dyer & Rice 1997; Eviner & Firestone 2007), but was more than sufficient to create stands that achieved 100% aerial cover in the first year. Each plot was $1.25 \times 1.25\,\mathrm{m}^2$, with 1 m spacing between plots. Plots were grouped into replicate blocks containing all treatments (within each set). Blocks were separated by 2 m.

In the first pair of experiments (1 and 2), there were four treatments, blocked together (Table 2): four native perennial grasses seeded alone (N), the native grasses seeded at the same time as a mix of four annual exotic grasses (NE), the exotic grasses seeded 2 weeks after than the native grasses (NtE), and the exotic grasses seeded 1 year after the native grasses (NttE).

In the second pair of experiments (3 and 4), there were five treatments, blocked together (Table 2): four native perennial grasses seeded alone (G), four native forbs seeded alone (F), the native grasses and forb seeded at the same time (GF), the native

**Table 1.** The species used in this experiment, and their seeding rates (seeds/m$^2$). The native species and their seeding rates are commonly used locally in grassland restoration.

| *Native Perennial Grasses* | *Exotic Annual Grasses* | *Native Forbs* |
|---|---|---|
| *Stipa* (*Nassella*) *pulchra* (100) | *Vulpia* (*Festuca*) *myuros*/*V. bromoides* (*Hopland*) (400) | *Eschscholzia californica* (125) |
| *Bromus carinatus* (100) | *Bromus hordeaceus* (400) | *Achillea millefolium* (175) |
| *Hordeum brachyantherum* (100) | *Hordeum murinum* (100) | *Croton* (*Euphorbia*) *setigerus* (50) |
| *Elymus glaucus* (100) | *Avena barbata*/*A. fatua* (*Davis*) (100) | *Asclepias fascicularis* (50) |

**Table 2.** The planting design of the two sets of experiments (each involving two experimental priority comparisons), each of which was identically implemented (with five replicates) at each of three sites.

| *Experiments 1 and 2*<br>*Treatment* | *Initial Seeding (November 2011)* | *Two Weeks Later* | *One Year Later (November 2012)* |
|---|---|---|---|
| N | Native grasses | | |
| NE | Native and exotic grasses | | |
| NtE | Native grasses | Exotic grasses | |
| NttE | Native grasses | | Exotic grasses |

| *Experiments 3 and 4*<br>*Treatment* | *Initial Seeding (November 2011)* | *One Year Later (November 2012)* |
|---|---|---|
| G | Native grasses | — |
| F | Native forbs | — |
| GF | Native grasses and forbs | — |
| GtF | Native grasses | Native forbs |
| FtG | Native forbs | Native grasses |

forbs seeded 1 year after the native grasses (GtF), and the native grasses seeded 1 year after the native forbs (FtG).

Seed was collected locally for each site in the spring and summer of each planting year. When local collections were insufficient, we purchased local seed. Seed mixes were hand sown into each plot, and then lightly raked.

All experimental blocks were replicated five times at each site in each year of initiation. The initial seeding occurred 18–20 November 2011. The 2-week priority seeding of annual grasses (NtE) occurred 5–7 December 2011. The 1-year priority seeding occurred 17–19 November 2012. All secondary seedings were done into plots with extant vegetation and litter, and were not raked after seeding. All plots were hand weeded during the first-growing season, removing seedlings of species not in the seed mixes. At peak flowering at the end of the growing season each spring, percent cover of all seeded species was visually estimated. These visual estimates correlate strongly with pin frame counts (Werner et al. in press).

### Statistical Analyses

For each experiment, we first tested the competitive effect of the target guild grown alone and grown with the target competitor guild, e.g. native grasses grown alone versus native grasses seeded together with exotic grasses. We then tested priority by comparing the success of the target guild seeded together with the competitor guild versus seeded earlier than the competitor guild. We also calculated "percent recovery." Using one of the experiments as an example, native cover in N is what can be achieved without competition, and this less native cover in NE (N−NE) is the "cost" of competition. If priority allows complete recovery (100%) from competition, then native cover in NtE would equal native cover in N, and NtE−NE would equal N−NE. Our "recovery" metric [(NtE−NE)/(N−NE)] quantifies how close to this competition-free cover is achieved by giving the natives priority. We ran analysis of variances (ANOVAs) with priority as a fixed effect, blocked by site (as a fixed effect). The initial analysis included survey year as a repeat measures factor. This analysis revealed multiple significant year by site by treatment interactions. Therefore we analyzed the two survey years separately, (1) one growing season after the addition of the second guild and (2) 4 years after initial planting.

### Literature Review

We summarized all plant priority experiments that we could find in the literature, using search terms "plant* and priority*," and following citation threads for relevant articles, both from this search and from our own knowledge of the literature. We limited ourselves to studies that experimentally manipulated plant species arrival, excluding articles that followed natural variation in arrival or emergence, or did seed additions over existing plant communities. Each paper was scored for the target and competitor species or guild, the length of the priority, the duration on the study, and the results. We also noted whether the research was done in greenhouses or in the field, and if the latter, in pots or in situ. The differences in methods between the different studies were sufficiently large (and the total number of studies insufficiently great) that we did not attempt formal meta-analyses.

## Results

### Two-week Priority of Native Grasses Over Exotic Grasses

Across all sites, the initial success of native perennial grasses was 96% lower when seeded together with exotic grasses (NE) as compared to natives seeded alone (N) after one growing season (Fig. 1; N, 53% cover, NE, 2% cover, $F = 41.17$, $p < 0.001$). After four growing seasons (the duration of this experiment), this competitive effect was still significant, though less pronounced as native cover generally increased in the NE plots over time. Native cover was 53% lower in NE plots as compared to N plots after four growing seasons (N, 50% cover, NE, 24% cover, $F = 28.59$, $p < 0.0001$). Total seeded cover initially differed strongly across sites, with Davis achieving the highest cover, and McLaughlin the least, but became more similar later.

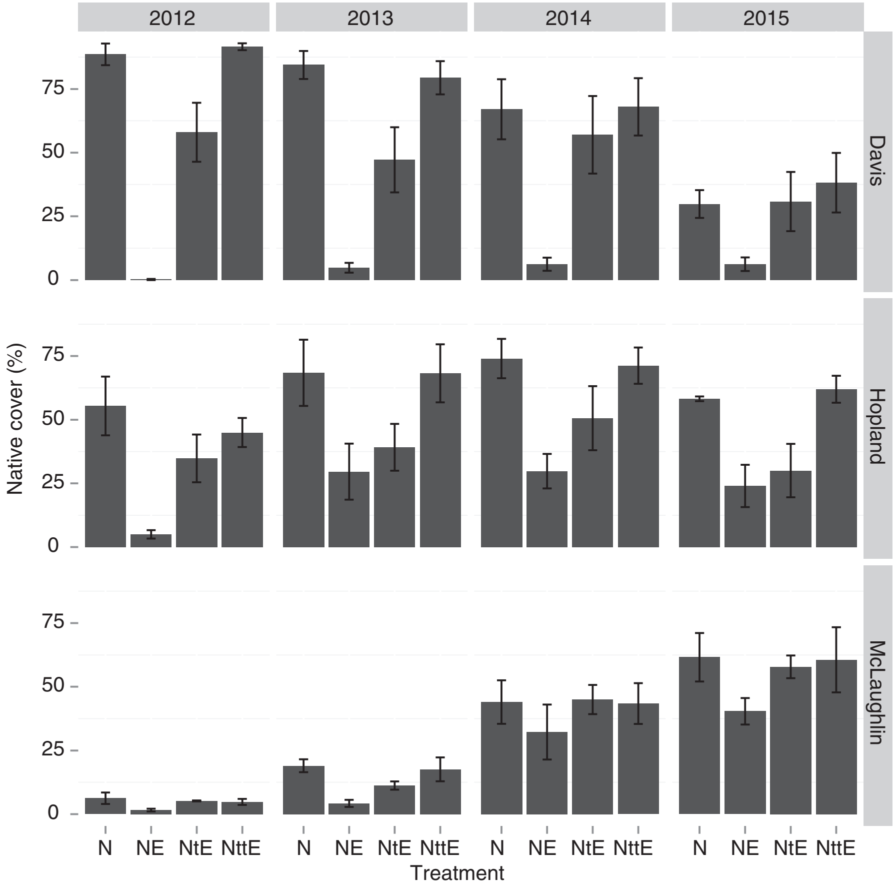

Figure 1. Percent cover of native perennial grasses in treatments initially seeded in 2011 testing the advantage of 2-week (NtE) and 1-year (NttE) priority over annual exotic grasses, in each of three sites in each of the four subsequent growing seasons. Treatment acronyms are explained in Table 2. Error bars represent ± 1 SE. Note that at the time of the 2012 data collection, the second seeding of the NttE treatment had not yet occurred, so only the last 3 years test this priority.

Giving the native perennial grasses a 2-week seeding advantage over the exotic annuals resulted in a 13-fold increase in native cover (NtE plots relative to NE plots) after one growing season (Fig. 1; NtE, 33% cover, NE, 2% cover, $F = 22.06$, $p < 0.001$). This represented a recovery of 60% of the cover lost to competition when planted together with the exotic annuals. After four growing seasons, the positive effects of priority were still pronounced with native cover in NtE plots 68% greater than in NE plots (NtE, 40% cover, NE, 24% cover, $F = 6.39$, $p = 0.02$), a 61% recovery in the native cover lost as a result of competition. The recovery was least in McLaughlin, where native cover was initially low, regardless of treatment.

### One-year Priority of Native Grasses Over Exotic Grasses

Giving the native perennial grasses a 1-year seeding advantage over the exotic annuals (NttE) resulted in a three-fold increase in relative cover of native grasses relative to plots in which native and exotic grasses were sown simultaneously (NE) two growing seasons after the natives were planted (one growing season after the addition of the exotic grasses) (Fig. 1; NttE, 55% cover, NE, 30% cover, $F = 31.08$, $p < 0.0001$). This represented a recovery of 95% of the cover “lost” to competition when planted together with the exotic annuals. Four growing seasons after initial planting (three growing seasons after the addition of exotics to the plots), native cover in 1-year priority plots (NttE) was 128% higher than in the plots in which natives and exotics were sown at the same time (NE) (Fig. 1: NttE, 54% cover, NE, 24% cover, $F = 19.52$, $p = 0.0002$) and native cover in these 1-year priority plots was actually slightly (but not significantly) higher than in the plots in which natives alone were sown (N, 50%). Though both 1-year and 2-week priority for native grasses over exotic grasses increased native cover, in the long-term 1-year priority was more positive than 2-week priority (NtE versus NttE). Both forms of priority were least pronounced at McLaughlin, where native cover was initially low, regardless of treatment (Fig. 1).

### One-year Priority of Native Grasses Over Native Forbs

The initial success of native perennial grasses was moderately reduced when seeded together with native forbs (G versus GF plots). Cover of native perennial grasses was 22% lower in GF plots than in grass-only plots two growing seasons after planting

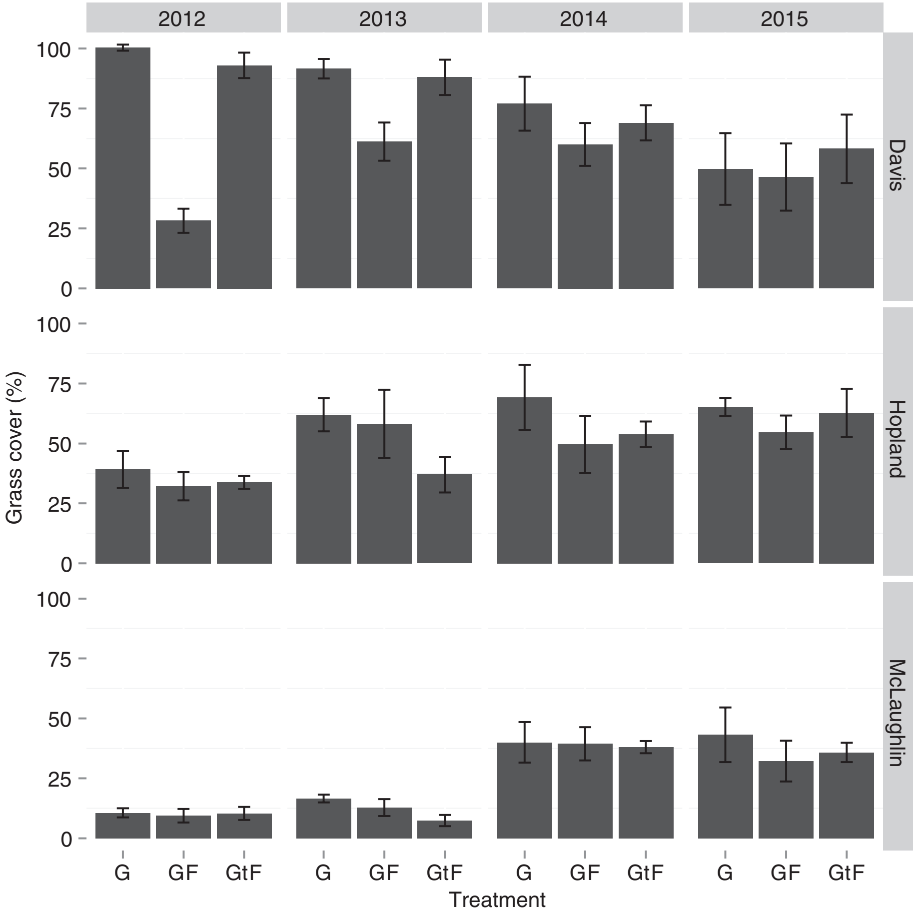

Figure 2. Percent cover of native grasses in treatments initially seeded in 2011 testing the advantage of 1-year priority of these grasses over native forbs, in each of three sites in each of the four subsequent growing seasons. Treatment acronyms are explained in Table 2. Error bars represent ± 1 SE. Note that at the time of the 2012 data collection, the delayed forb seeding (treatment FtG) had not yet occurred, so only the last 3 years test this priority.

(Fig. 2; G, 57% cover, GF, 44% cover, $F = 3.87$ cover, $p = 0.06$). Four growing seasons after planting, there was no longer a significant signature of forb competition on grass cover (G, 53% cover, GF, 44% cover, $F = 0.98$, $p = 0.33$).

Across all sites, giving the native perennial grasses a 1-year seeding advantage over native forbs did not increase in relative cover of the grasses two growing seasons after planting of the grasses (1 year after planting the forbs in the priority treatments) (GtF, 44% cover, GF, 44% cover, $F = 0$, $p = 0.993$). Four growing seasons after initial planting of the grasses, there was still no significant evidence of positive priority effects on native grasses (GtF, 52% cover, GF, 44% cover, $F = 0.94$, $p = 0.34$). Only at Davis (which had highest initial cover in general) was there a priority signal, and even there, it disappeared by the fourth year (Fig. 2).

### One-year Priority of Native Forbs Over Native Grasses

Across all sites, the initial success of native forbs was significantly reduced when seeded together with native grasses. After two growing seasons (the first growing season after the second seeding), cover of native forbs was 53% lower in GF plots than in F plots (Fig. 3; F, 41% cover, GF, 20% cover, $F = 8.28$, $p = 0.008$). After the full four growing seasons, there was still a 47% decrease in forb cover in GF plots as compared to F plots (F, 40% cover, GF, 21% cover, $F = 10.03$, $p = 0.004$).

Giving the native forbs a 1-year seeding advantage over native grasses resulted in a doubling of forb cover (FtG plots relative to GF plots) (FtG, 39% cover, GF, 20% cover, $F = 7.68$, $p = 0.01$), which represented a recovery of 91% of the cover “lost” to competition when planted together with the grasses. After four growing seasons, there was still a 63% increase in forb cover in forb priority plots (FtG) over plots in which forbs and grasses were planted at the same time (FtG, 35% cover, GF, 21% cover, $F = 5.21$, $p = 0.03$), representing a 70% recovery in forb cover lost to competition.

### Changes in Community Structure (Species Abundances)

Not only did co-seeding with a competing guild usually reduce the abundance of the target guild, it did so for some species more than others, resulting in a shift in within-guild community structure (Figs. S1–S3). In addition, within each experiment, the species most affected by competition often differed between

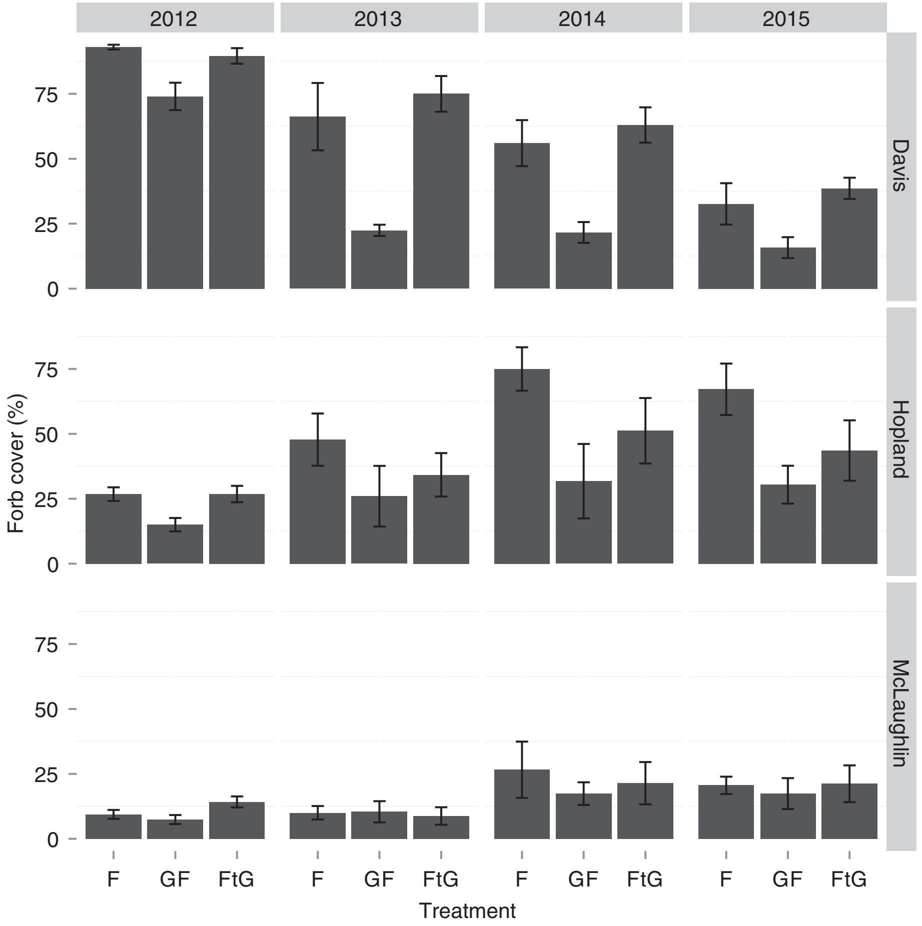

Figure 3. Percent cover of native forbs in treatments initially seeded in 2011 testing the advantage of 1-year priority of these grasses over native grasses, in each of three sites in each of the four subsequent growing seasons. Treatment acronyms are explained in Table 2. Error bars represent ± 1 SE. Note that at the time of the 2012 data collection, the delayed forb seeding (treatment GtF) had not yet occurred, so only the last 3 years test this priority.

sites. All forms of short-term and long-term priority tended to restore the within-guild community structure to one similar to that when seeded alone (e.g. N was more similar to NtE than to NE).

#### Literature Review

In addition to the four experiments described here, we found 14 priority research publications reporting 27 plant priority experiments (Table S2, Körner et al. 2008; Grman & Suding 2010; Dickson et al. 2012; Martin & Wilsey 2012; Kardol et al. 2013; Perkins & Hatfield 2014; Stevens & Fehmi 2011; von Gillhaussen et al. 2014; Schantz et al. 2015; Werner et al., in press). Although the length of time between plantings varied from 1 week to 3 years, the great majority (21/27, or 78%) tested short-term priority of 1–6 weeks between plantings. Only seven (26%) were monitored for longer than a single growing season, and three of those were from our study system (Young et al. 2015*a*, 2015*b*; Werner et al., in press). Fourteen of the 27 experiments (52%) were carried out in a greenhouse, five in outdoor pot mesocosms (19%), and eight in field plots (30%). Most demonstrated significant priority effects, but three of the five that did not were from the seven longer-term experiments.

### Discussion

Our priority experiments and review of the priority literature confirm the widespread ability of even short-term differences in arrival times (as little as 1 week) to shift interspecific relationships and therefore the structure of plant communities. Our experimental results also demonstrate, however, that these priority effects are strongly contingent (e.g. dependent on site), are sometimes asymmetrical (i.e. benefit some guilds more than others; see also Blaisdell 1949; Cleland et al. 2015; Vannette & Fukami 2014; Werner et al. in press), and are of variable persistence.

The likelihood and strength of priority effects depends in part upon whether conditions—both abiotic and biotic—allow for rapid growth and niche preemption by early-arriving species (Fukami 2015). For example, priority effects are expected to be stronger in less harsh, more productive environments that promote higher relative growth rates that accentuate competitive interactions (Chase 2003; Fukami 2015). In the experiments reported here, we observed variability in the strength (and occurrence) of priority effects among both planting sites and years consistent with this expectation. Priority effects were consistently weaker at McLaughlin, the least productive planting site (lowest initial plant cover), than at Hopland or Davis. Overall growth was lower at McLaughlin, where plots did not achieve full cover after the first growing season. Likewise, priority effects were weaker when initial sowing occurred in years with relatively less rainfall and produced less cover (unpublished data). In this same system, priority effects were weaker when no rainfall occurred in the interval between sowing of early- and late-arriving guilds (Vaughn & Young 2015). These results, and a watering experiment done in this system (Young et al. 2015*a*, 2015*b*), suggest that, in our study, water availability limited the ability of guilds sown early to preemptively utilize niche space and establish priority.

Conditions that promote increased population growth in early colonizers are only expected to yield priority effects if those increases are substantial relative to the rate of immigration by later-arriving species (Fukami 2015). In experiments 1 and 2, we experimentally delayed the arrival of exotic annual grasses for periods of 2 weeks or 1 year, and observed stronger expression of priority effects when immigration was delayed longer. In experiments 3 and 4, we delayed immigration of the later-arriving guild for 1 year, and found that the benefits of priority were asymmetrically expressed between the two guilds. Forb growth significantly decreased when forbs were sown simultaneously with grasses. In our study, the increased growth afforded to forbs by a 1-year delay in native grass arrival was sufficient to result in a longer-term (4 years) increase in forb cover. In contrast, simultaneous sowing only marginally reduced growth in grasses, so it is unsurprising that grasses did not benefit from delayed forb arrival.

Our review of priority literature indicates that often the imprint of early priority effects on community composition fades with time. Whether priority effects persist may depend on a variety of factors, including the mechanism underlying early colonists' initial success and whether strong competitive relationships exist among assembling species. For example, early-arriving species expressing short-term priority gained through niche preemption (rather than modification) will not maintain this initial advantage in the long term if late-arriving species are competitively superior (Fukami 2015). In our study system, the competitive relationships between native perennials and exotic annuals are known to depend on life stage (Vaughn & Young 2015): whereas exotic annuals can outcompete perennial seedlings (e.g. Dyer & Rice 1997), established perennials suppress exotic annuals (e.g. Seabloom et al. 2003). This difference played out across our three sites. In McLaughlin, where exotics were slower to grow, the 2-week priority produced an immediate native recovery, but in Davis, the priority effect in term of cover was delayed, perhaps because priority increased density of natives, but strong competition with exotics delayed the full growth (cover) of natives for a few years (see Vaughn & Young 2015). That previous study (Vaughn & Young 2015) also showed that the short-term advantage afforded to native perennials by delayed introduction of exotic annuals can persist for at least 4 years.

In restoration, where goals are based on long-term community structure and function, longer-term monitoring of priority effects for persistence is particularly advisable (see Werner et al. in press). Fukami et al. (2005) underscore the potential advantage of monitoring traits rather than simply species composition, and show that historical contingency may lead to divergent community structure, but longer-term convergence in function (guild structure), which in some cases may be the goal for restoration.

### "Inverse Priority"

Although it did not occur in our restoration experiments or the research covered by our literature review, one possible outcome of a priority experiment could be that later arrivals actually perform *better* when preceded by a given guild of early arrivals. The various expressions of such facilitative (as opposed to competitive) plant–plant relationships in the context of restoration have already been explored elsewhere (Padilla & Pugnaire 2006; Brooker et al. 2008; Ren et al. 2008; Yelenik et al. 2014), and may involve the suppression of weedy species by the earlier plantings that can assist in the establishment of later planted species (Kuusipalo et al. 1995; Parrotta et al. 1997; D'Antonio & Meyerson 2002; Jones et al. 2004; Wilsey et al. 2015).

### Implications for Restoration

As described in the Introduction section, there are situations arising in restoration where the ability to shift competitive relationships would be helpful. For example, it has been suggested that weighting the seed mix more heavily toward weaker competitors may increase their success (e.g. forbs, in tall grass prairie; Shirley 1994, p 42). In addition, several forms of temporal priority may prove useful in provided subordinate species a better chance at long-term success.

The most obvious of these manipulations is planting in two or more passes, introducing (seeding) the more subordinate species at some time interval before going back to seed the more dominant species, by which time the subordinate species might have established sufficiently to withstand competition, at least for a period of time. This is one of the recommendations for establishing forbs in grass-dominated prairies (Shirley 1994, p 42), and is being carried out in at least one Western prairie restoration site (http://appliedeco.org/seeding-the-prairies/). This requires additional costs and longer time frames, however; luxuries that many restoration projects may not be able to afford. Our experiments found that forbs in particular may benefit greatly from temporal priority, achieving significantly greater cover when given priority over native grasses in a California grassland. These effects were strong and lasting; obvious even 4 years after the initial planting. Native grasses (the dominant native guild in this system), on the other hand, did not show a strong response to priority, doing well with and without temporal priority.

Conversely, we have found examples where restoration practitioners have returned to over-seed "subordinate" forbs into prairies initially restored primarily with grasses (A. Fulks, J. Anderson, personal communication), with limited success. This may be done with "inverse priority" effects in mind (i.e. you establish the grasses first to keep out the invaders, then you add the more sensitive forbs). The idea of overplanting minor or missing species into restoration planting, however, faces a double hurdle of (1) trying to introduce often less competitive species, and (2) overcoming the additional competitive disadvantage of priority by the competitive dominants.

Planting grass plugs or container stock is sometimes done in order to reduce the time it takes individuals to reach a particular (sometimes contractual) size, but it can also be considered a form of priority planting, where the temporal head start (over non-native annuals, for example) is given to target species even before planting in the field. This technique has been shown to increase per plant survivorship (but see Young & Evans 2001), although not necessarily in a cost-effective way (Bainbridge et al. 1995; Palmerlee & Young 2010).

Another way to achieve temporal priority in a single planting pass is the use of aggregated plantings, where mono-specific patches (or seeding rows) of dominants and subordinates are planted at the same time. Because it takes some time for the dominant species to invade the other patches, subordinate species are essentially given more time to establish themselves (Grygiel et al. 2009, 2014; Porensky et al. 2012; Yurkonis & McKenna 2014; Seahra et al. 2016), thus achieving temporal priority in localized patches and resulting in higher levels of diversity at broader spatial scales. Such aggregated planting has been recommended by some practitioners, under the terms "mosaic planting" (Shirley 1994, p 42) and "Precision Prairie Reconstruction" (Grygiel et al. 2009, 2014).

Another potential use for priority within the context of restoration is to tip the competitive balance between native and exotic species by providing natives with short-term temporal priority over exotics. Experiments demonstrating the ability of native grasses to better compete with exotics if given temporal advantage may be analogous to pre-planting weed control, since the exotics usually reestablish within days to years after their control. In our experience in California grasslands, weed challenge is usually retarded for no more than a year after even fairly aggressive weed control. Even a late herbicide or light tilling pass after the first germinating rains (in the window between quick-germinating exotics and usually more slowly germinating natives) may provide the kinds of short-term windows of opportunity that these priority experiments suggest can be effective. Our experiments demonstrate that providing natives with only 2-week priority over exotics can provide significant benefits for native grasslands in a California grassland restoration, and that this benefit was still obvious within the restored communities a full 4 years after planting. This benefit has also been demonstrated by multiple short-term priority experiments (Table S2).

In addition, techniques that "pre-germinate" native seeds may provide a short-term priority that can offset some of the temporal advantage that exotic grasses seems to have over native grasses (or perhaps more accurately, can be described as off-setting the normal priority benefit enjoyed by early-germinating and fast-growing exotic annuals). These techniques include seed priming (Hardegree & Emmerich 1992; Hardegree 1994) and "cold-damp stratification" (Shirley 1994, p 43). Such "pre-germination" of native perennial grass seed can advance their germination times by several days, and has been demonstrated to (sometimes) take away at least some of the competitive advantage of the exotic annuals (Deering & Young 2006).

Although the experimental results reported here, combined with those from the literature (Table S2), provide strong evidence that even short-term priority usually results in an initial significant shift in species abundance in favor of the species planted earlier, the evidence that these positive outcomes will persist is less abundant, and more mixed. Are we truly overcoming competitive exclusion, or merely delaying it? It is worth noting that virtually none of the studies monitored for only a single growing season or less failed to show a priority effect (one or two out of 16). In contrast, two of the four publications in Table S2 that monitored priority experiments for more than one season suggested that the priority effects were short-lived. One long-term study of spatial aggregation as a priority technique also showed only temporary benefits (Porensky et al. 2012; Young et al. 2015*a*, 2015*b*). It is noteworthy, however, that one of the multi-year studies actually showed an increase in priority effect through time (Vaughn & Young 2015).

If restoration projects are to achieve sustainability, innovative techniques need to improve not just short-term but also long-term restoration success. Various restoration techniques that take advantage of temporal priority to alter restoration outcomes will need to demonstrate whether, and under what circumstances, their short-term gains can be parlayed into more permanent increases in restoration success.

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## Supporting Information

The following information may be found in the online version of this article:

**Figure S1.** Across the three study sites, relative cover in 2014 by the four species of native perennial grasses across the four experimental treatments: control (N), competition with exotic grasses (NE), short-term priority (NtE), and long-term priority (NttE).

**Figure S2.** Across the three study sites, relative cover in 2014 by the four species of native perennial grasses across the four experimental treatments: control (G), competition with native forbs (GF), and long-term priority (GtF).

**Figure S3.** Across the three study sites, relative cover in 2014 by the four species of native perennial forbs across the four experimental treatments: control (F), competition with native grasses (GF), and long-term priority (FtG).

**Table S1.** Site characteristics.

**Table S2.** Published plant priority experiments.

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