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RESEARCH ARTICLE

Vegetative spread is key to applied nucleation success in non-native-dominated grasslands

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Applied nucleation (i.e. planting vegetation patches) is a restoration strategy that better recreates natural ecosystem heterogeneity and requires fewer resources compared to planting the entire area. Whereas applied nucleation shows promise as a forest restoration strategy, this approach has received little study in grassland restoration, where the spread of planted vegetation nuclei may be impeded by aggressive non-native species. We compared the establishment and cover of restored native grass, forb, and rush species for 7 years in applied nucleation and full planting treatments in a former agricultural site dominated by non-natives along the central California coast. We planted seedlings of the same nine coastal prairie species in all treatments, but the applied nucleation plots had four nuclei with only 30% of the seedlings as the full planting plots. We also evaluated the effect of adding wood mulch to reduce non-native plant competition. Native forb cover increased over time and was similar across treatments in the final study year. Native grasses increased for the first 4 years and then declined sharply in all treatments. Native forb cover spread into unplanted areas in applied nucleation plots, whereas grasses showed minimal spread. Of the five planted forb species, the two that persisted until the final study year both spread via rhizomes. Wood mulch reduced non-native cover in the first 2 years and had a longer-term effect on species composition. Our results suggest that applied nucleation can be an effective restoration strategy at a small scale in non-native-dominated grasslands for species that spread vegetatively.

Key words: California, cluster planting, coastal prairie, restoration, spatially patterned planting, wood mulch

Implications for Practice

- Planting patches of vegetation (applied nucleation) is a promising approach for restoring some native grassland species.
- Species that spread vegetatively are well suited for use in applied nucleation or other spatially patterned planting strategies in sites where seedling recruitment is strongly limited by competition.
- Wood mulch suppresses non-native grasses for the first 2 years and increases native seedling establishment and clonal spread in a highly invaded California coastal prairie.

Introduction

Restoration efforts face the challenge of judiciously using limited resources to achieve the most successful ecological outcomes. A common approach to restoring degraded terrestrial systems where native propagules are lacking is to plant or seed the entire area in a homogeneous manner, but this approach is costly. An alternative approach is applied nucleation (Corbin & Holl 2012) or cluster planting (Saha et al. 2016) in which patches of vegetation are planted to mimic the natural nucleation process (Yarranton & Morrison 1974). In this approach, primary colonists establish in patches and spread outward clonally or from seed, and may facilitate the colonization

of other species. Not only does this methodology require fewer resources for planting and maintaining seedlings (Holl et al. 2020), it may better approximate the small-scale heterogeneity of natural ecosystem recovery (Holl et al. 2013).

Whereas the applied nucleation approach using woody species has shown promising results in a range of forest and shrubland ecosystems (e.g. Piironen et al. 2015; Corbin et al. 2016; Saha et al. 2016; Hulvey et al. 2017; Aradottir & Halldorsson 2018), it has received much less study as a strategy for grassland restoration. However, Grygiel et al. (2018) conducted a 15-year study of northern tallgrass prairie restoration in the midwestern United States and found that creating systematically spaced, small-scale

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(2.84 × 2.84 m) soil disturbances totaling 25% of the area and seeding these patches with grassland species produced similar total richness and higher native forb density as areas that were seeded throughout. In addition to vegetation nuclei increasing native cover, providing ecosystem services (e.g. pollination), and potentially resisting invasion (Hulvey et al. 2017), a key premise of the nucleation model of succession is that the planted vegetation patches spread over time. However, this can be challenging in arid ecosystems where seedling establishment is episodic (Hulvey et al. 2017), and in sites where planted patches do not enhance seed dispersal or shade out light-demanding non-native species that otherwise inhibit native vegetation establishment (Corbin & Holl 2012).

Low rates of native species establishment are a particular concern in Mediterranean-climate grasslands where many species do not have seeds with mechanisms for long-distance dispersal (Seabloom et al. 2003; Standish et al. 2007), and competition with invasive, non-native plants is a major barrier to restoration (Stromberg et al. 2007; Rayburn & Laca 2013; Gornish & Ambrozio dos Santos 2016). The vast majority of California grasslands are dominated by a mix of non-native grass and forb species that strongly inhibit the early stages of native seedling establishment, as the non-natives typically germinate earlier, grow faster, and outcompete most native species (Hamilton et al. 1999; Stromberg et al. 2007; Vaughn & Young 2015). If competition is reduced sufficiently at the young seedling stage, native species are more likely to be able to outcompete non-natives as the plants mature (Hamilton et al. 2002; Corbin & D'Antonio 2004).

Most studies focus on the first few years following restoration actions, even though ecosystems take longer to recover. In regions with high interannual variability and a substantial number of annual species, grassland composition is highly dynamic across years (Hallett et al. 2014; Dudley et al. 2017), particularly in the first few years of recovery. Often projects that appear to be successful in restoring native species for the first year or two become dominated by aggressive non-native species only a few years later (Rein et al. 2007; Holl et al. 2014b; Young et al. 2015).

We compared full planting and applied nucleation as strategies to restore coastal prairie in California and monitored vegetation composition for 7 years. We aimed to test whether a mix of native grass, forb, and rush species would establish and spread outside planted areas in a non-native dominated grassland. We also tested whether applying wood mulch to the soil surface at the time of planting would reduce competition with the existing non-native species and overcome the barriers to the initial establishment of native species, since surface mulch has been shown to suppress germination and growth of non-native species (Watkinson & Pill 2007; Holl et al. 2014b), as well as increase retention of soil moisture and prevent extreme temperature fluxes (van Donk 2011). It was unclear, however, whether wood mulch would also prevent the spread of native species. A prior study in this system showed that wood mulch increased native species establishment at the outset, but

the effects diminished within 2 years after planting (Holl et al. 2014b).

Methods

Study System and Site

California coastal prairies are biodiversity hotspots that historically hosted a mix of native perennial grasses and a diverse suite of native annual and perennial forbs (Ford & Hayes 2007), but large areas of coastal prairie have been converted to agricultural and urban uses. The remaining areas have been degraded by changes in disturbance regimes and invasion by non-native grass and forb species and have proven to be challenging to restore (Stromberg et al. 2007).

We conducted this experiment at Younger Lagoon Reserve (lat 36°57'03"N, long 122°03'57"W) in Santa Cruz, California, which is part of the University of California Natural Reserve System. The site is located on a coastal bluff adjacent to the ocean on the central coast of California and experiences a Mediterranean climate with a mean annual temperature of 14°C, mean annual rainfall of 400 mm with most of the precipitation falling between October and May, and frequent coastal fog in the summer. Years 1–3 of the study had below-average rainfall (Fig. S1) consistent with a historic drought period in California (Griffin & Anchukaitis 2014). The site is flat and the soils are classified as Watsonville loam underlain by Santa Cruz mudstone with a shallow water table (0.6–3 m). Before their incorporation into Younger Lagoon Reserve in 2009, the site was used for cattle grazing and row crop agriculture for several decades and then left fallow for 23 years. As a result of the intensive land use and subsequent invasion of non-native species, at the onset of this study, vegetation cover in the experimental areas was comprised nearly entirely of non-native annual grasses, such as *Festuca perenne* (perennial ryegrass) and *Bromus diandrus* (ripgut brome), and non-native forbs such as *Raphanus sativus* (wild radish) and *Helminthotheca echioides* (bristly oxtongue).

Experimental Design

In October 2011, prior to the start of the experiment, the entire study area was mowed and sprayed with broad-spectrum Glyphosate Pro 4 herbicide at 2% concentration to reduce the cover of mostly non-native background vegetation. The area was surrounded by an approximately 0.6-m tall wire mesh fence to exclude rabbits (*Sylvilagus bachmani*), which are common at the site. We added an approximately 10-cm layer of wood mulch (comprised mostly of *Sequoia sempervirens* [coast redwood], *Notholithocarpus densiflorus* [tanbark oak], *Umbellularia californica* [bay laurel], and *Hesperocyparis macrocarpa* [Monte-rey cypress]) to the mulched treatment plots. In January 2012, a few days before planting the experiment, we applied a second round of glyphosate to kill recent germinants.

We set up twenty 10 × 10-m plots with 1-m buffers between the plots; each plot was randomly assigned one of four main treatments with five replicates of each treatment: (1) fully planted with mulch, (2) fully planted with no mulch, (3) applied

Table 1. Mean percent survival (± 1 SE) of planted annual species in year 1 (2012) and perennial species in year 2 (2013). Nomenclature follows the Jepson Flora Project (2020); $n = 10$ mulch and no mulch plots. Survival of *Trifolium willdenovii* was zero in most plots preventing statistical comparison.

Species	Form	Lifespan	Rhizomatous	Year	Percent Survival		t	p
					No mulch	Mulch		
<i>Clarkia davyi</i>	Forb	Annual	No	2012	83.5 \pm 3.5	92.3 \pm 2.4	1.92	0.035
<i>Trifolium willdenovii</i>	Forb	Annual	No	2012	2.3 \pm 1.6	0.1 \pm 0.1	—	—
<i>Achillea millefolium</i>	Forb	Perennial	Yes	2013	46.7 \pm 9.4	66.6 \pm 6.4	1.78	0.047
<i>Grindelia stricta</i>	Forb	Perennial	No	2013	20.0 \pm 6.9	40.8 \pm 10.9	1.71	0.108
<i>Symphyotrichum chilense</i>	Forb	Perennial	Yes	2013	2.6 \pm 1.3	24.0 \pm 0.8	3.10	0.009
<i>Juncus patens</i>	Rush	Perennial	Yes	2013	40.0 \pm 5.7	36.7 \pm 5.3	0.10	0.923
<i>Bromus carinatus</i>	Grass	Perennial	No	2013	49.2 \pm 3.7	62.8 \pm 4.9	2.22	0.041
<i>Hordeum brachyantherum</i>	Grass	Perennial	No	2013	62.5 \pm 5.0	65.0 \pm 6.6	0.38	0.707
<i>Stipa pulchra</i>	Grass	Perennial	No	2013	38.8 \pm 5.7	46.7 \pm 4.9	1.12	0.279

nucleation planting with mulch, and (4) applied nucleation (hereafter “nucleation”) planting with no mulch. At the end of the second growing season, there was low survival of planted species and minimal recruitment outside of the planted areas in the nucleation no mulch plots, so we removed these plots from the study and focused our comparisons on the other three treatments.

We planted seedlings of three native perennial grass species, five forb species (two perennial and three annual), and one perennial rush species (Table 1). We collected native plant seeds during June–September 2011 from local coastal prairie sites (within 50 km) with similar soil and microclimate conditions. The seeds were cleaned by hand sorting and using sieves to remove the chaff. Seeds were then germinated in flats filled with Promix HP™ potting soil. Recently germinated seedlings with a minimum of two real leaves were transplanted into 3.8-cm diameter \times 14.0-cm tall Cone-tainers™ filled with Promix HP and grown at the UCSC Greenhouses and at a local native plant nursery (Central Coast Wilds). All seedlings except *Symphyotrichum chilense* (Pacific aster) were planted in late January 2012 at approximately 3 months old and had individual canopy covers of ≤ 25 cm². *S. chilense* had delayed germination and seedlings were planted in May 2012.

The entire 10 \times 10-m area of each fully planted plot was planted in a 22 \times 22 plant grid for a total of 484 plants per plot (Fig. S2). The seedlings were planted 45 cm from each other and plot boundaries. Each row was planted with a single species and plots were divided evenly into 11 rows of forbs/rushes and 11 rows of grasses. We used nine species in this experiment, which represent a mixture of grass, forb, and rush species, annuals, and perennials, and rhizomatous and non-rhizomatous species (Table 1). In each plot, there were two rows of *Achillea millefolium* (common yarrow), *Clarkia davyi* (Davy’s clarkia), *Grindelia stricta* (coastal gumweed), *Trifolium willdenovii* (tomcat clover), and *Juncus patens* (common rush); one row of *Symphyotrichum chilense*; four rows of *Hordeum brachyantherum* (meadow barley) and *Bromus carinatus* (California brome); and three rows of *Stipa pulchra* (purple needlegrass), with rows planted in a repeated alternating pattern. The forbs/rushes (Table 1) were planted on one side of each plot, and the grasses were planted on the

other side, as we had originally planned to control non-native species using grass- and forb-specific herbicides; however, soon after the initiation of the experiment UCSC banned use of herbicides at the site.

The nucleation plots were planted with four 2.25 \times 2.25-m nuclei (Fig. S3). There were two forb/rush nuclei on one half of the plot and two grass nuclei on the other half. The nuclei were separated by 2.5 m of unplanted land and a 1.5-m buffer was left unplanted between the nuclei and plot boundaries (Fig. S3). Each of the four nuclei had a 6 \times 6 plant grid for a total of 144 plants per plot that were planted at the same spacing (45 cm apart) as in the fully planted plots. Each nucleus had one row of each forb or rush species or two rows of each grass species planted in an alternating pattern.

We mowed half of every plot (10 \times 20 m) to a height of 8–10 cm at the end of peak growing season, late May to June from 2012 to 2018 in an attempt to reduce non-native competition, as herbicide use was not allowed. Plots were mowed perpendicular to planted rows (Figs. S2 & S3), so half of the forbs/rushes and half of the grasses were mowed. However, initial analyses suggested that mowing did not have a strong or consistent effect on plant community composition, likely because it was done once yearly after most species had set seed, so we did not include this factor in analyses.

Data Collection

Survival. In April 2012 (Year 1) and 2013 (Year 2) of the study, we measured the survival of all planted seedlings (12–24 seedlings per species in nucleation, 22–88 seedlings per species in full planting plots), after which time it was impossible to distinguish planted plants from newly germinated seedlings or ramets from existing plants. We report survival of *C. davyi* and *T. willdenovii* (annuals) from Year 1 and survival of the remainder perennial species in Year 2, after they had survived through a full dry season.

Recruitment. In April–May 2013 (Year 2), we measured seedling recruitment of four native forb species, *A. millefolium*, *C. davyi*, *G. stricta*, and *Symphyotrichum*

Table 2. Mean (± 1 SE) native forb recruits in all treatments in Year 2 (2013); $n = 5$ plots per treatment. Recruits were measured in both planted and unplanted areas of the nucleation plots as described in the Methods. Recruits of *Achille millefolium* and *Symphotrichum chilense* include both seedlings and ramets. *Trifolium willdenovii* was not observed in Year 2.

Species	Mulch		No Mulch	
	Full	Nuclei	Full	Nuclei
<i>Achillea millefolium</i>	1.7 \pm 1.2	4.9 \pm 3.0	0.04 \pm 0.04	0.3 \pm 0.2
<i>Clarkia davyi</i>	2.2 \pm 1.6	0.2 \pm 0.1	0.04 \pm 0.04	0
<i>Grindelia stricta</i>	0.1 \pm 0.04	1.0 \pm 0.7	0	0
<i>Symphotrichum chilense</i>	0	0.1 \pm 0.1	0	0

chilense. It was not possible to reliably identify new grass or rush seedlings, and no *T. willdenovii* survived to set seed in Year 1. We centered one 1 \times 0.25-m quadrat on a random location within the mowed and unmowed halves of each of the 11 forb rows (with the long edge parallel to individual species rows) per fully planted plot (22 quadrats per plot) and counted the number of seedlings and ramets of each species in each quadrat.

For nucleation plots, we likewise centered a quadrat on each forb row. We also placed two quadrats approximately 45 cm outside the rows nearest the outside edge of the plot and six additional quadrats outside the rows nearest the interior of the plot ($n = 20$ quadrats per nucleation plot). We did not measure recruitment in subsequent years as it was not possible to determine whether recruits were recently germinated from seeds or ramets from existing plants.

Plant Cover. In late April and early May of 2012–2018, we measured the percent cover of the native and non-native grass and forbs guilds. Since the one rush species, *J. patens*, was planted with the forbs it was included with native forb cover. From 2014–2018, we also recorded the cover of individual planted species. In the full planting plots, the central 8 \times 8-m area (excluding a 1-m buffer at all edges) was divided into eight 8 \times 1-m transects running parallel to planted rows (Fig. S4). An equal number of 1 \times 0.25-m quadrats were randomly distributed in each of the four subplots (grass-mowed, grass-unmowed, forb-mowed, forb-unmowed) with the long edge perpendicular to the planting rows; the number of quadrats varied by year (two per subplot in 2012, three in 2013, five in 2014, and four in 2015–2018). A similar sampling layout was used in 2013 and 2014 in nucleation plantings. Starting in 2015, we increased the sample size in nucleation plantings to six quadrats per subplot; these were distributed with two quadrats within the planted nuclei, two within 0.5 m of the edge, and two outside the nuclei (Fig. S5). Plant cover was estimated visually in 5% cover classes (e.g. 0–5%, 5–10%) and the midpoint used for analyses. Five plots were missing data in 2014 (one full-mulched, two full non-mulched, and two nucleation mulched); to enable us to include these data in repeated measures analyses we averaged values from 2013 and 2015 for these plots.

Analysis. The percent survival of individual plant species was calculated per plot and values were arcsine-square root

transformed. Initially, we analyzed the percent surviving using a two-way analysis of variance (ANOVA) with planting, mulch, and their interaction in the model. Because the planting and planting \times mulch interactions were not significant (all p values > 0.05), we compared values from mulched and non-mulched plots using a two-sample t test.

Native forb and grass cover were analyzed separately since they were planted in separate halves of the plots (Figs. S2 & S3); hence, we only report data for native forb and grass cover from quadrats in the half of the plot where they were planted. For analyses of location within nucleation plots, we averaged the two quadrats inside, at the edge, and outside nuclei. For all other analyses, we averaged cover quadrats within each plot prior to analysis so $n = 5$ for all treatments. We used repeated-measures multivariate analysis of variance (MANOVA) to test for the effects of three treatments (full planting with mulch, full planting without mulch, and nucleation planting with mulch) over time and use polynomial contrasts to specifically compare mulched vs. non-mulched full planted plots and mulched full planted vs. mulched nucleation plots. We report Wilks' lambda as the test statistic for the time \times treatment test. Likewise, we used repeated-measure MANOVA to test the effect of location within nucleation plots. Data were analyzed using JMP Pro v. 15.

Results

Overall survival of native perennial species in Year 2 (2013) was higher in mulched ($48.9 \pm 0.3\%$ [SE]) than unmulched ($37.1 \pm 0.3\%$) plots ($t = 3.8$, $p = 0.004$); this trend was strongest for *Achillea millefolium*, *Symphotrichum chilense*, and *Bromus carinatus* (Table 1). Almost all (95–100%) of the new recruits (seedlings and ramets) for the three perennial forb species (*A. millefolium*, *Grindelia stricta*, and *S. chilense*) in Year 2 were found in mulched plots (Table 2). One of the planted annual forbs, *Clarkia davyi*, had significantly higher survival in mulched plots in Year 1 (Table 1) and recruited almost entirely in mulched plots in Year 2 (Table 2), but most individuals did not survive to flower in Year 2, and no individuals were observed in subsequent years. The other native annual forb, *Trifolium willdenovii*, had only 1.6% survival in Year 1 across all treatments and was not observed in subsequent years. The one rush species, *Juncus patens*, had 38.3% overall survival in Year

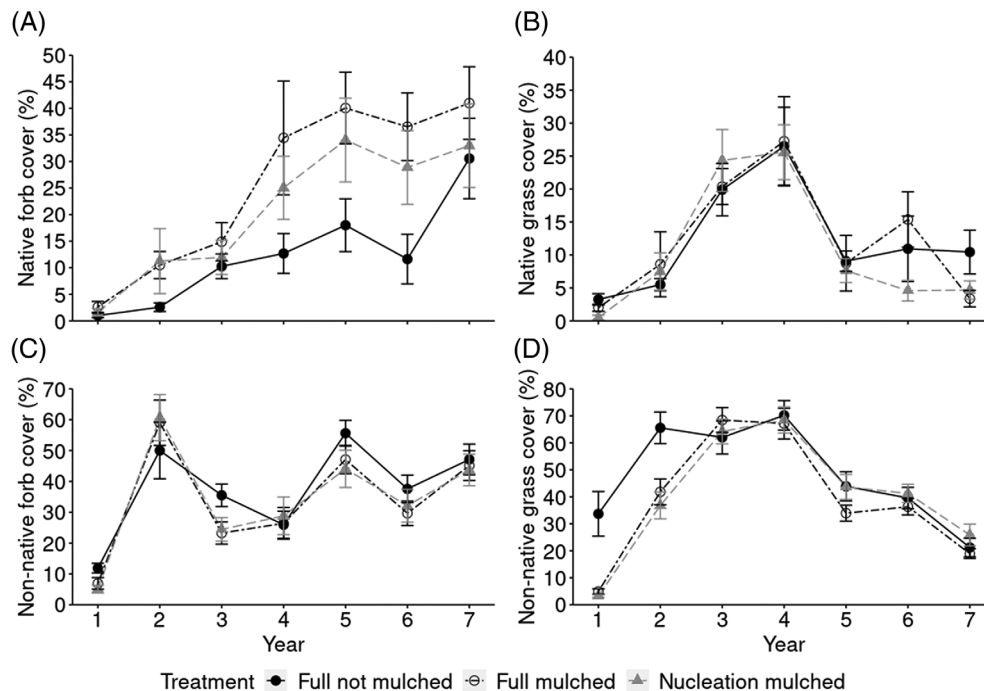


Figure 1. Mean cover (± 1 SE) of native and non-native forbs and grasses from Year 1 (2012) to Year 7 (2018); $n = 5$ plots per treatment. Cover was measured in both planted and unplanted areas of the nucleation plots as described in the Methods.

2 but the plants were small and the species was not observed after the second year.

Native forb cover increased in all treatments over time (Fig. 1A; $F_{6,7} = 4.7$, $p = 0.031$). Whereas native forb cover did not differ significantly across mulch treatments in the full model ($F_{2,12} = 1.7$, $p = 0.224$), the specific contrast between full mulched and full unmulched plots showed marginally higher cover in mulched plots (Fig. 1A; $F = 3.3$, $p = 0.093$). Planted native grass cover increased to approximately 25% cover in all treatments by Year 4 and then decreased over time to only $6.1 \pm 1.2\%$ cover across all treatments in the final study year, but there was no significant treatment or treatment \times time effect (Fig. 1B; Table S1). The cover of non-native forbs was highly variable across years but was similar across treatments (Fig. 1C; Table S1). There was a significant treatment \times time interaction for non-native grass cover ($F_{12,14} = 3.8$, $p = 0.011$), with mulched plots initially showing lower non-native grass cover, but the suppressive effect of mulch was lost by Year 3 (Fig. 1D; Table S1).

In the nucleation plots, native forb cover spread outside planted nuclei, and there was no significant differences in forb cover inside, at the edge, or outside planted nuclei overall in Years 4–7 of the study (Fig. 2; location: $F_{2,12} = 0.9$, $p = 0.453$; time: $F_{3,10} = 0.2$, $p = 0.558$, location \times time $_{6,20}$: $F = 0.8$, $p = 0.587$). Native grass cover was greatest inside nuclei, intermediate at their edges, and lowest outside of them in Years 4 and 5. In Years 4 and 5, native grass cover declined substantially in quadrats inside and at the edge of the planted nuclei. In turn, native grass cover was low in all treatments by the final 2 years (Fig. 2B; location: $F = 25.3$, $p < 0.001$; time: $F = 20.7$, $p < 0.001$, location \times time: $F = 2.3$, $p = 0.077$).

The three planted perennial forbs (*A. millefolium*, *G. stricta*, and *Symphyotrichum chilense*) persisted through Year 4 (Fig. 3A). *A. millefolium* cover increased in all treatments from Years 4 to 7. In Year 4, *G. stricta* and *S. chilense* had minimal to no cover in unmulched plots, but were found in mulched plots (Fig. 3A), although the distribution across plots ranged from 0 to 44% for *G. stricta* and 0 to 14% for *A. chilense*. In the subsequent 3 years (Years 5–7), cover of *S. chilense* increased substantially, whereas *G. stricta* declined and had $<1\%$ cover in all plots by Year 7 (Fig. 3A). All three native perennial grasses established successfully in most plots in the first few years of the experiment, but by Year 7, the grasses *B. carinatus* and *Stipa pulchra* were not found in any of the plots, and *H. brachyantherum* ranged from 0 to 11% cover across the three treatments (Fig. 3B).

Discussion

Our results show that applied nucleation was similarly effective to full planting in restoring native grasses over the first 4 years and native forb cover through the end of the 7-year study period, even though nucleation treatments were planted with only 30% of the number of seedlings as in the full planting treatment. This result is consistent with prior applied nucleation research in grasslands and forests (e.g. Corbin et al. 2016; Holl et al. 2017; Grygiel et al. 2018), as well as studies on other spatially patterned planting designs (Gornish et al. 2019; Shaw et al. 2020), showing that some species spread outside the planted areas. Using spatially patterned plantings is ecologically beneficial since it creates a more heterogeneous plant

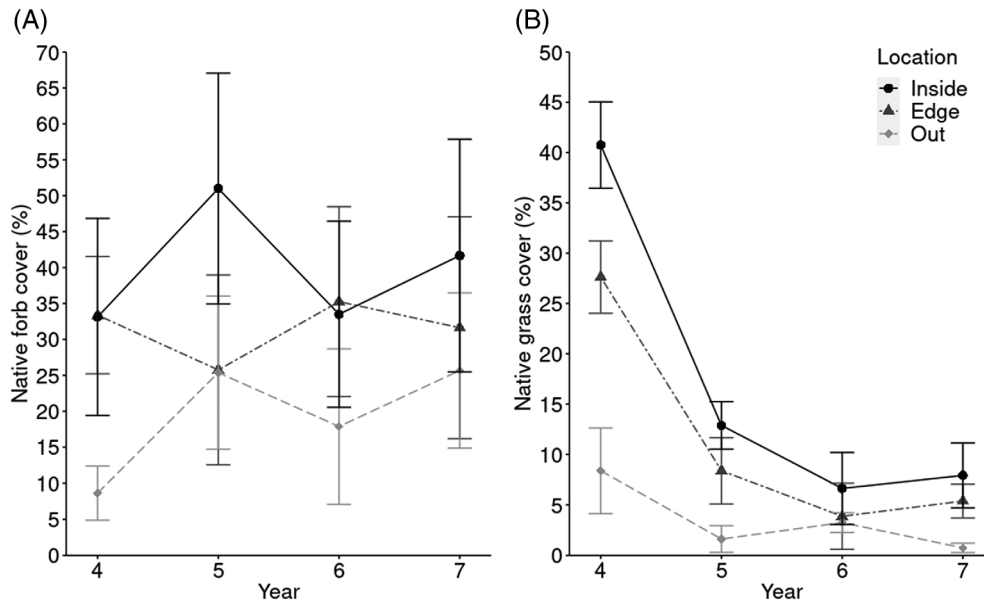


Figure 2. Mean native (A) forb and (B) grass cover (± 1 SE) inside, at the edge, and outside planted areas in nucleation plots from Year 4 (2015) to Year 7 (2018); $n = 5$ per location.

distribution that mimics the small-scale heterogeneity characteristic of grassland ecosystems (Seabloom et al. 2005; Gornish et al. 2019).

Most past studies of applied nucleation have focused on the role that woody vegetation nuclei play in facilitating the

establishment of new recruits through enhancing seed dispersal and increasing safe sites for seedling establishment (e.g., Holl et al. 2017; Aradottir & Halldorsson 2018). The evidence from our study suggests that most of the increase in native cover over time was due to vegetative spread. *Achillea millefolium* and

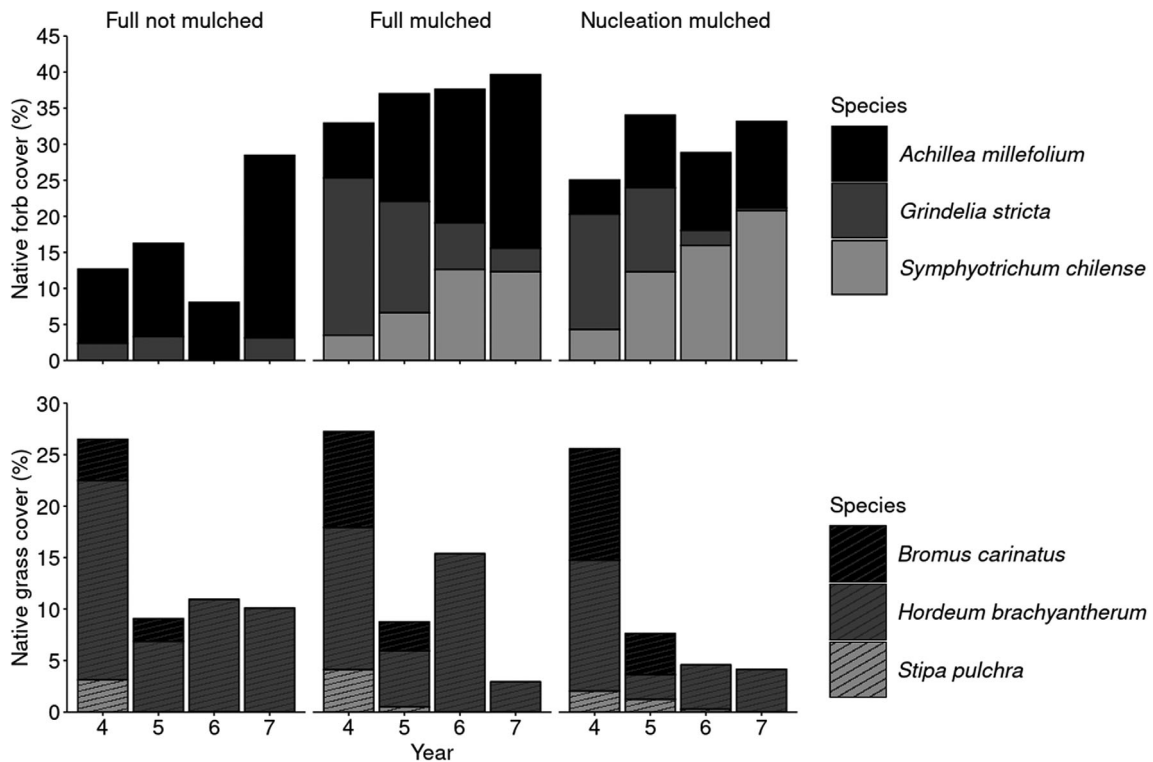


Figure 3. Mean percent cover (± 1 SE) of individual native (A) forb and (B) grass species across all plots of each treatment from Year 4 (2015) to Year 7 (2018).

Symphiotrichum chilense, the two native species that had the highest cover at the end of the study, both spread via rhizomes, despite the fact that *S. chilense* had low survival initially. While we were not able to reliably distinguish whether each new stem was a seedling established from seed germination or due to the vegetative spread of existing plants, the distribution of the plants within and across plots suggests that they mostly spread via rhizomes at our site. Like most California grasslands, our study site is dominated by non-native grasses and forbs that outcompete newly recruiting native seedlings (Carlsen et al. 2000; Cox & Allen 2008; Hiers et al. 2016). These conditions favor species that can spread vegetatively. Likewise, Grygiel et al. (2014) reported that rhizomatous species most commonly established outside seeded nuclei in tallgrass prairies.

This strong selection for species that propagate vegetatively raises a broader concern about biotic homogenization in restoration (McKinney & Lockwood 1999; Hiers et al. 2016). A common goal of restoration is to increase the cover and diversity of native species, but often the same generalist species are planted or recruit naturally at multiple locations across a given region (Holl 2002; Clavel et al. 2011; Lesage et al. 2018). This highlights the question of whether restoration will serve to restore the full suite of species across the landscape (β -diversity) if more locally restricted species are not planted or do not establish successfully (Polley et al. 2005; Lesage et al. 2018). Our results suggest that applied nucleation has the potential for restoring native cover in grasslands but may not be as effective in restoring the full diversity of species.

A long-standing debate in the succession and restoration literature is the degree to which initial conditions affect the long-term trajectory of ecosystem recovery (Temperton & Hobbs 2004; Collinge et al. 2011; Young et al. 2017). In our study, the inhibitory effects of mulch on non-native grass cover only lasted for 2 years, after which time the mulch had mostly decomposed, and the amount of native cover across treatments converged over time, trends that are consistent with prior research at this site (Holl et al. 2014b). At the same time, the presence of mulch at the beginning of the study enhanced the survival and early recruitment of a few species, which appeared to have a longer-term effect on species composition, in particular, the cover of *S. chilense*, which was not present in unmulched plots at the end of the study. This result is consistent with prior research suggesting that it is particularly important to reduce non-native competition at the initial stages of seedling establishment in California grasslands (Corbin & D'Antonio 2004; Lulow 2006).

The fact that the one rush, *Juncus patens*, which is a rhizomatous facultative wetland species, and the two annual forb species were not observed after the second year is likely due at least in part to the dry conditions early in the study, which was during the 1-in-1,200 year historic 2012–2014 California drought (Griffin & Anchukaitis 2014). The results highlight the challenge of reintroducing and maintaining annual species, particularly under highly variable rainfall conditions (Levine et al. 2008; Eviner 2014; Lesage et al. 2018).

The choice of restoration methods depends not only on ecological efficacy, but also on cost and logistical concerns, which are often site- and scale-specific. Applied nucleation and other

spatially patterned planting methods have lower plant propagation and planting costs compared to fully planting an area (Holl et al. 2020), but can be more logistically challenging and require additional staff training to implement given the non-standard planting designs (Ramírez-Soto et al. 2018). We planted seedlings rather than direct seeding nuclei, given that past cost calculations show that planting is the most cost-effective method at our site, due to low establishment from seed (Holl et al. 2014a) and the availability of volunteer labor to process native plant seed and plant seedlings. In other settings, it is more cost-effective to introduce nuclei by seeding (Grygiel et al. 2018). We tested applied nucleation at a small scale consistent with the size of many California coastal prairie restoration projects that are on the order of a few hectares or less. Comparisons of the ecological, logistical, and cost outcomes of applied nucleation versus other restoration strategies are needed at larger scales and in other grassland ecosystems.

In conclusion, applied nucleation and other spatially patterned planting designs show the potential to increase native cover of rhizomatous species in this and other grasslands (Grygiel et al. 2018; Gornish et al. 2019). However, grassland restoration is often quite challenging due to dispersal limitation and extensive competition from non-native species that are not shaded out by overstory cover (Gornish & Ambrozio dos Santos 2016; Sampaio et al. 2019), which is a mechanism that facilitates native seedling establishment in other nucleation studies (Holl et al. 2020). Successful restoration of these highly invaded systems will require long-term management and monitoring (Stromberg et al. 2007; Hayes & Holl 2011) and likely repeated introductions over time of species that do not readily establish (Wilson 2015; Stuble et al. 2017), regardless of the specific restoration methods used.

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Supporting Information

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

Table S1. Test statistics for repeated measures ANOVAs of native and exotic grass and forb cover over time.

Figure S1. Total rainfall from 1 October to 30 September of each rainfall year.

Figure S2. Full planting plot design. Green circles indicate the three grass species.

Figure S3. Applied nucleation plot design.

Figure S4. Full planting plant cover sampling layout.

Figure S5. Applied nucleation plant cover sampling layout.

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