

Persistent asymmetrical priority effects in a California grassland restoration experiment

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Abstract. The order of species arrival can dramatically alter the trajectory of community development. While there is experimental evidence that priority effects can be important drivers of community structure early on, the persistence and duration of these effects is unclear. Here we report on a community assembly experiment in which a mix of four native grasses and a mix of four native forbs were planted on their own, together, or with one-year priority over the other guild. We found positive effects of priority for both grasses and forbs in the initial years of the experiment. However, 6–8 yr after planting, the effectiveness of priority treatments were mixed. Some species became rare, persisting only in treatments in which they had been given priority; others continued to maintain high cover and exhibit a strong positive signal of priority effects; still others remained common but no longer showed a signature of the initial priority effects; and finally, some species became locally extinct across all experimental plots. Grass priority over forbs was strong and persistent, but not forb priority over grasses. Our results demonstrate that the long-term benefits of temporal priority can persist for at least 8 yr for some, but not all species, and these continued effects result in distinct community composition. Manipulating the trajectory of community assembly through priority in seeding has potential as a useful tool for restoration.

Key words: *Achillea*; *assembly*; *contingency*; *Hordeum*; *Lupinus*; *Nassella*; *Stipa*; *succession*.

INTRODUCTION

Community assembly can be an important driver of ecosystem structure and function, influencing which species establish and persist, as well as relative abundance (Connell and Slatyer 1977, Chase 2003). One of the central processes that drive community assembly is priority, or order of arrival. Species that receive priority (i.e., arrive earlier than others) often have a competitive advantage associated with greater individual size or density, allowing them to competitively suppress or exclude later-arriving species (Cole 1983, Fukami 2015). Mechanisms driving the benefits of priority appear to be a combination of size-asymmetric competition (Ellison and Rabinowitz 1989, Ejrnæs et al. 2006, Grman and Suding 2010, Wainwright et al. 2012), negative plant–soil feedbacks mediated by the soil microbial community (Grman and Suding 2010, van de Voorde et al. 2011), and ability of early arrivers to drastically reduce soil nutrients and water, thereby limiting competitor success (Fargione et al. 2003, Vannette and Fukami 2014, Fukami 2015).

It has been repeatedly demonstrated that priority effects can increase the establishment success of species

planted or seeded earlier than others (e.g., Deering and Young 2006, Grman and Suding 2010, Stevens and Fehmi 2011, Wainwright et al. 2012, Kardol et al. 2013, von Gillhaussen et al. 2014, Perkins and Hatfield 2014, Cleland et al. 2015). However, it might also be expected that in the longer term, convergent (e.g., successional) forces within the community could overcome the effects of priority on community composition (Young et al. 2001, Fukami et al. 2005). Previous experimental studies of priority effects in plant communities have typically only followed the resultant assemblages for a single growing season or less (those cited previously) and those extended for a couple years are mixed on whether priority persists, fades, or is dependent on site factors (Blaisdel 1949, Porensky et al. 2012, Pluckers et al. 2013, Vaughn and Young 2015), leaving unanswered the question of whether and when successional convergence swamps the effects of priority. More and longer-term studies of priority are required to tease apart these contrasting drivers of community structure.

A problem commonly encountered by restorationists is that in general, only a subset of seeded species persist aboveground in the long term. Often, competitive dominants quickly supplant less-dominant species, and this is particularly true in grassland ecosystems where restoration efforts often result in dominance by perennial grass species at the expense of forb cover (Menninger and Palmer 2006, Lulow et al. 2007). This is also true for

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restoration of California's Central Valley prairie, which is particularly troubling given recent evidence that these communities may historically have been forb-dominated (Hamilton 1997, Minnich 2008, Evett and Bartolome 2013), and at the very least contained a species-rich forb component (Lulow and Young 2009). As such, managing the order of species arrival has potential as a valuable restoration tool, allowing managers to enhance the establishment and likely success of desirable species by staggering the timing of planting (Palmer et al. 1997, Young et al. 2001, Vaughn and Young 2015), or by planting different species in separate but adjacent patches (Porensky et al. 2012).

Here, we report on the influence of priority effects on long-term community composition in a California grassland restoration site. Specifically, we manipulated the assembly order of native grasses and forbs in field-based mesocosms, alternatively providing grasses or forbs with one year of priority, seeding both guilds at the same time, or seeding guilds alone. Plots were followed for the first three years after planting and then resurveyed 6–8 yr after initiation to determine if initial priority effects had lasting impacts on community composition.

STUDY SITE AND METHODS

Study site

All plots were located in the Plant Sciences Agricultural Research Fields on the University of California, Davis campus (38.54° N, 121.78° W). The study site is located in the Central Valley of California, USA and experiences an interior Mediterranean climate with high inter- and intra-annual variability in timing and amount of precipitation. Mean annual precipitation is 442 mm, falling almost entirely between October and April (Menne et al. 2015). Summer (dry season) maximum temperatures average 32°C, and winter (wet season) minimum temperatures average 5°C (Menne et al. 2015). Soil at the study site is classified as Yolo Silt Loam (Natural Resources Conservation Service 2015). The study area was unplanted and tilled biannually for weed control for over three years prior to planting, before which it was used for agricultural cropping.

Experimental design and monitoring

We prepared 217 plots, each measuring 1.5 × 1.5 m and separated from each other by a 1-m buffer in a regular grid. Plots were tilled two weeks prior to planting. We randomly assigned each plot to one of three initiation years (2007, 2008, and 2009) and to one of six treatments (design in Appendix S1: Table S1): Grass Only (mix of four native perennial grasses), Forb Only (mix of native annual and perennial forbs), Simultaneous (combined mix of native grasses and forbs, planted simultaneously), Grass Priority (mix of native grasses and forbs, with forbs planted one year after the grasses), and Forb

Priority (mix of native grasses and forbs, with grasses planted one year after the forbs); Control plots were unseeded. There were 25–26 replicates of each seeded plot (127 seeded plots) and 90 unseeded control plots. Native species and local ecotypes were selected to represent those believed to be common in California interior grasslands prior to exotic annual invasion, as well as used commonly in local grassland restoration projects (J. Anderson, *personal communication*; seed densities in Appendix S1: Table S2). Seed was obtained from Hedgerow Farms (Winters, California).

In each year of initiation, we broadcast seed into tilled plots and raked them to ensure adequate soil contact. The priority treatments received a second seeding of the other guild (native grass or forb) ~1 yr later. In these plots we carefully broke up any bare soil surfaces (avoiding damage to already established plants) with a hard-tined hand rake, broadcast seed, and raked into the soil as with the initial seeding. Seeding in all 3 yr was conducted between 10 and 18 November. All plots were planted at a rate of 800 live seeds/m², with the Simultaneous, Grass Priority, and Forb Priority plots receiving 400 live seeds/m² each of grasses and forbs (Table S1). This seeding rate is comparable to the lower end of current grassland restoration practices in the region (typical range of 600–1600 total seeds/m²; J. Anderson, *personal communication*).

All plots were hand weeded for two growing seasons (November–June) following establishment to reduce competition from unplanted species. Additionally, areas between and around plots were tilled annually for the first 3 yr. To minimize the influence of plot edge effects, we collected data only from the inner 1 m² of each plot. In June 2008, 2009, and 2010 and May 2015 we visually estimated aerial cover for native grasses and forbs at the species level, weeds (a combination of exotic grasses and forbs), and bare ground in all plots. To corroborate our visual cover measurements, we simultaneously collected pin hit data in June 2008; these two estimates had strong *r*² correlations of 0.98 for grass cover, 0.98 for forb cover, 0.99 for weed cover, and 0.96 for bare ground, thereby supporting the accuracy of our visual cover estimates.

Statistical analyses

We compared mean cover of grasses and forbs, both as guilds and as individual species, between contrasting treatments using an *F* test comparison of means, with a *P* value of 0.05 as the threshold for significance (R Core Team 2013). We conducted multivariate analysis of community composition with a permutational analysis of variance test (PERMANOVA; Oksanen et al. 2015). The test was run on the results of a Bray-Curtis similarity matrix for plots measured in 2015. Data were permuted 1000 times to calculate the pseudo-*F* and *P* values for this test. We used nonmetric multidimensional scaling (NMDS) to visualize plot dissimilarity based on the Bray-Curtis similarity index.

RESULTS

Initial effects of priority

We monitored species cover in plots established in Year 1 (2008) at 1, 2, 3, and 8 yr after initial seeding to track the effects of priority through time. Two years after initial seeding (1 yr after the addition of round-two seeding in the priority plots), native grass cover in the Grass Priority treatment was almost twice that of the Simultaneous treatment where grasses and forbs were planted at the same time (Fig. 1a; $F = 7.13$; $P = 0.02$; $n = 20$). Although there was 23% greater cover of native forbs in the Forb Priority treatment than in the Simultaneous treatment, this difference was not statistically significant (Fig. 1b; $F = 2.9$; $P = 0.11$; $n = 20$). Three years after the initial seeding, these effects of priority increased: native grass cover in the Grass Priority treatment was more than double that in the Simultaneous treatment ($F = 33.5$; $P < 0.01$), and native forbs continued the trend of higher cover in the Forb Priority treatment, with 17% higher cover than the Simultaneous treatment ($F = 3.82$; $P = 0.07$).

Priority persistence in overall community composition

At the final cover survey, 6–8 yr after seeding, some species had disappeared entirely from all treatments; other grass species persisted only in the Grass Only and Grass Priority treatments (Table 1). Total native cover of all grasses and forbs was lower 6–8 yr after seeding than 2–3 yr after seeding (Fig. 1). Even with this overall loss of native cover, seeded native communities differed substantially in composition across treatments.

The cover of planted species in 6–8 yr after seeding differed significantly across priority treatments (PERMANOVA analysis results in Appendix S2: Table S1, pseudo- $F = 8.88$, $P = 0.001$) with Grass Only and Grass Priority plots tending to have relatively more

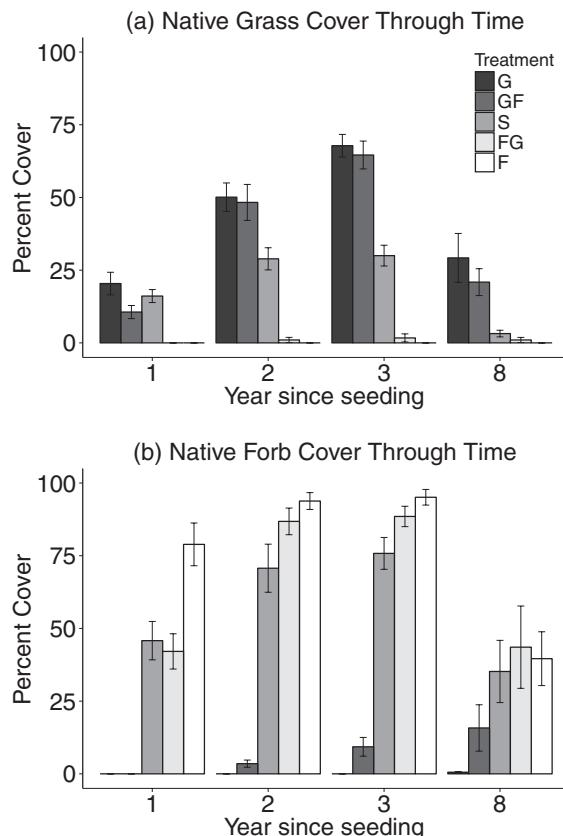


FIG. 1. Percent cover through time of the Year 1 seeding of (a) native grasses and (b) native forbs, with grass only (G), grass priority (GF), seeded simultaneously with the other native guild (S), forb priority (FG), and forb only (F) treatments. Average cover is shown by treatment, with standard error (SE). Plots were weeded to remove exotics for the first 3 yr after seeding, and left unweeded for the following 5 yr.

Stipa pulchra, *Poa secunda*, and *Hordeum brachyantherm*, Forb Only and Forb Priority plots tending to have more *Lupinus formosus* and *Achillea millefolium*,

TABLE 1. Percent cover (means with standard error) of native species in 2015 by treatment, across all years of establishment.

	Treatment					
	Grass Only (%)	Grass Priority (%)	Simultaneous (%)	Forb Priority (%)	Forb Only (%)	Control (%)
Total native grasses	29.2 ^A ± 4.6	18.7 ^B ± 3.5	9.32 ^C ± 2.5	2.80 ^C ± 1.2	1.38 ^C ± 1.1	2.13 ^C ± 0.67
<i>Stipa pulchra</i>	28.2 ^A ± 4.4	17.8 ^B ± 3.5	9.1 ^{B,C} ± 2.5	2.80 ^C ± 1.2	1.38 ^C ± 1.1	2.12 ^C ± 0.66
<i>Hordeum brachyantherum</i>	0.60 ^A ± 0.34	0.64 ^A ± 0.44	0 ^A	0 ^A	0 ^A	0.0 ^A
<i>Poa secunda</i>	0.36 ^A ± 1.4	0.24 ^A ± 0.20	0.20 ^A ± 0.1	0 ^A	0 ^A	0.01 ^A ± 0.01
<i>Koeleria macrantha</i>	0 ^A	0 ^A	0 ^A	0 ^A	0 ^A	0 ^A
Total native forbs	4.28 ^A ± 1.4	11.4 ^A ± 3.2	33.0 ^B ± 5.0	33.0 ^B ± 6.1	34.7 ^B ± 5.3	16.5 ^A ± 1.7
<i>Lupinus formosus</i>	0.16 ^A ± 0.09	5.56 ^{A,B} ± 0.29	18.5 ^{B,C} ± 4.4	18.8 ^{B,C} ± 5.9	20.8 ^C ± 5.8	1.61 ^A ± 0.8
<i>Achillea millefolium</i>	4.12 ^A ± 1.4	5.84 ^{A,B} ± 1.2	14.4 ^{B,C} ± 2.3	14.2 ^{B,C} ± 2.1	13.9 ^{B,C} ± 2.1	14.9 ^C ± 1.5
<i>Lotus purshianus</i>	0 ^A	0 ^A	0 ^A	0 ^A	0 ^A	0 ^A
<i>Calandrinia ciliata</i>	0 ^A	0 ^A	0 ^A	0 ^A	0 ^A	0 ^A
Exotic species	65.2 ^A ± 4.1	69.0 ^A ± 4.4	55.9 ^A ± 5.4	63.1 ^A ± 5.7	62.5 ^A ± 5.0	80.5 ^B ± 1.8

Note: Superscripted uppercase letters indicate significant differences across rows.

and Simultaneous plots showing intermediate distributions of species (Fig. 2a). There was also significant variability in community composition across years in which the plots were established (pseudo- $F = 6.66$, $P = 0.001$). Plots initiated in the first year had the highest cover of *L. formosus* and the lowest cover of *A. millefolium*, those initiated in the third year showed the opposite pattern, and those initiated in the second year were intermediate for both species. Cover of *S. pulchra* was highest in plots initiated in the second year, and cover of *H. brachyantherum* was highest in plots initiated in the third year. However, there were no significant interactions between priority treatment and year of initiation

(pseudo- $F = 1.19$; $P = 0.28$), so for subsequent analyses we combined the final cover data (6–8 yr after seeding) across all years of initiation.

The competition and positive priority effects for native grasses persisted 6–8 yr after initial seeding (Fig. 2b). Native grasses averaged 70% lower cover in the Simultaneous treatment than the Grass Only treatment ($F_{51} = 15.9$; $P < 0.01$) (Table 1). The Grass Priority treatment had double the mean native grass cover of the Simultaneous treatment, which represented most of the difference in grass cover between the Simultaneous and Grass Only treatments (Fig. 2b; $F_{50} = 4.78$; $P = 0.03$). In contrast, the priority trend observed earlier for dominant

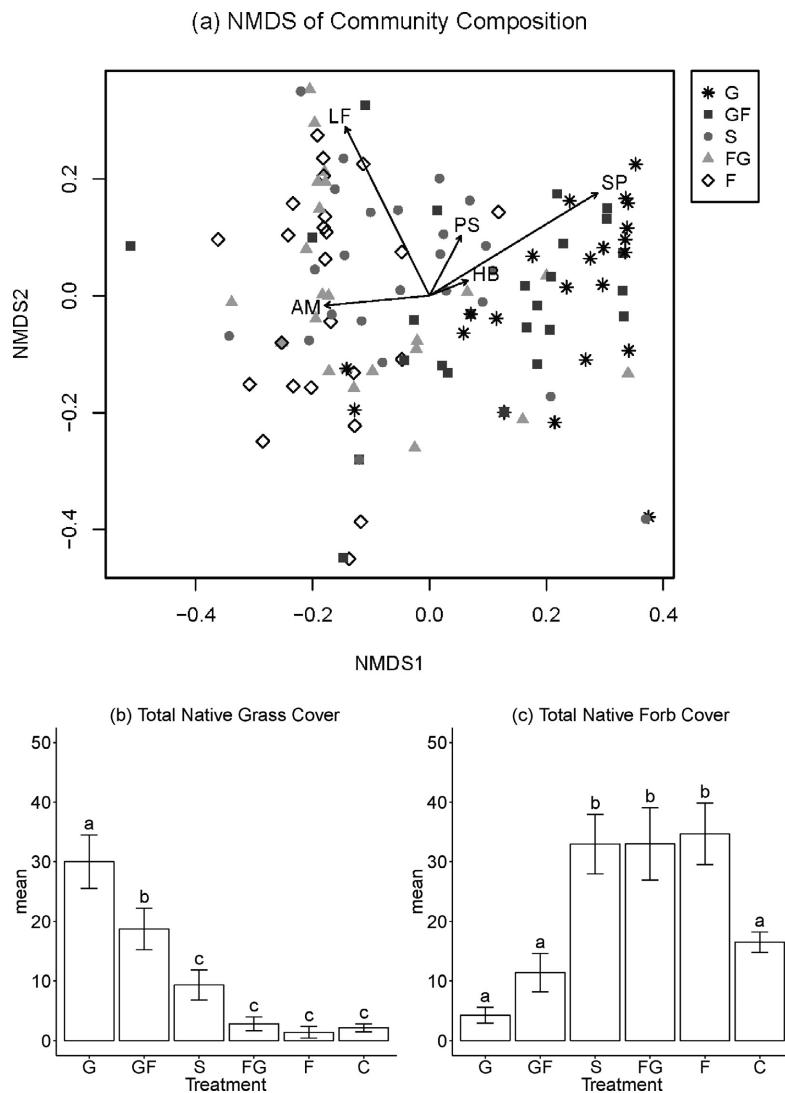


FIG. 2. (a) Nonmetric multidimensional scaling (NMDS) of differences in compositional similarity of native plant community 6–8 yr after seeding (2015) by treatment, with all seeding years combined. Vectors show abundances of forbs *Lupinus formosus* and *Achillea millefolium*, and grasses *Stipa pulchra*, *Hordeum brachyantherum*, and *Poa secunda*. Ordination stress across two dimensions is equal to 0.164. (b) Percent native grass cover (\pm SE) by treatment 6–8 yr after seeding. (c) Percent native forb cover 6–8 yr after seeding. Bars not sharing a lowercase letter were significantly different. Treatments are grass only (G), grass priority (GF), simultaneous (S), forb priority (FG), forb only (F), and control (C).

native forbs essentially disappeared; forbs performed equally well in the Simultaneous treatment as in the Forb Priority treatment and the Forb Only treatment (Fig. 2c; $F_{50} = 0.23$; $P = 0.64$). Mean cover for native forbs was lower in the Grass Priority treatment (Fig. 2c; $F_{50} = 13.1$; $P < 0.01$). In 2015, cover of exotics was significantly lower in all seeded treatments than in the Control treatment ($P < 0.05$), but otherwise did not depend on treatment (Table 1; $F = 0.94$; $P = 0.44$). In summary, the long-term priority effect of grasses over forbs persisted after 6–8 yr, but the priority effects of forbs over grasses did not, largely because forb cover was not reduced in the long-term when forbs were seeded together with grasses.

Long-term priority effects on individual species

In addition to seeded native grasses on the whole, strong priority effects remained evident for some individual native grass species 6–8 yr after initial establishment. Mean cover of *S. pulchra* was 69% less in the Simultaneous treatment as compared to the Grass Only treatment ($F_{51} = 15.8$; $P < 0.01$) (Table 1). Cover in the Grass Priority treatment was intermediate to these two treatments, and double that in the Simultaneous treatment ($F_{50} = 4.22$; $P = 0.045$; Fig. 3a).

The cover of native forb dominants *A. millefolium* (Am.) and *L. formosus* (Lf.) was 70% and 60%, lower, respectively, in the Grass Priority treatment as compared to the Simultaneous treatment (Fig. 3c,d; Am. $F_{50} = 11.2$; $P = 0.002$; Lf. $F_{50} = 6.09$; $P = 0.017$). Despite this, neither of these forb species had lasting benefits from early arrival in the Forb Priority treatment (Am. $F_{50} = 0.004$; $P = 0.95$; Lf. $F_{50} = 0.001$; $P = 0.97$).

Subordinate native grasses *H. brachyantherum* and *P. secunda* were present at very low cover values (<0.3%, and <0.2% overall), and in only 13% of seeded plots, but their pattern of occurrence (Fig. 4, $\chi^2 = 2.47$, $P = 0.12$) paralleled that of native grasses overall (Fig. 2b, almost entirely *S. pulchra*). Their presence was higher (albeit not significantly) in the Grass Only treatment (35% of plots) than in either the Simultaneous treatment (12% of plots) or the Grass Priority treatment (20% of plots). The seeded species *Koeleria macrantha* (a perennial grass), *Calandrinia menziesii*, and *Lotus purshianus* (seeded annual forbs) were absent from all plots sampled in 2015.

DISCUSSION

This long-term study revealed that shifts in community composition caused by priority effects can persist for at least eight years. However, the extent and duration of the effects of priority were variable across species and guilds.

Asymmetric competition between grasses and forbs

Efforts to restore species-rich grasslands may be hindered by competitive interactions among native

species, with dominant species suppressing the establishment or growth of subordinates. In our seed mixes, competition with native forbs resulted in lower cover and persistence of native grass species. For example, grass cover was lower in the Simultaneous treatment than the Grass Only treatment, beginning in the first year after seeding and continuing through the extent of the study.

In contrast, cover of native forbs was not strongly impacted by competition with native grasses. Lower cover of forbs in the Simultaneous treatment than the Forb Only treatment in the first few years likely reflects the difference in seed count, as the Simultaneous treatment seed was split between forb and grass. Six to eight years after seeding, forb cover was similar in the Forb Only and Simultaneous treatments, indicating competition was primarily asymmetric, with forbs reducing native grass cover but not being impacted by them. Our results complement evidence that California grasslands may have originally been forb-dominated (Minnich 2008, Evett and Bartolome 2013). However, competitive interactions are often species-specific, so broader conclusions on competitive dominance of native forbs and grasses would require examination of larger suites of native species.

Asymmetric priority

Providing a one-year priority to native grasses over seeded forbs shifted the competitive balance such that grasses achieved and maintained higher cover throughout the duration of this eight-year study. The observed higher cover in the Grass Priority treatment may be due to increased seedling establishment rates (Seabloom et al. 2003, Vaughn and Young 2015) or faster growth rates of individuals under lower competitive stress (Dyer and Rice 1999).

The responses of individual species to competition and priority demonstrate a qualitative disconnect between short- and long-term results. Early effects of priority benefited both native grasses *S. pulchra* and *H. brachyantherum* for the first three years. During this time, percent cover of these grasses increased in the Simultaneous treatment and the Grass Priority treatment, but increased more quickly in the latter treatment, resulting in increased strength of priority effects over the first three years. Six to eight years after seeding, cover of *S. pulchra* had decreased substantially in the Simultaneous treatment plots relative to previous years, but declined only slightly in the Grass Priority plots. However, the cover of *H. brachyantherum* had decreased dramatically in all treatments such that, while cover still followed patterns of priority, the differences were no longer statistically significant.

Asymmetric persistence of priority effects

Our results of short-term priority effects are consistent with previous work in this system demonstrating

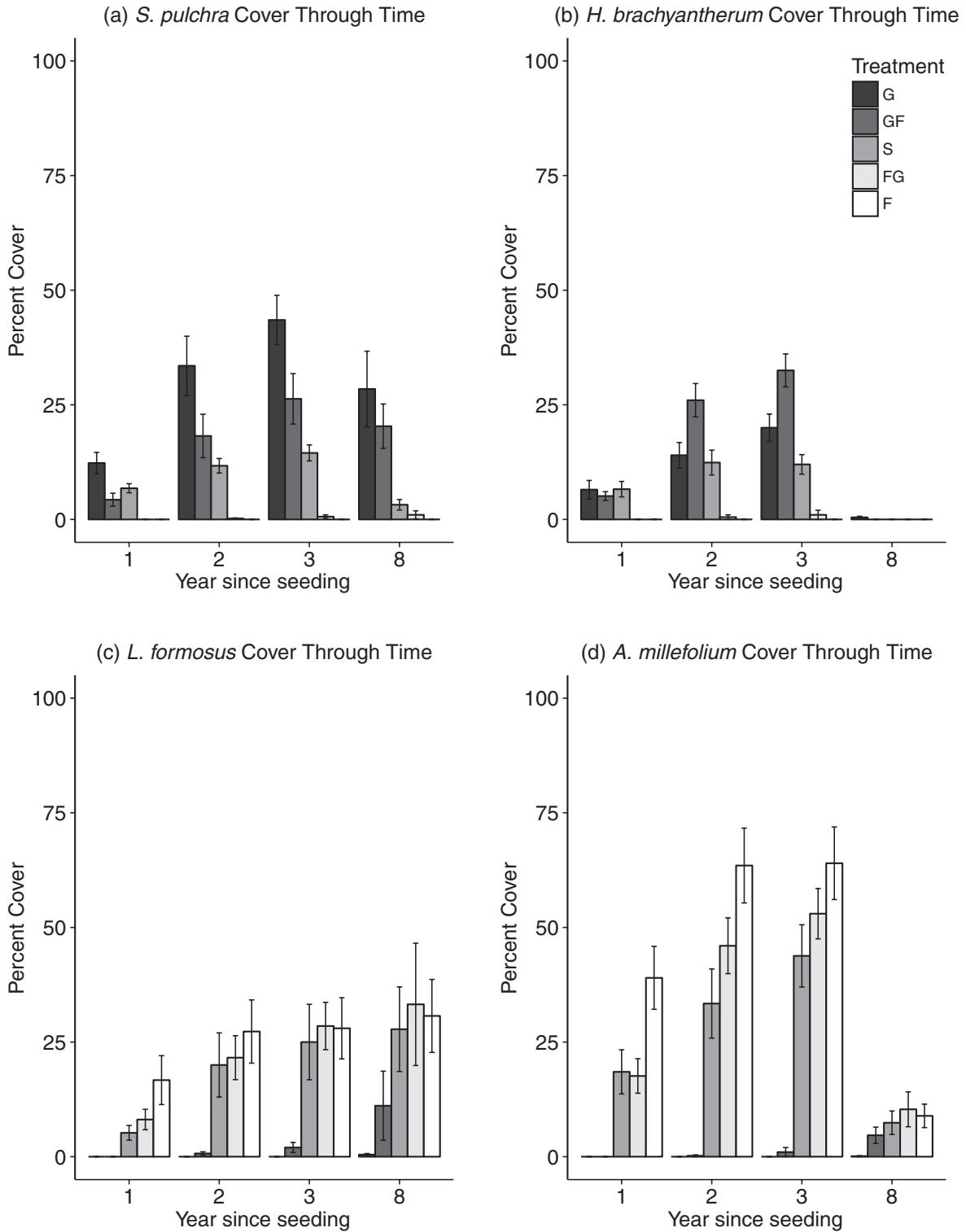


FIG. 3. Percent cover through time of the Year 1 seeding of native grasses (a) *S. pulchra* and (b) *H. brachyantherum*, and native forbs (c) *L. formosus* and (d) *A. millefolium*, with standard error. Treatments are as in Fig. 1, with the addition of control (C). Plots were weeded to remove exotics for the first 3 yr after initial seeding, and left unweeded for the following 5 yr.

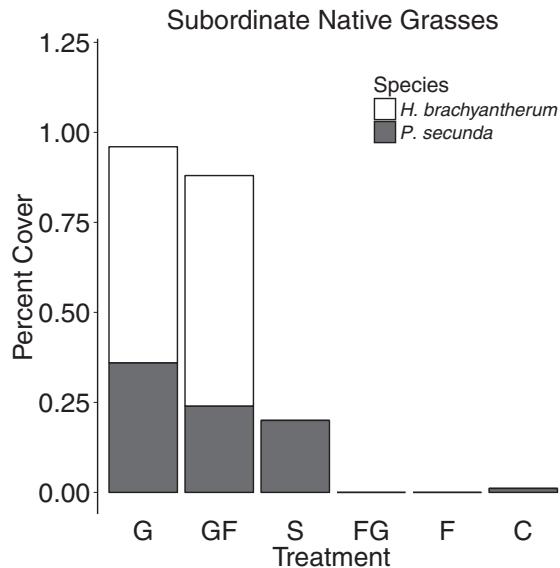


FIG. 4. Percent cover of the subordinate native grasses *H. brachyantherum* and *P. secunda* by treatment, 6–8 yr after seeding (2015). All treatments had < 1% cover of subordinate native grasses Treatments as in Fig. 3.

recruitment limitation of native grasses (Seabloom et al. 2003, Vaughn and Young 2015), with higher seedling establishment rates in the priority treatment resulting in consequently higher cover as perennial adult plants grew. The extended duration of our study reveals a more complicated process, particularly following the establishment of exotics allowed after the third year. Higher cover in the priority treatment, due to more individual seedlings or larger plant size, seems to have improved the ability of *S. pulchra* to compete with exotics. But the dramatic decrease in cover of *H. brachyantherum* following three years of initially increasing cover indicates that priority was insufficient to maintain cover, although persistence may have been slightly improved. We note that *H. brachyantherum* is a fairly short-lived perennial, and many of these original individuals may have simply failed to replace themselves, especially in the absence of disturbance (Darris 2004).

Though arrival before grasses (Forb Priority) was not particularly helpful for dominant forb species, arrival after grasses (Grass Priority) was strongly detrimental. While the cover of dominant or subordinate forbs was not enhanced by forb priority over native grasses, when native grasses were given priority over forbs, the cover of both forb dominants *L. formosus* and *A. millefolium* was lower for the first three years and total forb cover remained lower in 2015. This strong difference indicates that the established native grasses decreased establishment of young forb seedlings. The mechanisms for this competition could include water or nutrient limitation (Fargione et al. 2003) or plant–soil feedbacks mediated by the soil microbial community (Grman and

Suding 2010). Space limitation is less likely, as first year grasses in priority treatments only covered an average of 11% of the plots.

Similar patterns in the first three years for the forbs *L. formosus* and *A. millefolium* resulted in differences in the longer term. While both these species had lower cover (nonsignificant) in the Grass Priority treatment, and significantly lower cover in the Grass Only treatment, *L. formosus* also had lower cover in the Control treatment, while *A. millefolium*'s cover in the Control treatment was similar to its cover in the Forb Only, Forb Priority, and Simultaneous treatments. The cover of *A. millefolium* in the Control treatment suggests that this species successfully spread into these plots where it was not initially seeded. In contrast, the lower cover of both forb species in the Grass Priority and Grass Only treatments indicates that established native grasses are suppressing not only the initial seedling establishment of these forbs, but also subsequent colonization attempts.

This sharp tradeoff between native grass and forb cover indicates that there may be no way to avoid competitive exclusion by native guilds in the context of high exotic competition. Despite the observed drop in dominant forb cover, weed cover was not dependent on treatment, indicating that, while subordinate to native forbs, native grasses may be equivalent to forbs in their ability to compete with exotic grasses.

Implications for management

Planting of targeted species early in the course of restoration can facilitate the establishment of competitive subordinates (e.g., *S. pulchra*) that might otherwise be rapidly lost from the species pool, particularly in the face of early competition for resources by exotic species, thereby increasing longer-term species richness. However, highly subordinate species (e.g., *P. secunda*, *H. brachyantherum*, *K. macrantha*, *C. menziesii*, and *L. purshianus*) were still lost or decreased precipitously over time. We tended to see the greatest effects of priority for larger and longer-lived species, which may have been more adept at maintaining their early advantages through time. However, a larger species pool and more direct competitive pairings would be necessary to make strong conclusions as to which species are most likely to benefit from priority.

Additional management strategies may be required to increase presence and abundance of these more subordinate species: e.g., grazing, mowing, prescribed fire, summer irrigation, and interspecific aggregation (Hayes and Holl 2003, Wainwright et al. 2012, Funk et al. 2015, Young et al. 2015a). Practitioners should also be mindful that the advantages of priority may result in lower cover of late-arriving dominant species (e.g., *S. pulchra*, *L. formosus*). This tradeoff may ultimately reduce cover of the native species most capable of effectively competing with exotic annual grasses and forbs.

Increased heterogeneity, richness, and native cover, along with decreased invasive annual grass cover, are generally common restoration goals in grasslands (Stromberg et al. 2007), but increased cover of native competitive dominants may come at the cost of native species richness.

Practices that not only increase native cover, but also support heterogeneity and native richness, could include a combination of planting strategies (e.g., including areas with both Grass Priority and Forb Priority, and some without any priority; D'Antonio and Chambers 2006, Porensky et al. 2012, Vaughn and Young 2015, Young et al. 2015b). Weed management in the initial years after planting may be particularly important for maintaining the effects of priority over dominant natives. Weed management effectively provides native species with priority over exotics, and intensive weed management may be required for longer time periods post-planting if increased native species richness is an important goal of the restoration effort. Priority planting and weed management require increased time and labor and must be factored into restoration budgets and balanced by trade-offs of increased invasive cover and decreased richness. However, our results suggest that providing desirable species with priority may have long-lasting effects on many native grassland species and can serve as a valuable tool to promote desirable species and shape community composition.

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