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Permalink

<https://escholarship.org/uc/item/82d07019>

Journal

Restoration Ecology, 22(1)

ISSN

1061-2971

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Publication Date

2014

DOI

10.1111/rec.12022

Peer reviewed

RESEARCH ARTICLE

Establishment and Management of Native Functional Groups in Restoration

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Abstract

The limiting similarity hypothesis predicts that communities should be more resistant to invasion by non-natives when they include natives with a diversity of traits from more than one functional group. In restoration, planting natives with a diversity of traits may result in competition between natives of different functional groups and may influence the efficacy of different seeding and maintenance methods, potentially impacting native establishment. We compare initial establishment and first-year performance of natives and the effectiveness of maintenance techniques in uniform versus mixed functional group plantings. We seeded ruderal herbaceous natives, longer-lived shrubby natives, or a mixture of the two functional groups using drill- and hand-seeding methods. Non-natives were left undisturbed, removed by hand-weeding and mowing, or treated with herbicide to test maintenance methods

in a factorial design. Native functional groups had highest establishment, growth, and reproduction when planted alone, and hand-seeding resulted in more natives as well as more of the most common invasive, *Brassica nigra*. Wick herbicide removed more non-natives and resulted in greater reproduction of natives, while hand-weeding and mowing increased native density. Our results point to the importance of considering competition among native functional groups as well as between natives and invasives in restoration. Interactions among functional groups, seeding methods, and maintenance techniques indicate restoration will be easier to implement when natives with different traits are planted separately.

Key words: coastal sage scrub, community assembly, competition, functional traits, invasive species, Mediterranean-climate shrub-land.

Introduction

Niche-based community assembly theory predicts communities should be resistant to invasion by non-native species if they contain native species that have traits similar to the common non-natives (Abrams 1983; Fargione et al. 2003; Emery 2007). At larger spatial scales, successful non-natives should have adaptations similar to native species that are appropriate to the novel environment (Diez et al. 2008). Several studies have identified traits of successful invaders that are different from traits of native species at the community level, indicating that invasives are filling vacant niches (Prinzing et al. 2002; Leishman et al. 2007; Kuster et al. 2010). In restoration, this concept may guide the selection of native plants, supporting the use of diverse natives with a range of traits and especially traits similar to those of common invasives (Young et al. 2005; Funk et al. 2008; Roberts et al. 2010). Yet ruderal natives have many of the traits associated with successful non-natives,

including high dispersal abilities, growth rates, and reproductive rates (Grime 1977; Sakai et al. 2001; Prinzing et al. 2002) and may thus interfere with the establishment of later successional natives. Consequently, the efficacy of planting mixed functional groups is somewhat uncertain.

Ruderal, non-native grasses and forbs have invaded many semiarid shrub ecosystems, such as the Coastal Sage Scrub communities of southern California (Stylinski & Allen 1999; Cox & Allen 2008). Restoration of heavily degraded Mediterranean-climate shrublands can be difficult, even after non-native grazers are removed or fire frequency is reduced (Eliason & Allen 1997; Minnich & Dezzani 1998; Sharma et al. 2010). Non-native removal methods are labor intensive and expensive, so maximizing their efficiency is important (Simmons et al. 2007; Wilson et al. 2011). While trait-based restoration theory suggests including ruderal, early-successional native species in restoration to assist in controlling invasive species (Funk et al. 2008), the planting of native ruderals decreases trait differences between natives and non-natives, making it more difficult to apply a non-native-control strategy without simultaneously damaging natives (Kaeser & Kirkman 2010; Cox & Allen 2011).

Using different seeding methods (drill vs. hand seeding) and maintenance methods (hand weeding and mowing vs. herbicide) we tested initial establishment, growth, and

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reproduction of natives from seed mixes that contained ruderals, shrubs, or a combination of the two. We used an additive design to maintain constant intraspecific (and intra-functional group) competition in separate and mixed plantings (Goldberg & Scheiner 2001). While a subtractive design (aka replacement) tests the hypothesis that intra- and inter-functional group interactions are equal, additive designs test the hypothesis that different functional groups do not compete because they use different resources (Snaydon 1991; Hamilton 1994). Additive designs are commonly used in restoration (Haggar & Ewel 1997; Fehmi et al. 2004; Murphy 2005). While manipulating densities of both functional groups (aka a response surface design) carries the benefits of both additive and subtractive designs (Inouye 2001), this was not feasible because all density combinations were crossed factorially with seeding and maintenance methods (Goldberg & Scheiner 2001; Inouye 2001; Murphy 2005).

With an additive design, we addressed the following questions: (1) Do different functional groups of natives (ruderals versus shrubs) have greater first-year establishment and reproduction when seeded alone or mixed together? (2) What seeding method results in greatest establishment of each functional group? and (3) When labor time is kept constant, what maintenance technique results in greatest native establishment and reproduction and do results differ between groups when planted alone or in a mix? Unlike previous tests of limiting similarity and applications to trait-based restoration (Fargione et al. 2003; Turnbull et al. 2005; Firm et al. 2010), our approach investigated the relationship between different functional groups of natives and potential interactions with seeding and maintenance methods. Plots with both ruderals and shrubs may have greatest native establishment because different functional groups utilize different resources (Abrams 1983; Pacala & Tilman 1994). Alternatively, plants with different growth strategies may compete more with one another, such as through successional change that allows one life form to restrict the resources available to another (Huston & Smith 1987; Tyler 1996; Keeley et al. 2005). Our results will clarify effectiveness of native establishment when planting natives with a range of traits in restoration, the germination response to seeding method, and potency of different maintenance techniques.

Methods

Study Site and Experimental Design

The study was within the Irvine Ranch Natural Landmark in southern California (117.7382°N, 33.7647°W). Long-term (1902–2003) mean annual precipitation was 327 mm (Tustin Irvine Ranch Station, Coop ID # 049087, 33°43'N, 117°47'W, elev. 36 m), and rainfall for 2011 (year of study) was 500 mm (Santiago Dam Station, Coop ID # 047987, 33°47'N, 117°43'W, elev. 26 m). Cattle grazing occurred from at least the mid-1800s until 2002. Fires within the last 50 years occurred in 1967 and 2007.

Prior to restoration, the 66 × 30 m experimental area had 255% cover non-native annual grasses (primarily *Bromus*

diandrus, *Brachypodium distachyon*, and *Avena fatua*), 95% cover non-native forbs (all *Brassica nigra*), and 3% native cover. Remnant native vegetation in the watershed indicated a mosaic of grassland and coastal sage scrub. Site preparation to reduce the number of non-native seeds in the seed bank consisted of 2 years (2009 and 2010) of pre-germination mowing and post-germination spraying with glyphosate at 0.25 qts/ac (1.17 L/ha). The site had a gentle slope of -18° . We used a fully factorial design with three independent variables: (1) native seed mix (ruderals, shrubs, or a combination of the two in an additive design); (2) seeding method (drill seeder or hand-broadcast with tamping); and (3) maintenance treatment (herbicide-wick, hand/mow, or control). The resulting 18 treatment combinations were applied in $3.7 \times 5 \text{ m}^2$ plots, replicated in each of six blocks (Fig. S1).

Each seed mix consisted of six native species based on those occurring in the vicinity of the restoration site, in addition to a third mix consisting of all species, additively (Table S1, nomenclature follows Baldwin et al. 2012). Species were seeded on 13 and 14 December 2010. For the drill-seeded treatment, we first removed excess thatch with a Rowse® (Burwell, NE, U.S.A.) hydraulic rake tractor attachment, designed to gather hay. Raking was immediately followed with seeding with a Truax® FLEXII Grass Drill (New Hope, MN, U.S.A.), which included concave blades in front of each seed disc to facilitate no-till seeding. For the hand-seeded treatment, we hand-raked thatch, broadcast seed (measured out for each seed strip per mix), lightly raked, and used McLeods to tamp seeds into the soil.

For the herbicide-wick strategy (hereafter “wick”), we applied concentrated glyphosate (20%) with The Red Weeder® (Harrisburg, OR, U.S.A.) weed wiper. This hand held tool consists of a tube with an herbicide solution and a sponge at the end, which allows the applicator to treat individual plants with a single dab on a leaf. We applied this treatment once a month (February–May). For the manual and mowing strategy (hereafter “man/mow”), we hand-pulled non-natives in February and March, and used weed whackers to cut non-natives to the height of natives in April and May. For wick and man/mow treatments, we standardized quantity of time applied to each plot (7 minutes for first three events and 5 minutes for the last event).

Data Collection

Data on emergent seedlings, early summer plant density, and estimated seed set (for species that reproduced) were collected in all plots. Height of shrubs (and diameter of the perennial grass, *Elymus condensatus*) was determined in shrub and mixed plots. Two weeks post-germination following late-December rain, prior to application of maintenance treatments, we recorded all seedlings in a 25 × 25 cm quadrat in the center of each plot. Mid-June 2011, three 25 × 25 cm quadrats were placed in each plot along a diagonal from the upper left corner, through the middle, and in the lower right of each plot. Quadrats were placed 1 m from plot edges, and all plants in each quadrat were recorded. Average number of individuals

and species richness (S) per plot was calculated and used as the dependent variable in analyses.

Reproductive output was estimated in July and August, 2011, in one 25 × 25 cm quadrat in the center of each plot for all species that reproduced except for *Eschscholzia californica*, whose seeds dispersed earlier in the season. To determine seed production by *Phacelia cicutaria*, we counted infructescences and measured their length. Seed number was highly correlated with infructescence length ($N = 27$, $R^2 = 0.9018$, $p < 0.0001$), so we used length to estimate seed set. For *Malacothrix saxatilis* and *Deinandra fasciculata*, we counted composite flowers per infructescences on an average-sized individual in each plot and used average seed number/infructescence ($N > 25$) to estimate seed production per plot. Seed production estimates were natural log-transformed to improve normality. Flowers were counted on all reproductive *Eriogonum fasciculatum* individuals. Height of native shrubs and diameter of *E. condensatus* were measured in the central quadrat.

Data Analysis

Counts of native and non-native seedlings were square-root transformed to improve normality. Proportion of native plants was approximately normally distributed. All data (square-root transformed number of seedlings, average density, ln-transformed seed estimates, and average size) were analyzed with fully factorial mixed-model analysis of variances (ANOVAs) using proc mixed in SAS (version 9.3, SAS Institute, Cary, NC, U.S.A.). The three treatments (seed mix, seeding method, and maintenance technique) were included as fixed factors, and block (replicate) was included as a random factor. Maintenance treatment was not included in analysis of seedling data, which were collected prior to treatment application. We also performed an ordination, implemented with PC-ORD (McCune & Mefford 1999), using the June density data to evaluate patterns of community composition after several months of growth with different maintenance techniques and seeding methods. We used non-metric multi-dimensional scaling on Bray–Curtis distances to find a two-dimensional ordination in which the graphic distances from one plot to the next represent the dissimilarities in the plant associations.

Results

Large numbers of seeded natives germinated in response to January rains. Two native ruderals (*Calandrinia ciliata* and *Lupinus succulentus*) and one shrub (*Acmispon glaber*) did not establish well (six or fewer seedlings in February censuses). Seventeen non-native volunteer species also germinated in study plots. *Brassica nigra* was by far the most abundant non-native, germinating in every plot with up to 20 individuals per sampling quadrat. Few natives germinated from the seed bank, in fewer than five plots (Table S1).

Main Effect of Native Functional Groups

Both functional groups had greater establishment, growth, and reproduction when grown alone than in mixed plantings. In

February, there were more shrub seedlings in plots without native ruderals than in mixed plots (Fig. 1, Table S2). This was true for both the number of individual shrubs as well as the number of shrub species (S , Table S2). Although this was an additive design in which mixed plots received more seeds, the sum of all native seedlings was highest in shrub-only plots, intermediate in mixed plots, and lowest in ruderal plots (Fig. 2, Table S2). There was no significant difference in numbers of native ruderal seedlings in plots with or without shrubs (Table S2, Fig. 1). Each functional group had higher density in June (four months post-germination), when grown alone than in combination (Table S3, Fig. 3). Species richness (S) of shrubs was higher in shrub-only plots, while ruderal S did not differ among seed mixes (Table S3). As expected, S of all natives combined (calculated with both shrubs and ruderals) was greater in mixed plots (Table S3). The sum of all native plants was highest in shrub-only plots, intermediate in mixed plots, and lowest in ruderal plots (Fig. S2, Table S3).

Abundance of non-native seedlings was not significantly influenced by native seed mix (Table S2). This was true for the most abundant non-native, *B. nigra*, as well as the non-native grasses. Non-native abundance in control plots in June (without maintenance) was also not significantly influenced by the native community (Fig. S3, Table S4).

Native ruderals *Phacelia cicutaria* and *Malacothrix saxatilis* had higher seed production in ruderal-only plots than in mixed plots (*Phacelia* $F_{1,40} = 6.68$, $p = 0.014$, *Malacothrix* $F_{1,35} = 11.9$, $p = 0.002$, Fig. S4). For *Deinandra fasciculata*, there was no significant effect of seed mix ($F_{1,35} = 0.01$, $p = 0.953$). *Eriogonum fasciculatum*, the only native shrub to reproduce the first year, produced an average of 8 inflorescences/plant in shrub-only plots, and did not reproduce at all in mixed plots. *Eriogonum fasciculatum* and *Elymus condensatus*, were larger in shrub-only plots (ERFA $F_{1,32} = 9.21$, $p = 0.005$, ELCO $F_{1,23} = 4.63$, $p = 0.04$, Fig. S4), while *Salvia apiana* and *Artemisia californica* did not differ in size depending on seed mix (SAAP $F_{1,29} = 0.13$, $p = 0.720$, ARCA $F_{1,30} = 1.84$, $p = 0.177$).

The ordination of plots in species space sorted plots along Axis 1 by seed mix, from ruderal-only to shrub-only (Fig. 4). Some species, such as *S. apiana* and *E. fasciculatum*, were particularly highly correlated with Axis 1 ($R > 0.88$), indicating these species were more likely to occur in shrub-only plots (Table S5). *Phacelia cicutaria* was highly negatively correlated with Axis 1 ($R = -0.77$), indicating that it was more abundant in ruderal-only plots. Axis 2 of the ordination separated plots according to whether they contained more *B. nigra* (control plots) or native species (plots with some type of maintenance treatment, Fig. 4).

Seeding Method, Maintenance Technique, and Interactions with Seed Mixture

There were more native seedlings in hand-seeded than drill-seeded plots and in shrub-only plots than ruderal-only plots (Table S2, Fig. 2). There were also more seedlings of the most abundant non-native, *B. nigra*, in hand-seeded plots,

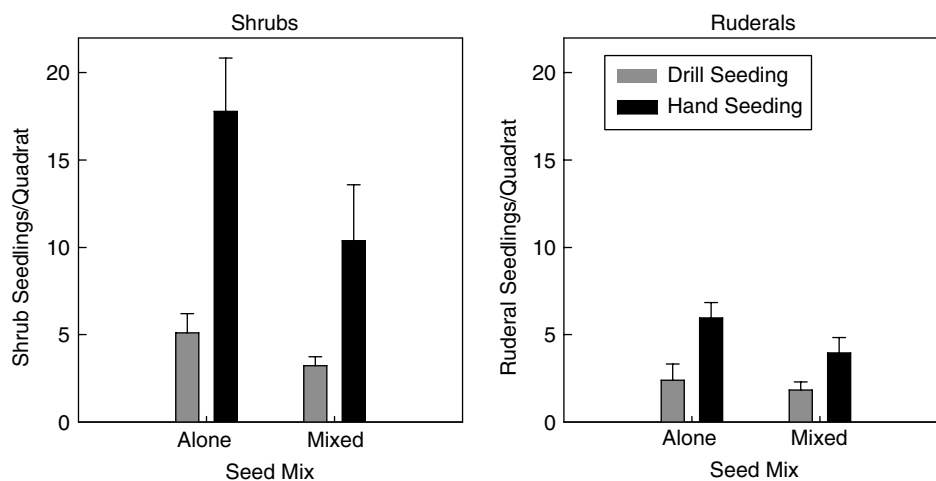


Figure 1. Emergent seedlings of native ruderals and shrubs planted alone and in a mixture in drill- and hand-seeded plots. Data are means + SE.

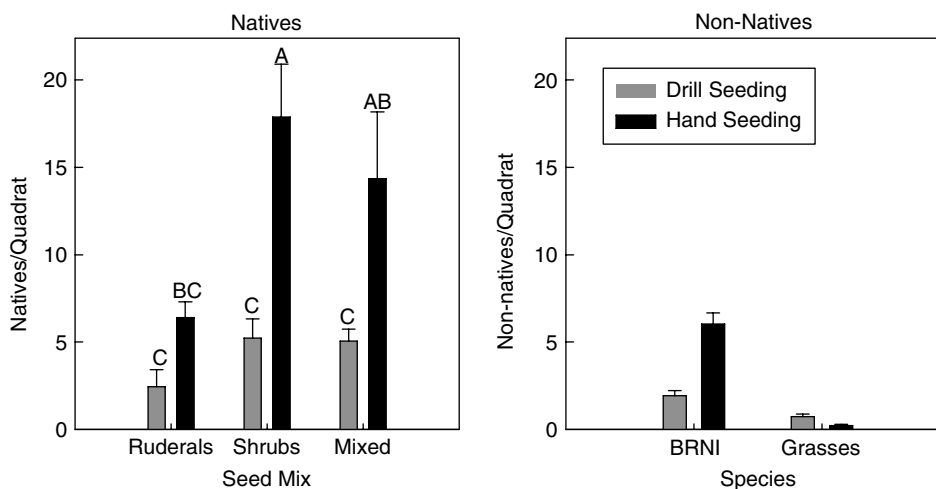


Figure 2. Number of native (left) and non-native (right) emergent seedlings recorded in February in drill- and hand-seeded plots. For natives, the x-axis lists the seed mix, and letters indicate results of a Tukey post-hoc test, where different letters indicate a statistically significant difference between group means. Numbers of *Brassica nigra* and of non-native grass species were graphed separately. Values are means + SE.

while non-native grasses germinated more in drill-seeded plots (Table S2, Fig. 2). Differences in abundance depending on seeding method persisted through June (Figs. S2 & S3, Table S3).

Both man/mow and wick reduced density of non-natives (Table S3, Fig. S3). Wick reduced *B. nigra* and increased non-native grasses, presumably due to reduction of *B. nigra* (Fig. S3, Table S3). Natives were most abundant in man/mow plots and had higher diversity in plots that received any weed maintenance (Fig. S2, Table S3). *Eriogonum fasciculatum* only reproduced in wick plots, and *Malacothrix saxatilis* had greater seed production in wick plots (Fig. S4). Native response to maintenance varied depending on seed mix and seeding method, as was evident in significant three-way interactions for density of shrubs, ruderals, and all natives combined (Table S3, Fig. 3). In hand-seeded plots, man/mow resulted in greater native density than wick. Drill plots treated with

wick and man/mow had higher native density than control plots. Effectiveness of man/mow varied depending on seed mix, with man/mow resulting in greater native density than wick in shrub-only plots, but no significant difference between the maintenance treatments in mixed plots (Fig. 3, Table S3).

Discussion

Success of native establishment and first-year performance varied depending on trait diversity of natives used in restoration. That native ruderals, whose traits are similar to non-natives, did not reduce non-native germination or abundance more than native shrubs contradicts other trait-based restoration studies (Bakker & Wilson 2004; Young et al. 2009; Ammond & Litton 2012; Mason et al. 2012). It will be interesting to monitor this through time, as the influence of native plant community on non-natives may change with

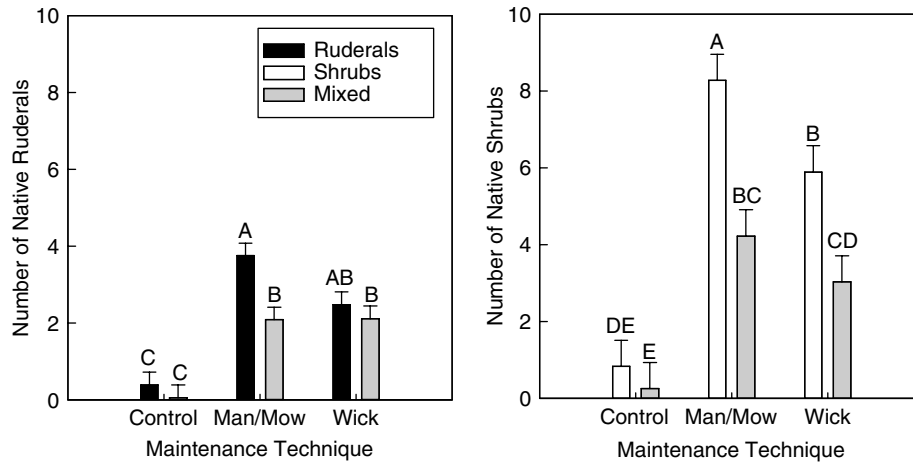


Figure 3. Density of ruderals and shrubs planted alone and in mixed groups. The *x*-axis indicates maintenance technique (control plots with no removal of non-native species, man/mow, or wick treatments). Values are means + SE. Letters indicate results of a Tukey post-hoc test, where different letters indicate a statistically significant difference.

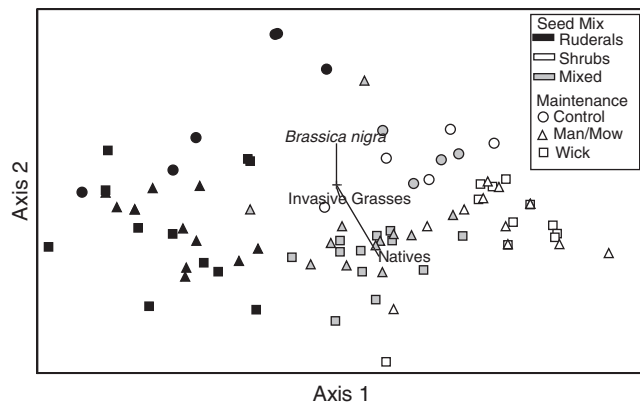


Figure 4. Ordination of plots, coded by seed mix and maintenance technique, based on abundance of species. The plots-by-species matrix was Beals smoothed, and the transformed matrix was ordinated using nonmetric multidimensional scaling of Bray–Curtis distances. Vectors represent correlations between abundance of *Brassica nigra*, non-native, invasive grasses, and native species and axes of the ordination. The length of the vector represents the strength of the correlation. Correlations for the abundance of each species with the ordination axes are given in Table S5.

shrub growth. Each native functional group had greatest establishment, growth, and reproduction when planted separately. This was an additive design in which intra-specific and intra-functional group competition remained constant, so reduced establishment of each functional group in mixed plots demonstrates competition among plants from different functional groups (Goldberg & Scheiner 2001). Reduced performance of each functional group in mixed plantings may seem contrary to niche-based coexistence and community assembly theories that predict competition within functional groups to be stronger than competition between functional groups (Chesson 2000; Fargione et al. 2003; Adler et al. 2009). As mentioned in the introduction, one possible explanation with an additive design

is that greater plant density in mixed plots decreased available resources (Marquez & Allen 1996; Goldberg & Scheiner 2001). We seeded both functional groups at relatively high rates in comparison to other CSS restoration studies, making it unlikely that establishment was seed limited (Cione et al. 2002; Montalvo et al. 2002; Cox & Allen 2011).

Resulting plant density depended on seed mix, with greatest overall density in shrub-only plots. Density differences were apparent in February and continued through June. While reduced establishment and success of shrubs in mixed plots cannot be explained by density (since density of all plants was greatest in shrub-only plots), density may explain reduced establishment and performance of ruderals in mixed plots (density was lowest in ruderal-only plots). It is more difficult to understand how this could have resulted in the differences observed in February, when seedlings had emerged only weeks prior to data collection. Controlled competition experiments and measurements of germination phenology could determine the mechanism by which each native functional group reduced performance of the other (Goldberg 1996).

Our results are consistent with another study of emergence and survival of ruderals and shrubs in CSS, in which ruderals had increased survival when shrubs were removed (Tyler 1996). However, in that study and in studies of post-fire succession in semi-arid shrublands, negative correlations between ruderals and shrubs were caused by shade-intolerance of ruderals (Westman 1981; Tyler 1996; Keeley et al. 2005). In contrast, ruderals in this study grew quickly and were taller than shrub seedlings. If light competition influenced results, shading was likely the cause of reduced performance of shrubs, rather than ruderals, in the mixed plantings. Our result that shrubs performed better without ruderals may explain why shrubs did not establish in another CSS restoration project, where shrubs were seeded along with natives from other functional groups (Cox & Allen 2008). In temporally variable environments such as Mediterranean climates (Keeley et al.

2005), the limiting similarity concept that predicts competition within functional groups is complicated by changes in available resources (Abrams 1983; Pacala & Tilman 1994). This experiment was conducted in a high-rainfall year, presumably favoring establishment of all species. High-rainfall may have resulted in light, rather than water, being the primary limiting resource. In a different type of year, we may expect more intense competition for water, and taller plants may create favorable microhabitats resulting in facilitation rather than competition (Padilla & Pugnaire 2006; Maestre et al. 2009).

Greater germination of natives in hand-seeded plots corresponds with another study comparing seeding methods in CSS (Montalvo et al. 2002). We were surprised that our test of drill- and hand-seeding methods resulted in differences in volunteer, non-native species. The more thorough raking of the top 5–10 mm of soil with the finer pronged hand-rake (vs. the hay rake tractor attachment) probably brought *Brassica nigra* seeds to the surface, exposing them to light and increasing germination. Differences in native germination may be due to planting depth, since the drill seeder tends to plant seeds deeper in the soil (Sheley et al. 2006; Yurkonis et al. 2008). Non-native grasses have greater germination under thatch while natives exhibit decreased germination under thatch (Reynolds et al. 2001; Levine & Rees 2004). Although thatch was removed from both hand and drill seeded plots, differences in exposure to sunlight caused by planting depth and/or raking methods may be similar. Lower emergence of natives in drill-seeded plots may be due to decreased sunlight exposure or decreased distances between seeds planted in rows in drill-seeding versus hand-seeding, which involves scattering seeds evenly and more natural distances between neighbors (Yurkonis et al. 2010).

Our results clearly support maintenance to reduce non-natives during native establishment, but there was no clear answer to the question of whether man/mow or wick was most effective. Effectiveness varied depending on seeding method (and resulting differences in plant density) and functional group. Natives were most abundant in the shrub-only man/mow plots, while there was no difference in native density in man/mow or wick treatments in mixed plots. We think this is because mowing occurred at the height of the tallest native and there was greater height discrepancy between shrubs and non-natives. As shrubs grow taller through time, we may expect mowing height to be more similar among treatments. Natives, regardless of functional group, tended to have highest density in man/mow plots, but higher fecundity in wick plots. In the ordination graph, man/mow and wick plots are scattered throughout the bottom half, indicating no difference in community composition. Wick herbicide removed more *B. nigra* but not non-native grasses. The wick method used a broad-spectrum herbicide applied directly to the non-native plant. Targeted herbicides applied aurally to areas where natives differ from non-natives, such as broad-leaf-specific or graminoid-specific herbicides, may be more efficient (Ansley & Castellano 2006), although aerial herbicides may have un-intended, negative side effects on native species (Kaesler & Kirkman 2010). Maintenance techniques are often more successful in communities where natives are very different from non-natives

(Sandel et al. 2011), supporting the concept of separating out native shrubs from those whose traits overlap with non-natives. The efficiency of selective herbicides is especially important given that restored CSS may require long-term maintenance (Allen et al. 2005).

In conclusion, data collected during the first year of native growth in this restoration experiment demonstrated that native shrubs and ruderals had greater germination, survival, and, for some species, greater seed production in separate than in mixed functional group plantings. We are continuing to monitor these plots to determine whether the pattern we observed during initial establishment, early growth, and first-year reproduction continues through time. We repeated the experiment on a larger scale in a different year to determine the role of environmental variation on our results, something that is especially important in temporally variable environments such as southern California (Keeley et al. 2005). Continued monitoring will clarify the long-term importance of competition between natives with different life histories and growth strategies in restoration.

Implications for Practice

- Planting native shrubs and herbaceous ruderals in separate strips may result in greater establishment and would allow for selective maintenance options.
- Hand seeding and raking may lead to greater germination of Coastal Sage Scrub species than drill seeding.
- Hand raking may be useful in the site-preparation phase to flush out seeds of *Brassica nigra*.
- Weed maintenance may be essential to establishment of all native plants in restoration.

Acknowledgments

We are grateful to UC Irvine Center for Environmental Biology faculty members and Irvine Ranch Conservancy staff, and especially to Diane Pataki and Jutta Burger. Kathleen Treseder commented on a draft of the manuscript. Rosemary Garcia and Roxanne Murillo assisted with data collection in the field. Funding was provided through CEB, which was founded in 2010 by a grant from Donald Bren and the Irvine Company. Irvine Ranch Conservancy provided additional funding, through the Irvine Company and Orange County Parks.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Layout of the experimental design.

Figure S2. The density of native plants in June.

Figure S3. The density of all non-native plants.

Figure S4. Estimated reproductive output of *Phacelia cicutaria* and *Malacothrix saxatilis* and size of *Eriogonum fasciculatum* and *Elymus condensatus* in plots with single vs. mixed plantings.

Table S1. List of species found in our study plots.

Table S2. Results from mixed-model ANOVAs on data collected in February on the number of emergent seedlings.

Table S3. Results from mixed-model ANOVAs on data collected on plant density (number of plants) in June.

Table S4. Results from mixed-model ANOVAs on data collected on density of non-native plants in June.

Table S5. Correlations of each species with ordination axes.