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TOWARD PREDICTION IN THE RESTORATION OF BIODIVERSITY

Every restoration is unique: testing year effects and site effects as drivers of initial restoration trajectoriesKatharine L. Stuble^{*1,2}, Stephen E. Fick^{1,3} and Truman P. Young¹¹Department of Plant Sciences, University of California, Davis, CA 95616, USA; ²The Holden Arboretum, 9500 Sperry Road, Kirtland, OH 44094, USA; and ³Stockholm Environmental Institute, Box 24218, 104 51 Stockholm, Sweden**Summary**

1. The outcomes of restoration efforts are contingent on the specifics of the restoration practices utilized, but also on uncontrolled contingencies such as site effects and year effects. Although restoration practitioners have long been aware that the successes of their projects vary from site to site and from year to year, there have been few direct experimental tests of these contingencies.

2. We established grassland restoration plots identically across three sites in northern California, in each of four establishment years (for 12 site-year combinations).

3. The resulting plant communities differed significantly across sites and across establishment years. As a consequence of these community differences, there were ‘forb years’ and ‘grass years’, although these sometimes differed among sites. Multivariate analysis identified mean annual temperature and total precipitation as likely drivers of some of these differences.

4. *Synthesis and applications.* Our results not only confirm the idiosyncratic nature of the results of restoration efforts (and ecological experiments in general) but also demonstrate that some of this variation can potentially be related to measurable environmental conditions. Understanding the drivers of this variability can ultimately aid restoration practitioners by allowing them to focus restoration efforts on years and sites most likely to yield desired outcomes.

Key-words: community assembly, community composition, contingency, ecosystem function, grassland, multivariate analysis, restoration, site effects, year effects

Introduction

Restoration practitioners know that community assembly is a strong driver of ecosystem structure and function (Chase 2003; Fukami *et al.* 2005). Both propagule pressure and order of species arrival have been shown experimentally to be important drivers of divergence in community composition (Drake 1990; Chase 2003; Foster *et al.* 2004; Fukami *et al.* 2005; Ejrnaes, Bruun & Graae 2006; Vaughn & Young 2015), and can be used to manipulate community trajectories to achieve the goals of ecological restoration (Young, Petersen & Clary 2005; Young *et al.* 2017). Environmental conditions during community establishment can be another important, yet experimentally underexplored, determinant of community composition (Berlow 1997; Belyea & Lancaster 1999; Chase 2003). Such contingencies (in particular, site effects and year effects) in the early stages of community establishment can challenge restoration efforts, creating variable and enduring species composition outcomes

across sites and years even when restoration efforts are otherwise identical (Young, Petersen & Clary 2005; Matthews & Spyreas 2010; Vaughn & Young 2010; Grman, Bassett & Brudvig 2013), limiting our ability to generalize restoration prescriptions. Conversely, analysis of sufficiently replicated restoration experiments across space and time may help to reveal patterns of causation across divergent outcomes that may allow for more informed restoration.

In particular, restoration outcomes can be driven both by abiotic conditions, including rainfall and temperature, and by biotic factors such as herbivory and competition, during community establishment (Bakker *et al.* 2003; Howe & Lane 2004; MacDougall, Wilson & Bakker 2008; Baeten *et al.* 2010). In addition to interannual variability, such conditions can also vary from site to site, creating a strong spatial signature in restoration outcomes (Seabloom 2011). These contingencies are evident not only in restoration experiments but also in the trajectories of ecosystems recovering after disturbance events such as fire or flooding (Savage & Mast 2005; Trowbridge 2007; Harvey, Donato & Turner 2016).

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Variation in community composition appearing early in community establishment has the potential to persist, generating long-term divergence in community composition (Hoelzle, Jonas & Paschke 2012; Werner *et al.* 2016). It is likely that the factors limiting the establishment of (particularly perennial) individuals are more restrictive than the factors that affect their persistence (Young, Petersen & Clary 2005; Donohue *et al.* 2010). By extension, community structure might thus be expected to be particularly sensitive to environmental conditions during establishment, resulting in long-term divergent trajectories among communities established in different sites and/or years.

California's grassland ecosystems are thought to have been dominated by some combination of perennial bunchgrasses and annual/perennial forbs prior to extensive conversion for agriculture and invasion by exotic annual grasses from Europe (Minnich 2008). Cover of grasses and forbs, and even their above-ground presence or absence, in this ecosystem can vary substantially across years and are strongly driven by growing-season precipitation and temperature (Pitt & Heady 1978; Zavaleta *et al.* 2003). Interannual variability in these environmental drivers may be important in maintaining species coexistence and promoting the persistence of rare forbs in California grasslands (Levine & Rees 2004). In particular, it has been suggested that there are 'forb years' (years in which forbs perform particularly well) and 'grass years' (years in which grasses perform particularly well) in heavily invaded California annual grasslands (Pitt & Heady 1978; Hanson 1986; Zavaleta *et al.* 2003). Likewise, interannual variation in weather conditions may generate multiple restoration outcomes, dependent on the year and site in which a restoration was initiated (Polis *et al.* 1997; Bakker *et al.* 2003). However, these year and site contingencies have rarely been formally tested, and most ecological experiments are only carried out in a single year at a single site (Vaughn & Young 2010). This lack of experimental replication runs the risk that the results of ecological experiments may be idiosyncratic, but not recognized as such.

Here, we report on the results of a set of field-based experiments in which we initiated identical seeding treatments in each year for 4 years across three sites to examine the potential for site and years effects to drive the composition of resulting communities. Specifically, we tested how site effects and year effects drove variability in community composition in newly restored California grasslands, and which environmental factors may help explain these differences.

Materials and methods

EXPERIMENTAL DESIGN

In 2011, 2012, 2013, and 2014 we established a series of experimental plots to study site effects and year effects in the context of grassland restoration. These year-replicated experiments were further replicated over three sites in north-central California: UC

Davis Agricultural Experiment Station in Davis, CA (38.543°N, 121.756°W), the McLaughlin Natural Reserve near Lower Lake, CA (38.868°N, 122.420°W), and Hopland Research and Extension Center in Hopland, CA (38.983°N, 123.086°W). These sites have similar clay loam soils, but differ moderately in elevation and climate (temperature and rainfall; see Fig. S1, Supporting Information) and weed challenge (the abundance of weed species competing with sown species during restoration) (see Young *et al.* 2015 for site details). 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. Study areas were surrounded by grasslands dominated by exotic annuals.

In March–September of each initiation year, we collected seed of local provenance at each of the three sites (where possible) from four native perennial grasses and four perennial forb species (Table 1). For a few of these 96 provenances (8 species × 3 sites × 4 years) for which local reproductive populations could not be located, we purchased ecotype-appropriate seed from local native seed providers. Each year, we tested viability of seeds from all three sites and used this in calculating our sowing rates such that we added the same number of viable seeds for each species to our study plots across sites and years.

At each site, we established a grid of 20 blocks (five replicate blocks for experimental initiation in each of four different years). Each plot had several planting combinations, but here we report only on plots seeded simultaneously with all eight native species (one replicate plot per block for a total of five plots established per site in each year). Each experimental plot was 1.25 m on a side, separated from adjacent plots by 1 m. Blocks were separated by 4 m.

Prior to planting, all sites were tilled to control weeds, both before and 1–2 weeks after the first germinating rains in the fall; a practice common in restoration efforts in these ecosystems. We sowed the seeds of all eight species together within 1 week of the second tilling (within a 4-day period each year; dates ranged from 17 November to 6 December). These overall seeding rates of live seed are within the range of current grassland restoration practices in the region (J. Anderson, pers. comm.). Each plot was lightly raked, sown and then raked again to increase seed-soil contact.

Over the following weeks, plots were weeded of volunteer non-target forbs. 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.

Surveys were carried out after the main winter's rain had ceased in the spring, at a time of peak flowering. For the Davis and Hopland sites, this was between 5 May and 6 June each year. The phenology of the plants was delayed at the higher elevation

Table 1. Seeding rates of sown plants species (species abbreviations used in text are given in parentheses)

Grasses	Forbs
<i>Bromus carinatus</i> Hook. & Arn. (100) (Brca)	<i>Achillea millefolium</i> L. (175) (Acmi)
<i>Elymus glaucus</i> Buckley (100) (Elgl)	<i>Asclepias fascicularis</i> Decne. (50) (Asfa)
<i>Hordeum brachyantherum</i> Nevski (100) (Hobr)	<i>Croton setigerus</i> Hook. (125) (Crse)
<i>Nassella pulchra</i> (Hitcch.) Barkworth (100) (Napu)	<i>Eschscholzia californica</i> Cham. (125) (Esca)

McLaughlin site, which was surveyed between 19 May and 14 June each year. The percent areal cover of each seeded species was visually estimated for each plot by T. Young. Visual estimation of areal cover is a reliable measure of cover in this system (Werner *et al.* 2016).

STATISTICAL ANALYSIS

To examine variability in composition of the plant community across sites and planting years, we conducted a two-way permutational multivariate analysis of variance (PERMANOVA) examining community composition as a function of site, planting year and their interaction. This PERMANOVA was calculated based on a Bray–Curtis similarity matrix of data collected in 2015 (across the three sites and four planting years). Pseudo- F and P values were calculated based on 10 000 permutations of the data using the *adonis* function in R (vegan package: Oksanen *et al.* 2015). We used similarity percentage analysis (SIMPER; the *simper* function in vegan) to determine the identity of species contributing most to community dissimilarity among plots and planting years.

Across planting years, plots measured in 2015 represent plots of different ages (i.e. in the 2015 data set used above, plots planted in 2011 were 4 years old, while plots planted in 2012 were 3 years old). Because plot age may influence community composition as plots mature along a chronosequence, we also ran the analysis while holding plot age constant at 2 years, comparing composition of plots planted in 2011, 2012 and 2013, 2 years after planting (measurements taken in 2013, 2014 and 2015 respectively) with site and planting year as factors.

To examine the stability of community composition through time, we ran a series of PERMANOVAs comparing composition

of plots established in 2011 as those plots aged (composition data collected in 2012 vs. 2013, 2013 vs. 2014, and 2014 vs. 2015), blocking by site.

We used canonical correspondence analysis (CCA) to examine the importance of climate conditions as drivers of community composition. The number of rainy days per year and mean temperature in the year of planting, with sums and means per year calculated from July 1 through June 30, were included as abiotic variables in the model. Significance was determined by permuting the data 10 000 times using the *anova.cca* function in *vegan*.

To examine how the ratio of forbs to grasses in a community might be contingent on conditions during establishment, we pooled the four grass species and the four forb species separately for each plot, and calculated the natural log of the ratio of forbs to grasses ($\ln(\text{forbs/grasses})$) using the compositional data collected in 2015. Using a two-way analysis of variance (ANOVA), we examined the variation in the ratio of forbs to grasses across sites, planting years and their interaction. All statistical analyses were performed in R version 3.3.1 (R Development Core Team 2016).

Results

Despite identical site preparation, seed species mixes, and restoration planting techniques and timing, we found substantial variability in species composition driven both by site effects and year effects, as well as their interaction (Figs 1 and 2). Across the plots surveyed in 2015, the composition of communities varied significantly across sites (pseudo- $F_{2,44} = 9.07$, $P < 0.0001$) and establishment year (pseudo- $F_{3,44} = 8.85$, $P < 0.0001$), and there was a

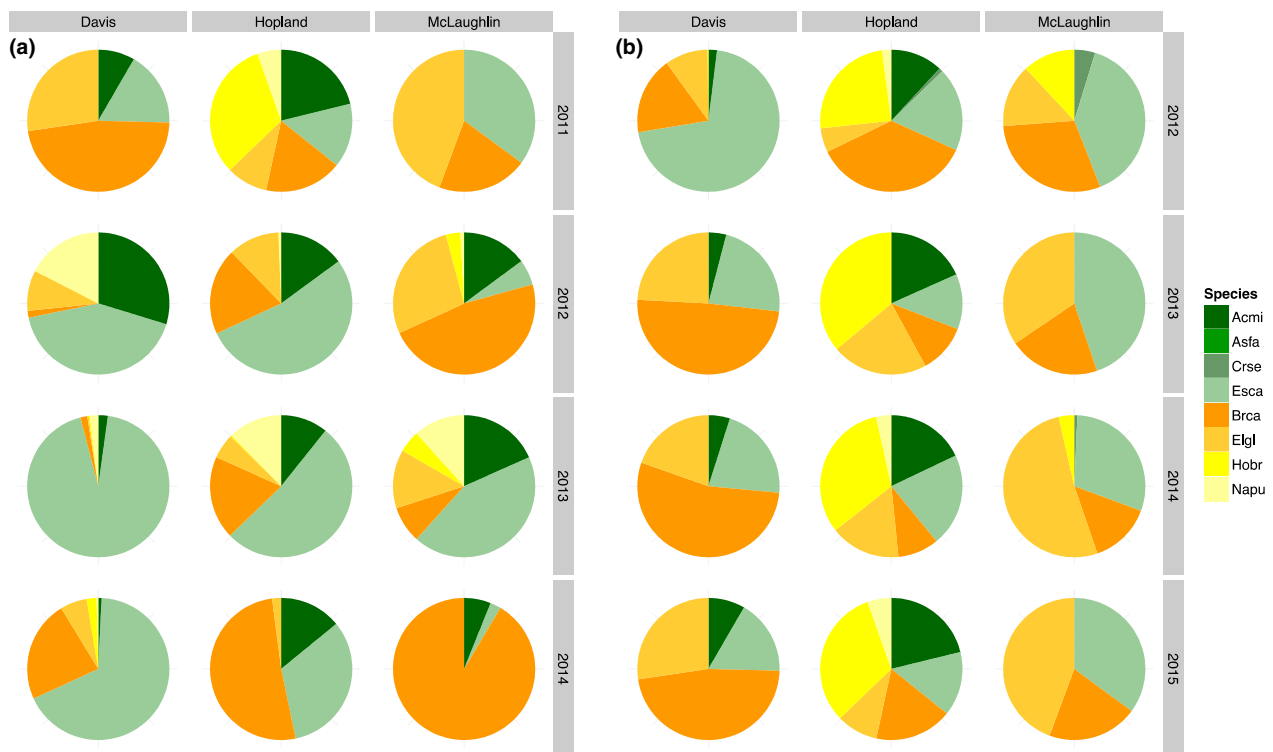


Fig. 1. Composition of (a) plots surveyed in 2015 across the three sites and four planting years and (b) plots established in 2011, surveyed through time from 2012 through 2015.

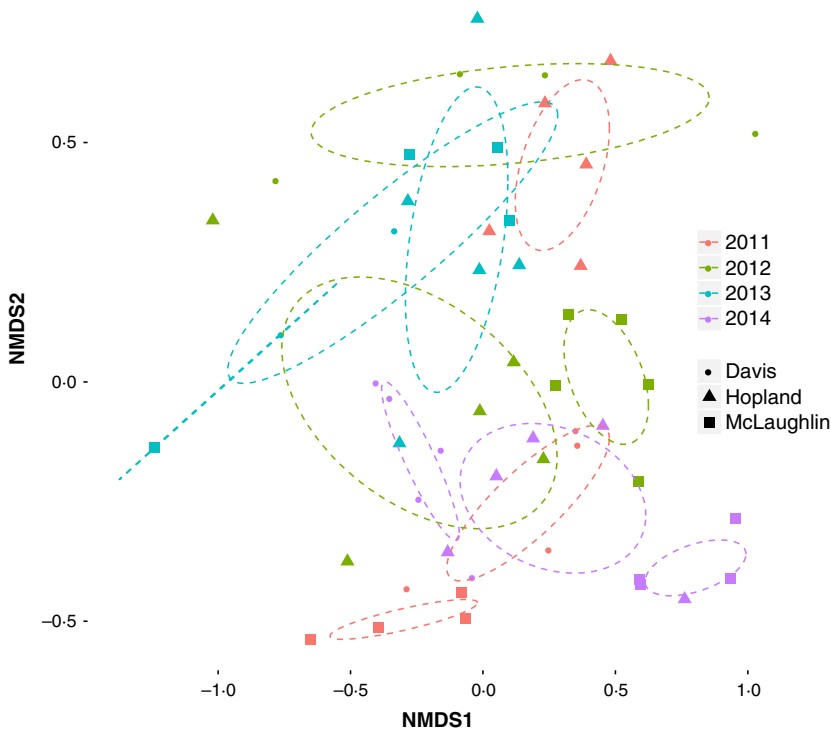


Fig. 2. Non-metric multi-dimensional scaled plot based on Bray–Curtis dissimilarity, across sites and planting years for plots surveyed in 2015. Ellipses represent 95% confidence limits based on the standard deviation of individual points. Ordination stress across two dimensions = 0.15. [Colour figure can be viewed at wileyonlinelibrary.com]

significant interaction between these factors (pseudo- $F_{6,44} = 5.92$, $P < 0.0001$).

Because these significant year effects could have been due, in part, to differences in plot age rather than planting year, we examined differences in community composition across planting years while holding plot age constant at 2 years. When we examined 2-year-old plots (which required dropping the 2014 planting year), we found again that community composition differed significantly among these plots of the same age based on site (pseudo- $F_{2,35} = 7.07$, $P < 0.0001$), year (pseudo- $F_{2,35} = 7.37$, $P < 0.0001$) and their interaction (pseudo- $F_{4,35} = 8.32$, $P < 0.0001$) (see Fig. S2). Finally, examination of the plots initiated in 2011 through time (Fig. 3) revealed that, while there were significant shifts in community

composition between the first and second years after planting (2012–2013: pseudo- $F_{1,26} = 4.60$, $P < 0.001$), composition stabilized thereafter (2013–2014: pseudo- $F_{1,26} = 0.87$, $P = 0.49$; 2014–2015: pseudo- $F_{1,26} = 0.04$, $P = 0.98$). Taken together, the analysis of the 2-year-old plots and composition of the 2011 plots through time suggest that it is indeed year of initiation, not plot age, that drive differences in mature plots surveyed in a given year (as in our analysis of 2015 survey data).

Eschscholzia californica and *Achillea millefolium* accounted for virtually all of the forb cover, with *E. californica* usually the more abundant of the two (Fig. 1). All four seeded grasses occurred in the experimental plots, but their relative abundances differed substantially across sites and planting years. Grasses were most often

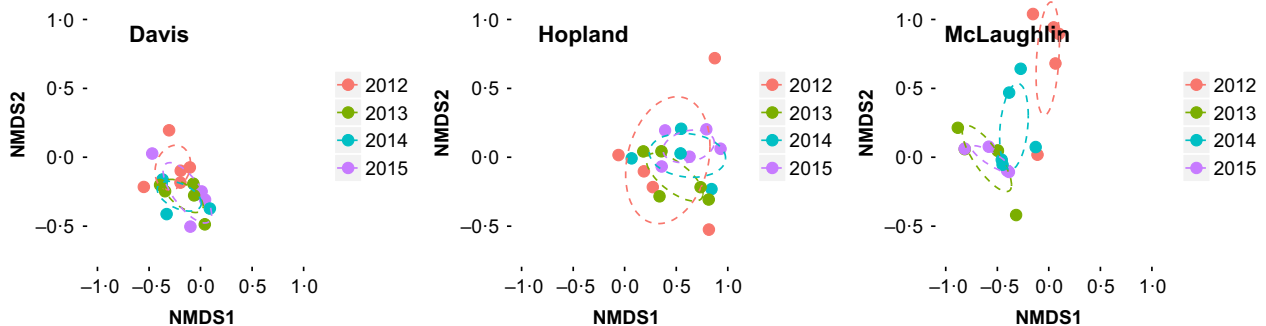


Fig. 3. Non-metric multi-dimensional scaled plot based on Bray–Curtis dissimilarity, for plots established in 2011 through time (surveyed in 2012 through 2015) at each of the three sites. Ellipses represent 95% confidence limits based on the standard deviation of individual points. Ordination stress across two dimensions = 0.14 for all three sites combined. [Colour figure can be viewed at wileyonlinelibrary.com]

dominated by *Bromus carinatus*, but occasionally *Elymus glaucus* was the dominant grass. The grass species *Hordeum brachyantherum* was often absent from plots, but was the most common grass at Hopland in plots established in 2011. Simper analysis revealed that, for all pairs of planting years (e.g. 2011 vs. 2012; 2011 vs. 2013, etc.), the two species contributing most to dissimilarity across planting years were the forb *E. californica*, and the grass *B. carinatus* (Table 2).

Canonical correspondence analysis of data collected in 2015 revealed that both the number of rainy days and mean annual temperature were marginally significant correlates of dissimilarity in community composition across sites and planting years (from 2015 survey data) (number of rainy days: $F = 2.74$, $P = 0.08$; mean annual temperature: $F = 3.14$, $P = 0.06$) (Fig. 4). The first two CCA axes explained 39% of the variation in seeded plant community structure (CCA1: 26%, CCA2: 13%).

Table 2. Simper analysis indicating the contribution (proportion) of *Eschscholzia californica* (Esca) and *Bromus carinatus* (Brca) to dissimilarity in community composition across planting years. These were the top two species contributing to community dissimilarity in community composition for all pairs of planting years

Planting year comparison	Ecsa	Brca
2011–2012	0.15	0.14
2011–2013	0.22	0.14
2011–2014	0.17	0.15
2012–2013	0.28	0.12
2012–2014	0.22	0.17
2013–2014	0.33	0.20

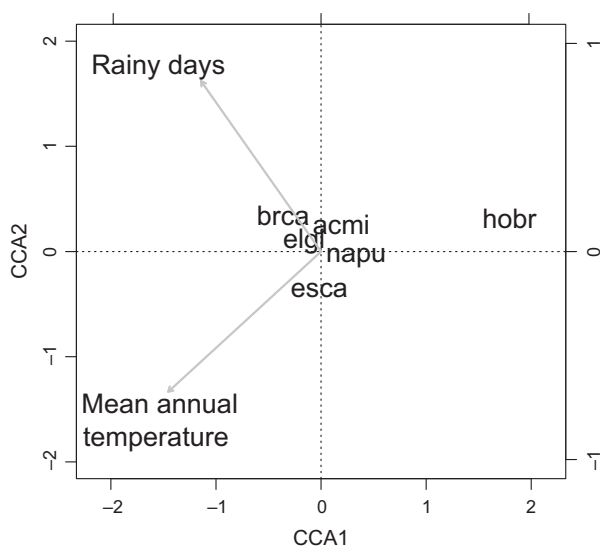


Fig. 4. Canonical correspondence plot reveals that both the number of rainy days and mean annual temperature are strong drivers of community composition. Combined, these two canonical correspondence analysis (CCA) axes explained 39% of variation in community composition.

We found significant variation in the ratio of forbs to grasses in plots across sites and planting years (site: $F_{2,44} = 19.68$, $P < 0.0001$; year: $F_{3,44} = 14.84$, $P < 0.0001$; site \times year: $F_{6,44} = 6.16$, $P < 0.0001$) (Fig. 5). Six (of twelve) site \times year combinations yielded communities that were dominated by forbs, while the other six yielded communities that were dominated by grasses. All three sites experienced some planting years that came to be dominated by forbs, and others dominated by grasses. Across all three sites, plots established in 2011 yielded grass-dominated plots, while planting in 2013 yielded forb-dominated plots. In 2012 and 2014, the balance of grasses to forbs was variable across sites. For example, grass dominance was strongest in plots planted in 2014 at McLaughlin, while in the same planting year forbs were the dominant functional group at Davis.

Discussion

STRONG SITE EFFECTS AND YEAR EFFECTS

This study revealed substantial variability in community composition among identically prepared and seeded grassland plots driven by both site effects and year effects, along with their interaction (Fig. 2). In addition to overall variability in community composition, site effects and year effects drove the ratio of forbs to grasses. Some site-by-year combinations yielded a community dominated by forbs, while native grasses dominated other site-by-year combinations (Fig. 5). These results provide compelling direct evidence for what restoration practitioners (and some ecologists) have long known; that the outcomes of restoration efforts, and ecological experiments more generally, are highly contingent on the spatial-temporal

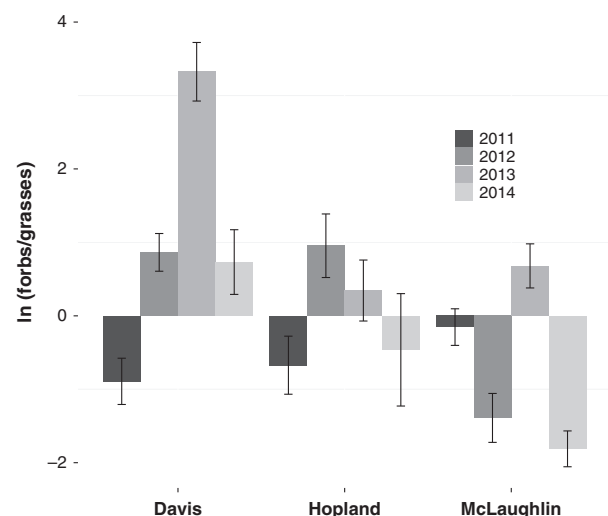


Fig. 5. Ratio of forbs to grasses (\pm standard error) in plots planted across sites and years (surveyed in 2015) reveals broad compositional variability across sites and planting years. Positive values indicate a greater abundance of forbs than grasses, while negative values indicate more grasses than forbs.

context in which they are conducted (Bakker *et al.* 2003; Brudvig 2011; Grman, Bassett & Brudvig 2013). Such contingencies can complicate the quest by land managers restore ecosystems to particular states (Brudvig 2011), but these contingencies may also contribute to overall patterns of diversity on the landscape.

ENVIRONMENTAL CORRELATES OF COMMUNITY VARIATION

In California grasslands, rainfall and temperature during the growing season have been previously identified as strong drivers of community establishment and growth (Pitt & Heady 1978; Zavaleta *et al.* 2003). While all four of our study years were drier than the historical averages for each respective site (see Fig. S1), conditions across the experimental years varied considerably. Furthermore, while three of our four study years were warmer than the historic average, one of the study years (2011 planting year) was cooler (see Fig. S1). Layered onto this interannual variability in climatic conditions were site-level differences. These two sources (site and year) of variation in abiotic conditions likely played an important role in driving divergent community composition across our plots. Mean temperature and the number of rainy days were important drivers of community dissimilarity; the first two axes of our CCA incorporating these two environmental parameters accounted for 39% of the variation in community structure. This is simultaneously not only indicative of the importance of mean annual temperature and the number of rainy days but also suggests the importance of other unmeasured environmental factors contributing to compositional differences across sites and years (e.g. biotic interactions, soil properties, weed challenge).

Our experimental results support past descriptive research suggesting that grasses tend to benefit from wetter conditions during establishment ('grass years'), while forb species in California grasslands are better able to capitalize on hotter and drier conditions during establishment ('forb years') (Pitt & Heady 1978). To the extent that such yearly variations may be increasingly predictable (e.g. El Niño and La Niña events and climate change projections), we may be able to more realistically adjust restoration goals, or more appropriately time restoration activities.

The observed divergence in community composition across sites and years may be driven by direct species-specific responses to environmental conditions, which can influence germination, emergence and establishment, as well as survival (Hobbs & Mooney 1991; Zavaleta *et al.* 2003; Classen *et al.* 2010). However, in addition to direct responses by species to abiotic conditions, indirect responses mediated by interspecific interactions can also be important drivers of site and year effects. These interspecific interactions may include competition (Goldstein & Suding 2014) and shifts in the relative importance of priority effects (Kardol, Souza & Classen 2013).

STABILITY OF ESTABLISHED (PERENNIAL) PLANT COMMUNITIES

At the time of the 2015 surveys for this experiment, the oldest of our plots had been established more than 4 years prior. We found compositional differences among plots across sites and establishment years were persistent throughout this study, providing strong evidence that early differences in community composition can persist, at least in the short term. Furthermore, after the second growing season, there was little change in community composition among plots established in the same year and at the same site, demonstrating that plots established with these native perennials tend to be relatively stable following initial establishment. Although it is possible that they may yet converge, given enough time, and disturbance may affect the process (Wassenaar *et al.* 2005), we suspect that this stability may well last for at least the life spans of the constituent perennial species (Young, Chase & Huddleston 2001). Data from an older parallel restoration experiment revealed that community differences were still striking and significant 8 years after initiation (Werner *et al.* 2016). Regardless, our initial data are consistent with the hypothesis that strong site and year effects can drive differences in community composition that have the potential to persist, shaping the composition of California's native grasslands.

Conclusions

The data presented here provide strong evidence that restoration outcomes are highly contingent on external conditions that vary both spatially and temporally. The extent to which these factors can drive important restoration outcomes, including diversity and community composition, is substantial, and largely beyond the control of the restoration practitioner. These contingencies may seem vexing, but as more data are collected we can move towards developing models to predict environmental conditions that will promote desired restoration outcomes and perhaps enlighten our understanding of how climate change may influence the structure of future plant communities.

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Data accessibility

Plant cover data are available from figshare: <https://dx.doi.org/10.6084/m9.figshare.4309490.v1> (Young 2016).

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Supporting Information

Details of electronic Supporting Information are provided below.

Fig. S1. Mean temperature and total precipitation for each growing year.

Fig. S2. Non-metric multi-dimensional scaled plot based on Bray–Curtis dissimilarity, across sites and planting years.