Using filter-based community assembly models to improve restoration outcomes

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Summary

1. Ecological filter models derived from community assembly theory can inform restoration planning by highlighting management actions most likely to affect community composition. Despite growing interest in these models, many restoration studies solely manipulate a single assembly filter – the biotic filter by altering interspecific competition – while ignoring abiotic and dispersal filters that may also influence restoration success.

2. To examine how manipulating all three assembly filters (biotic, abiotic, dispersal) affected restoration in an annual-type grassland, we seeded native forbs from the same functional group as a target invader to increase biotic resistance to invasion (biotic filter), cut standing biomass and either removed it or returned it to plots as litter to alter light conditions (abiotic filter), and added native forbs at different seeding rates to alter density of establishing native populations (dispersal filter). We measured grassland restoration success by recording native species and invader cover in plots.

3. The addition of native species with phenological and morphological traits similar to the target invader reduced invasion and increased native populations, but only in litter-free plots when high densities of native seed were added.

4. Seeding two species with functional traits similar to the invader was more effective for achieving restoration goals than seeding just one functionally similar species. As such, trait differences among restoration species, even species belonging to the same functional group, may increase biotic resistance to invasion in restored communities.

5. Litter removal altered native–invader interactions. When litter was left on the plots, added natives did not reduce invader cover. However, when litter was removed, added natives led to declines in invader cover.

6. Increasing native seeding rates led to larger native populations and increased invasion resistance.

7. Synthesis and applications. In this study, simultaneously manipulating biotic, abiotic and dispersal filters was necessary to optimize grassland restoration outcomes. In particular, the biotic filter only contributed to successful restoration outcomes under abiotic and dispersal conditions that were created through management actions specifically targeting these two additional filters. Restoration planning based on filter models should incorporate actions that target all three assembly filters, rather than solely focusing on the biotic filter.

Key-words: assembly filter, Centaurea solstitialis, community assembly, competition, filter model, functional trait, grassland restoration, litter, seeding rate

Introduction

Ecosystem restoration often requires strategies that encourage native species establishment while resisting non-native species invasion. Assembly theory, by focusing on processes that influence community development, provides a rich foundation of ideas that can inform restoration strategies (Temperton & Hobbs 2004). In particular, the concept of ‘ecological assembly filters’ – processes that sort and narrow the pool of potentially establishing

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species based on their traits – provides a framework for understanding factors that contribute to final species composition, abundance and diversity in restored ecosystems (Keddy 1992; Diaz, Cabido & Casanoves 1998) (Fig. 1). Three assembly filters commonly identified in the restoration literature are as follows: (1) dispersal limitation – barriers preventing species from reaching a restoration site (Funk et al. 2008; Oster et al. 2009), (2) abiotic site conditions – environmental conditions that differentially favour the establishment and survival of species at a site (Hobbs & Norton 2004; Cleland, Larios & Suding 2013) and (3) biotic interactions – interactions among species that limit the persistence and abundance of individual species (Funk et al. 2008; Cleland, Larios & Suding 2013). By identifying the biotic, abiotic and dispersal filters that contribute to community assembly, filter-based assembly models (filter models) highlight suites of actions practitioners could implement to reach ecosystem management goals (Fig. 1).

To date, restoration studies that use filter models to inform community assembly mainly focus on the biotic filter by manipulating resident composition to alter biotic resistance in restored communities (Funk et al. 2008; Hooper & Dukes 2010; but see Cleland, Larios & Suding 2013). An increasing number of studies, particularly in the biodiversity–ecosystem functioning literature, find that adding resident species with functional traits similar to exotics reduces invasion (Young et al. 2009; Hooper & Dukes 2010). This literature highlights two mechanisms that contribute to biotic resistance: complementary resource-use by resident communities (Hooper 1998; Fargione & Tilman 2005) and the limiting similarity of resident species and invaders (Tilman 2004; Hooper & Dukes 2010). In both cases, resident species decrease the chance of invasion by reducing available resources.

Drawing on these ideas, managers may be able to increase biotic resistance to invasion by filling niches in restored sites with native species that use resources similarly to non-natives (Funk et al. 2008) (Fig. 1).

In contrast to the biotic filter which can limit trait similarity in assembling communities, the dispersal and abiotic filters are predicted to favour assembly of natives and exotics with similar traits (Funk et al. 2008; Laughlin et al. 2012). Because of this, it may not be obvious how managers can use these filters to favour natives while limiting exotic invasion. For example, dispersal filters may lead to species with similar dispersal syndromes reaching assembling sites (e.g. species with wind-dispersed seeds). Similarly, the abiotic filter can lead to successful colonisation by any arriving species that can survive existing site conditions. It may be possible in a restoration context, however, to manipulate both the dispersal and abiotic filters through management designed to favour natives and inhibit exotics.

The dispersal filter, which in natural settings influences assembly by affecting species arrival to sites, can be manipulated in restoration settings through native seeding rates (Oster et al. 2009) (Fig. 1). While invasion research often focuses on the propagule pressure of exotic species as a driver of invasion (Von Holle & Simberloff 2005), competition between native and exotic plants may equally depend on native abundance (Simmons 2005; Hulvey & Zavaleta 2012). Low native propagule pressure leading to sparse native populations can result in little competition for limiting resources and reduced biotic resistance to invasion. In restoration settings, adding natives at high seedling densities might increase the competitive interactions between functionally similar natives and invaders.

Successful restoration will also depend on how both seeded natives and targeted exotics respond to site

Fig. 1. Community assembly filter model. Community assembly theory can be used to explain the sorting of the available species pool to determine final composition in unmanaged grassland communities. Species must pass through a series of ‘filters’ that narrow the pool, including dispersal, abiotic and biotic filters. In a restoration setting, managers can manipulate filters to influence the final composition of restored sites.
conditions that comprise the abiotic assembly filter (Fig. 1). Because species belonging to the same functional group can possess strongly overlapping traits, such as rooting depth or phenology, management designed to make a site suitable for added native species may also favour the establishment of functionally similar exotics. Species classified in the same functional group, however, can differ in many traits (Evinaer & Chapin 2003) leading to differences in establishment and survival under the same abiotic conditions. Management that targets these differences, particularly actions that favour natives over exotics, may be the key to increasing restoration success.

In this study, we build on initial work linking filter-based assembly models to ecosystem restoration by testing how manipulating all three assembly filters (dispersal, abiotic and biotic), rather than solely the biotic filter, can increase restoration success. We focus on grassland ecosystems, where limiting similarity of resident species and invading exotics has often been tested as a mechanism contributing to biotic filtering (Young et al. 2009; Hooper & Dukes 2010). Similar to past grassland studies, we manipulate the biotic assembly filter by planting different native seed-mixes with functional traits similar to targeted exotic species and test how seed-mix composition can affect the biotic filter. We additionally target the dispersal and abiotic filters by manipulating native seeding density (dispersal filter) and altering the amount of litter in restoration plots (abiotic filter).

We chose to manipulate the abiotic filter via litter removal because grassland restoration projects often require some site preparation (mowing, ripping, burning) (Stromberg et al. 2007) that alters the presence of litter. The effects of litter removal can vary, with some studies finding litter decreases seedling survival by reducing light levels or creating a mechanical barrier to germinating seeds (Xiong & Nilsson 1999; Amatangelo, Dukes & Field 2010). Similar to past grassland studies, we manipulate the biotic assembly filter by planting different native seed-mixes with functional traits similar to targeted exotic species and test how seed-mix composition can affect the biotic filter. We additionally target the dispersal and abiotic filters by manipulating native seeding density (dispersal filter) and altering the amount of litter in restoration plots (abiotic filter).

We were interested in determining whether manipulating all filters together led to synergistic effects on restoration outcomes.

**Materials and methods**

**STUDY SYSTEM**

To explore the restoration benefit of manipulating multiple assembly filters, we focused on the restoration of a Californian annual-type grassland dominated by non-native *Centaurea solstitialis* L. Like many grassland ecosystems, the composition of Californian annual grasslands has changed drastically due to ongoing invasions (Schiffman 2007). *Centaurea solstitialis* is a target for control because it competes with native plants, is spreading and can interfere with cattle grazing (DiTomaso, Kyser & Pitcairn 2006). Our goal was to reduce the abundance of *C. solstitialis* while simultaneously increasing populations of native species.

The study took place from November 2007 to August 2008 and was located at the Skyline Ridge Open Space Preserve, Palo Alto, California, in the Central Coast Range (37°18′44.19″N, 122°10′36.94″W, 640 m elevation). The area has a Mediterranean climate with rain occurring November–March, followed by a dry season April–October. Rainfall for the duration of the study was 71–86 cm. See Appendix S1 in Supporting Information for a list of species occurring at the site.

**ASSEMBLY FILTER MANIPULATION**

**Biotic filter**

We examined whether the addition of native forbs [*Hemizonia congesta* DC. ssp. *luculfolia* (DC.) Babc. & H.M. Hall (hayfield tarplant) and *Madia gracilis* (Smith) Keck (slender tarplant)] with resource-use characteristics similar to *C. solstitialis* could reduce *C. solstitialis* cover and also whether both native forbs seeded together had a greater effect on *C. solstitialis* than *H. congesta* alone.

*Centaurea solstitialis*, *H. congesta* and *M. gracilis* can all be classified in the same functional group – late-season annual forbs – based on a number of phenological and morphological characteristics that make possible spatial and temporal competition for resources throughout the growing season (Dukes 2001). All three species bolt and flower between May and September after many other grassland plants have senesced (Gulmon et al. 1983; Hickman 1993; DiTomaso, Kyser & Pitcairn 2006) and each has a taproot that allows it to survive during the summer drought common in California’s Mediterranean climate.

**Dispersal filter**

We altered the dispersal filter by varying native forb seeding rate. Seeding densities included no addition, low-density addition (500 seeds m$^{-2}$) and high-density addition (2000 seeds m$^{-2}$). *Hemizonia congesta* has a laboratory germination rate of c. 10% (K. Huvev, unpublished data) resulting in an estimated live seeding rate of 50 and 200 seeds m$^{-2}$, respectively. These numbers are lower than the recommended 600 live seeds m$^{-2}$ for grass seed in Californian restoration projects (Stromberg et al. 2007); however, because neither *M. gracilis* nor *H. congesta* are commonly grown by seed suppliers, seeding rates may be limited by the amount of seed that can be locally collected. We aimed to investigate whether these relatively low seed densities could result in positive restoration effects. We matched the total seeding rates in the two-species treatment to those in the one-species treatment and chose to use equal amounts *H. congesta* and *M. gracilis* to allow for differences in germinability.

**Abiotic filter**

We manipulated the abiotic assembly filter by cutting the previous year’s dead standing biomass and either removing it or adding it back as an even layer of cut-litter. Past studies determined that *C. solstitialis* grows better in high light environments (DiTomaso, Kyser & Pitcairn 2006), so we expected litter removal to favour re-invasion. Because *H. congesta* and *M. gracilis* share a number of phenological and morphological traits with
**C. solstitialis**, we also expected litter removal to favour their establishment but were interested in possible differences among species.

**EXPERIMENTAL DESIGN**

In November 2007, we established 30 1 \times 1 \text{ m} plots, leaving at least 1 \text{ m} between plots and seeded them with locally collected *H. congesta* (Fig. 2). After these plots were seeded, we added a two-species native seeding treatment to the experiment. Because we could no longer randomize this treatment across the previously seeded plots, we established a second set of 30 plots adjacent to the first and added a 1:1 mix of locally collected *H. congesta* and *M. gracilis*. The cover of senesced *C. solstitialis* was similar across all pre-treatment plots and ranged from 75% to 95%. This pre-planting cover represented accumulated growth from previous growing seasons since *C. solstitialis* stems degrade slowly (DiTomaso, Kyser & Pitcairn 2006). Although similar amounts of senesced *C. solstitialis* across plots did not guarantee similarly dense populations the following year due to the influence of annual growth conditions, we used senesced *C. solstitialis* cover as an indication that the seed bank in plots was relatively similar. We did not attempt to alter *C. solstitialis* seed densities in the seed bank.

Within each set of plots, we crossed seeding density \times litter treatments (three seed densities and two litter treatments) to test how manipulating the dispersal filter and abiotic filter in addition to the biotic filter might influence restoration outcomes. We lightly raked added seed into exposed soil after cutting litter. We included five randomized replicates of the six seeding density \times litter treatments for both the one- and two-species additions (60 plots total). We additionally compared these restoration treatments to five unmanipulated grassland control plots interspersed among the 60 manipulated plots. Recruitment of *C. solstitialis* occurred naturally from the seed bank. Although we did not analyse the seed bank prior to planting, we did not find evidence of *H. congesta* at the site before seeding (i.e. live or dead plants). *Mudia gracilis* occurred at low levels throughout the site. Our seeding rates, however, resulted in *M. gracilis* populations that were an order of magnitude greater than background levels 75% of the time.

On 6 and 7 August 2008, we recorded *C. solstitialis* abundance by measuring cover using 5% cover classes plus a 1 and 3% cover class to accurately characterize low-cover plots. To measure native species establishment, we counted individuals belonging to each seeded forb species and recorded total cover of all native species found in plots. To reduce the influence of edge effects, we collected all data from 0.50 m² (0.71 \times 0.71- \text{m}) interior subplots.

**ANALYSIS**

Due to our staged experimental set-up, the one- and two-species seeding treatments were not randomized with respect to the experimental plots. To assess the likelihood of site effects, we compared final 2008 *C. solstitialis* cover between the one- and two-species plots using one-way ANOVA in the most similar conditions: litter-free, no-seed addition treatments. Because there was no significant difference in *C. solstitialis* cover in these plots, we assumed there was no confounding site effect and included both one- and two-species plots in a single analysis.

Following the examination of confounded site effects, we used three-way means model ANOVAs (with native species number, seeding density and litter treatment as factors) to determine the effectiveness of included restoration treatments and compare them to unmanipulated grassland control plots. The unmanipulated control plots represented a litter treatment (no manipulation) that was not fully crossed with seeding density. In particular, our experiment did not include the following treatments: uncut-litter with low or high seeding density. A means model ANOVA allows for examination of such experimental designs by first testing the null hypothesis that cell means are equal to control the experiment-wise type I error rate and then allowing for custom orthogonal contrasts that are balanced across non-missing cells to test specific hypotheses about treatment effects (Searle 1987). Separate means model ANOVAs were conducted for the two response variables: *C. solstitialis* cover and native cover.

We tested specific hypotheses about treatment effects with planned orthogonal contrasts. To assess the effect of seeding with one vs. two species, we averaged cover values across nonzero seeding densities (500 and 2000) and compared these values between the one- and two-species treatments. We assessed the effect of litter treatment by comparing the mean responses among all three litter treatments at the zero seeding density. We examined the litter \times seed-mix interaction by examining only treatments in which seed was added and litter treatments were fully crossed. We assessed the role of native seeding density on
invasion and native cover by using polynomial contrasts, which allowed us to determine whether seeding density had linear or quadratic effects on cover. These contrasts also allowed us to examine whether these effects differed between the one- and two-species treatments and between the two litter treatments that were fully crossed with seeding density.

To better meet statistical assumptions, we arcsine square-root-transformed C. solstitialis and native species cover. We analysed all data using SYSTAT 12 and 13 (Systat Software Inc 2007).

**Results**

**SIMILARITY OF SITE CONDITIONS**

*Centaurea solstitialis* cover in litter-free, no-seed addition plots did not differ between one- and two-species treatments (*N* = 10, *F* = 0.557, *P* = 0.477). We therefore concluded that site effects were minimal and the effect of species richness (one- or two-species additions) primarily represents the real effect of seeding one vs. two species. This allowed us to analyse our data via a three-way means model ANOVA.

**PHENOLOGICAL AND ESTABLISHMENT DIFFERENCES AMONG FUNCTIONALLY SIMILAR SPECIES**

While *H. congesta*, *M. gracilis* and *C. solstitialis* can all be classified in the same functional group of late-season annual forbs, they differed slightly in phenology. By mid-June, *H. congesta* was mostly in basal rosette form, while *M. gracilis* and *C. solstitialis* had bolted and *M. gracilis* had started to flower. *Centaurea solstitialis* started to bloom by late June and reached peak biomass by late July. By late July, *H. congesta* had bolted and was starting to flower, while most *M. gracilis* had senesced. In treatments seeded with the two-species seed-mix, *M. gracilis* had a higher average establishment rate than *H. congesta* (Fig. 3). The average establishment rate for each native forb in litter removal treatments was 19.6% (±9.7%) and 10.3% (±5.1%) (*M. gracilis* and *H. congesta*, respectively). In litter retention treatments, rates were 4.8% (±3.1%) and 1.6% (±1.4%), respectively. High-density additions of the two-species seed-mix resulted in an average of 290.4 native forbs m−² (Fig. 3). High-density additions of the one-species seed-mix (*H. congesta* only) resulted in an average of 164.8 native forbs m−². When *H. congesta* was planted alone, an average of 9.5% (±4.7%) established and survived in litter removal treatments, while 3.8% (±2.7%) established and survived in litter retention treatments.

**CENTAUREA SOLSTITIALIS ABUNDANCE**

**Biotic filter**

*Centaurea solstitialis* cover (averaged across low- and high seeding densities and both litter treatments) was about five percentage points lower in the two-species mix (12.6%) compared to seeding *H. congesta* alone (17.5%; i.e. significant ‘seed-mix composition’ effect, Table 1).

**Abiotic filter**

In the absence of native seed addition, *C. solstitialis* cover in plots where litter was cut and retained was equal to that in the unmanipulated controls where litter was left standing (Table 1; Fig. 4a–c). In addition, in the absence of native seed addition, *C. solstitialis* cover was 17 percentage points greater where litter was removed (30.5%) than in plots where litter was retained (13.5%; i.e. the average of cut and retain treatments and unmanipulated controls where litter was left standing; significant ‘Litter treatment, Average of retain and control vs. remove’ effect, Table 1).

**Synergy among dispersal, abiotic and biotic filters**

For both the one- and two-species seed-mixes, the effect of seeding density on *C. solstitialis* reinvansion was mediated by the presence of cut-litter (i.e. significant ‘seed density × litter’ linear interaction, Table 1). When litter was removed, adding native seed resulted in steep linear declines in *C. solstitialis* cover (Fig. 4b,c). For each 1000 seeds added, *C. solstitialis* cover was reduced by 9.2 percentage points. In contrast, when cut-litter was retained, adding native seed only slightly reduced *C. solstitialis* cover (Fig. 4b,c); each 1000 seeds added reduced *C. solstitialis* cover by 0.9 percentage points.
Table 1. Means ANOVA table for Centaurea solstitialis cover

<table>
<thead>
<tr>
<th>Effect</th>
<th>d.f.</th>
<th>MS</th>
<th>F-ratio</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Means model</td>
<td>12</td>
<td>220.4</td>
<td>6.64</td>
<td>&lt;0.000001*</td>
</tr>
<tr>
<td>Seed-mix composition</td>
<td>1</td>
<td>186.1</td>
<td>5.61</td>
<td>0.021596*</td>
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<tr>
<td>(at nonzero seed density)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Seed density</td>
<td>2</td>
<td>299.1</td>
<td>9.01</td>
<td>0.000435*</td>
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<td>17.76</td>
<td>0.000100*</td>
</tr>
<tr>
<td>Seed density (quadratic)</td>
<td>(1)</td>
<td>9.1</td>
<td>0.27</td>
<td>0.603426</td>
</tr>
<tr>
<td>Litter treatment (at zero seed</td>
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<td>525.4</td>
<td>15.84</td>
<td>0.000004*</td>
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<tr>
<td>density only)</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Cut and retain vs. control</td>
<td>(1)</td>
<td>65.6</td>
<td>1.98</td>
<td>0.165560</td>
</tr>
<tr>
<td>Average of retain and control vs.</td>
<td>(1)</td>
<td>985.6</td>
<td>29.71</td>
<td>0.000001*</td>
</tr>
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<td>remove Seed-mix x seed density</td>
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<td>44.4</td>
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<td>Seed-mix x litter (at nonzero</td>
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<td>0.494515</td>
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<tr>
<td>seed densities)</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Seed density x litter</td>
<td>2</td>
<td>192.4</td>
<td>5.80</td>
<td>0.005323*</td>
</tr>
<tr>
<td>(linear)</td>
<td>(1)</td>
<td>384.4</td>
<td>11.59</td>
<td>0.001286*</td>
</tr>
<tr>
<td>Seed density x litter (quadratic)</td>
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<td>0.01</td>
<td>0.911748</td>
</tr>
<tr>
<td>Seed-mix x seed density x litter</td>
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<td>47.7</td>
<td>1.44</td>
<td>0.246857</td>
</tr>
<tr>
<td>Error</td>
<td>52</td>
<td>33.2</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Significant effects at $P \leq 0.05$ are marked with an asterisk.

NATIVE FORB ESTABLISHMENT

Planted native forbs comprised the majority of native cover (95–100%) at the end of the growing season. Madia gracilis occurred at low levels throughout the site and was present in seven no-seed addition plots and three control plots (cover was ≤3% except in one plot where cover was 5%). Elymus glaucus Buckley, a native bunchgrass, comprised ≤5% cover in seven plots.

Biotic filter

Seeding with two native species resulted in larger native populations when compared with single-species treatments regardless of seeding densities and litter treatment (i.e. significant ‘seed-mix composition’ effect, Table 2).

Abiotic filter

In the absence of seeding, cutting and retaining or removing litter had no effect on native cover likely because natives were largely absent in these plots.

Synergy among dispersal, abiotic and biotic filters

For both seed-mixes, native cover had a positive curvilinear relationship with seeding rate (i.e. significant ‘seed density’ linear and quadratic effects, Table 2). The slope of this increase, however, depended on seed-mix; native cover increased more sharply in two-species seedings at high densities than in one-species seedings at high densities (i.e. significant ‘seed-mix x seed density’ linear effect, Table 2; Fig. 4e,f). The relationship was

Table 2. Means ANOVA table for native species cover. Hemizonia congesta and Madia gracilis comprised the majority of cover. The native bunchgrass Elymus glaucus contributed ≤5% cover in seven plots across seeding treatments

<table>
<thead>
<tr>
<th>Effect</th>
<th>d.f.</th>
<th>MS</th>
<th>F-ratio</th>
<th>P-value</th>
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<td>16.25</td>
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<td>Seed-mix composition</td>
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<tr>
<td>(at nonzero seed density)</td>
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<tr>
<td>Seed density</td>
<td>2</td>
<td>1600.9</td>
<td>55.54</td>
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<td>density only)</td>
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<tr>
<td>Seed-mix x seed density</td>
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<td>364.0</td>
<td>12.63</td>
<td>0.000034*</td>
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<tr>
<td>(linear)</td>
<td>(1)</td>
<td>673.6</td>
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<td>184.8</td>
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<td>seed densities)</td>
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<td>Seed density x litter</td>
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<td>155.9</td>
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<td>Seed-mix x seed density x litter</td>
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<td>2.94</td>
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<tr>
<td>Error</td>
<td>52</td>
<td>28.8</td>
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</tbody>
</table>

Significant effects at $P \leq 0.05$ are marked with an asterisk.

curvilinear rather than strictly linear because native cover began to saturate at high seeding densities. The relationship between native cover and seeding rate also depended on litter treatment: native cover increased more at higher seeding densities when litter was cut and removed compared to when cut and retained (i.e. significant ‘seed density × litter’ linear effect, Table 2; Fig. 4e,f). Because of these relationships, native populations were largest in treatments that included high-rate additions of the two-species mix into plots where litter had been removed.

Discussion

By identifying the biotic, abiotic and dispersal filters that contribute to community assembly, filter-based assembly models highlight management actions that can contribute to ecosystem restoration. One factor potentially limiting the useful application of these models is a focus on the biotic filter’s contribution to ecosystem restoration without also considering how the dispersal and abiotic filters may synergistically contribute to restoration outcomes. In our study, we aimed to maximize native species cover and minimize reinvasion by a target invader. We show that while solely manipulating the biotic filter via seed additions and seed-mix selection can impact both native plant establishment and exotic species control, optimal outcomes required actions that targeted all three filters. For example, the largest gains in native populations and reduction in reinvasion occurred when native seeds were added via the two-species mix, at high seeding rates, to plots where litter was removed. Such findings suggest that management targeting all filters, and not solely the biotic filter, can alter the strength of biotic resistance in restored communities and improve restoration outcomes.

Did Manipulating the Biotic Assembly Filter Affect Restoration?

In grasslands, there is growing evidence that plant communities including resident species with resource-use traits similar to a target invader can resist invasion more successfully than communities lacking a functional analogue (Dukes 2002; Fargione, Brown & Tilman 2003; Tilman 2004; Zavaleta & Hulvey 2007; Young et al. 2009). Our study adds support to this idea by providing an example where planting native species with phenological and morphological traits similar to invading exotics simultaneously reduced invasion and increased native populations. In litter-free plots, high-density additions of either of the native seed-mixes significantly reduced invasion and increased native populations compared to treatments with no-seed addition.

The greater success of the two-species seed-mix compared with the one-species mix, suggests, however, that additional manipulations of the biotic filter beyond simple functional group matching may increase its effectiveness in grassland restoration. In particular, the choice of species, even between those that belong to the same functional group, appears to influence restoration outcomes. Two well-defined mechanisms stemming from studies of biodiversity–ecosystem functioning offer plausible explanations for the pattern of greater invasion resistance in the two-species treatments. First, multiple studies at small spatial-scales have found that increased species diversity can lead to increased invasion resistance through resource-use complementarity (Naeem et al. 2000; Dukes 2001). In our study, although the two added native forbs belonged to the same functional group, their life cycles and phenologies differed slightly. Madia gracilis bolted, flowered and senesced earlier than H. congesta. Therefore, the two-species treatment may have resulted in greater competition with the target invader through greater resource-use complementarity stemming from slight differences in phenology.

It is also possible that seed diversity favoured invasion resistance by increasing the chance of including a single species that strongly competed with the invader for resources (Aarssen 1997; Huston 1997). In the two-species mix, one of the natives (M. gracilis) bolted and flowered in closer temporal proximity with the invader than the second seeded native (H. congesta) possibly leading to a more temporally similar use of resources and more competition (Cleland, Larios & Suding 2013). Madia gracilis also had higher establishment rates than H. congesta, and adding it to the seed-mix may have increased competition by increasing the abundance of functionally similar plants in plots (Hulvey & Zavaleta 2012). Including an M. gracilis-only treatment might have clarified whether invasion resistance was driven by this single species, or alternatively by the combination of the two native species. Regardless, our results suggest that although functional group matching can increase biotic resistance in restored communities, the differences among individual species even within the same functional group can also influence restoration outcomes.

While our results suggest that the different seed-mixes affected invasion resistance, because one- and two-species plots were not intermixed it is also possible that differences in C. solstitialis cover were due to site heterogeneity not accounted for in our experimental design. For example, factors correlated with plot locations could have resulted in C. solstitialis cover that was either greater in one-species plots or reduced in the two-species plots. Our finding that C. solstitialis invasion was equal across one- and two-species plots in the litter-free, no-seed addition treatments, however, suggests that this is not the case. It appears, rather, that growth conditions were similar for the invader across both treatment areas and that differences in C. solstitialis cover were due to seed additions. Additional studies that fully randomize seed-mix treatments would be a useful next step to this work.
Management actions that solely focused on the biotic filter via the direct manipulation of restoration species did not optimize restoration goals. Litter removal and native seeding density also affected restoration outcomes by altering how effectively native seed additions reduced invasion and increased native populations.

Litter removal was designed to alter light levels in restoration plots, and past studies have found that high light conditions increase *C. solstitialis* populations (DiTomaso, Kyser & Pitcairn 2006; Young et al. 2011). Of interest for restoration planning, litter removal directly altered interactions between planted natives and the invading exotic. When litter was retained, native species additions had little impact on exotic invasion, regardless of seeding density. Litter removal, however, favoured both seeded natives (increased cover and abundance) and the invader (increased cover), but also led to strong interactions between the species when grown together. This suggests that in high resource conditions (high light levels), greater species performance led to more competition, while in resource-poor plots (low light levels), lower performance reduced or eliminated the effects of functionally similar natives on exotic invasion, possibly by decreasing the strength of their neighbourhood-scale interactions. Our findings are consistent with multiple studies showing abiotic gradients can alter competition intensity (Pugnaire & Luque 2001; Callaway et al. 2002). While we aimed for the litter treatment to affect light conditions, litter may also affect other site characteristics such as soil moisture. Because of this, research exploring the mechanisms by which litter affects establishment could help inform restoration strategies that target site abiotic conditions.

The manipulation of abiotic site conditions highlights a unique challenge of using native species with functional traits similar to target invaders to mitigate exotic species reinvasion in restoration projects. While it is possible that natives and exotics might respond differently to site manipulations (Hayes & Holl 2003), we found the invader and natives responded similarly to litter removal. As such, restoration species that are chosen to have functional traits similar to invaders may be more likely to respond similarly to such actions than restoration species without trait overlap. Despite this challenge, in our study, the favourable growth conditions created for the invader by removing litter were mitigated by increased competition with the seeded native forbs.

The strong influence of litter on invasion additionally suggests that an alternative to increasing biotic resistance by seeding competitive natives is to create poor growing conditions for invaders. We found that litter could directly limit invasion to a degree that equalled that found in native seed addition treatments. This option may have some advantages – particularly reduced seed costs and planting activities. There are also disadvantages, however, such as the lack of direct enhancement of the native community or lack of future biotic resistance stemming from competitive species establishment. As such, future studies that examine not just how the presence of litter affects native and exotic establishment but also how litter depth might differentially alter establishment might inform how to best alter abiotic site conditions.

Finally, the biotic filter's influence on restoration outcomes was dependent on dispersal filter manipulations via native seeding rates. In a restoration setting, seeding competitive natives at rates high enough to reduce invasion may be vital to project success. In litter-free treatments, adding larger amounts of native seed resulted in higher invasion resistance compared to treatments with low-or no-seed addition (39-3% declines in one-species treatments and 69-2-75-7% declines in two-species treatments). One explanation for the increased influence of natives at high seeding rates is that these high rates translated into larger populations of established native forbs, and thus increased competition. While we did not measure the mechanisms leading to reduced invasion, past work in microcosms found that large populations of *H. congesta* reduced *C. solstitialis* invasion by competing more strongly than small populations for limited soil moisture (Hulvey & Zavaleta 2012).

**CONCLUSIONS**

Restoration projects often strive to balance multiple restoration goals including reducing weeds, increasing native plant cover and increasingly, restoring desirable ecosystem processes such as invasion resistance (Menninger & Palmer 2006; Hobbs & Cramer 2008). A growing number of studies show that directly altering biotic interactions at restoration sites via manipulation of the biotic filter can both increase native populations and reduce invasion. Our study builds on such results and indicates that employing filter models that target the dispersal and abiotic filters for management action in addition to the biotic filter can result in optimal gains in multiple restoration outcomes. In particular, the biotic filter only contributed to successful restoration outcomes under abiotic and dispersal conditions that were created through management actions specifically targeting these two additional filters. Ultimately, incorporating ideas from assembly theory, such as the existence of multiple assembly filters, into restoration planning can help managers simultaneously reach multiple management goals.

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Data accessibility

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

Appendix S1. List of species occurring at the Skyline Ridge Open Space Preserve restoration site.