

Enhancing plant diversity in a novel grassland using seed addition

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Abstract

1. Restoration of novel ecosystems to a historical benchmark may not always be possible or advisable. Novel ecosystems may be managed by targeting specific components and accepting the novelty of other ecosystem attributes. The feasibility of this component-wise management of novel ecosystems has rarely been tested.
2. In a novel grassland, where C₃ grasses have replaced C₄ grasses, nutrients have been elevated, and diversity has been lost due to a history of agricultural land use, we aimed to return diversity using seed addition, without altering the dominant grass matrix or nutrient status. Using direct seeding, with and without soil disturbance, we assessed the ability of 10 species of native forbs to establish.
3. Eight of the 10 seeded species established in the first year. Soil disturbance increased establishment success by 50%, while high levels of exotic cover decreased it by 24%. Establishment was inversely related to total plant cover at sowing, with a 10% increase in initial plant cover decreasing establishment by 47%.
4. By the third year, six of the eight species persisted and five were flowering. Survival and reproduction in the third year was not associated with the soil disturbance treatment or plant cover.
5. *Synthesis and applications.* We show that native plant species can be re-established in grasslands where abiotic and biotic conditions are novel relative to their reference state. This suggests that the conservation value of novel ecosystems can be enhanced using simple restoration tools that target specific ecosystem components.

KEYWORDS

eutrophication, fire, grassland, introduced species, native species, novel ecosystem, plant diversity, restoration, seed addition, soil disturbance

1 | INTRODUCTION

Ecosystems globally have been transformed by human activity, leading to novel assemblages with previously unassociated biotic and abiotic features (Hobbs, Higgs, & Harris, 2009; Williams & Jackson, 2007). These novel ecosystems may be irreversibly changed (Hobbs et al., 2009), or in alternative states of varying stability (Hallett et al., 2013; Suding, Gross, & Houseman, 2004). Restoring such altered systems to their prior state may be difficult or impossible (Hobbs et al., 2009,

2014). In the absence of an achievable past reference state for restoration, managers of these novel ecosystems must re-imagine the ecosystem and formulate new goal states (Hobbs et al., 2009, 2014).

Frameworks for guiding novel ecosystem management decisions have been proposed (Hobbs et al., 2014; Hulvey et al., 2013) and applied (Trueman, Standish, & Hobbs, 2014). These frameworks identify three core management goals of novel ecosystems: protecting biodiversity, recovering ecosystem function or services, or managing for novel species composition, function or services (Hulvey et al., 2013).

These new goals imply management actions that target specific components, while accepting the novelty of other ecosystem attributes. However, the feasibility of component-wise management of novel ecosystems has rarely been explored or empirically tested.

Grasslands are particularly relevant to novel ecosystem management. Extensive agricultural practices have modified native grasslands across all continents (Dorrough & Scroggie, 2008; Ellis, Goldewijk, Siebert, Lightman, & Ramankutty, 2010; Prober, Lunt, & Thiele, 2002), but most retain their essential character as grass-dominated ecosystems (Ellis et al., 2010). Grazing, fertilizer application, species introductions and cropping of grasslands cause substantial changes in soil chemistry (Falkengren-Grerup, ten Brink, & Brunet, 2006), plant diversity (Borer et al., 2014; Dorrough & Scroggie, 2008) and exotic plant abundance (Seabloom et al., 2015).

Testing management actions aimed at increasing native forb diversity in temperate Australian grasslands provides an ideal case study for testing novel ecosystem management, with a focus on a specific system component. Extensive conversion for agriculture and human settlement has substantially reduced the extent of grasslands across south-eastern Australia with remaining grasslands in various stages of modification (Department of Sustainability, Environment, Water, Population and Communities, 2011; Department of the Environment and Heritage, 2006). Native forb richness and cover were high in the pre-agricultural environment (Patton, 1935), but are low in modified grasslands that also have elevated soil fertility and high exotic species cover (Dorrough & Scroggie, 2008; Prober, Thiele, Lunt, & Koen, 2005; Smallbone, Prober, & Lunt, 2007). Forb richness and cover are perceived as valuable components of the grassland ecosystem, (Lindemann-Matthies, Junge, & Matthies, 2010; Sinclair, Griffioen, Duncan, Millett-Riley, & White, 2015) and are thus good candidates for management investment.

Native forb decline in temperate Australian grasslands is associated with multiple concurrent factors, which may present barriers to their return. First, competition from grasses causes competitive exclusion in the absence of appropriate regular disturbance that limits grass cover (Morgan, 1998b; Stuwe & Parsons, 1977). Second, species palatable to grazing have likely been eliminated and many do not possess sufficient soil seed banks from which to recover (Dorrough, McIntyre, & Scroggie, 2011; Dorrough & Scroggie, 2008; Vesk & Westoby, 2001). Third, the combination of elevated soil nutrient levels from fertilization and exotic species result in competitive exclusion of many native species that are adapted to lower nutrient soils (Bakker & Berendse, 1999; Prober et al., 2005; Seabloom et al., 2015). Soil nutrients, particularly phosphorus, may remain in grassland soils for decades and are difficult to remove by management (Coad, Burkitt, Dougherty, & Sparrow, 2014; Falkengren-Grerup et al., 2006). Finally, these grazed Australian temperate grasslands generally move from dominance by C_4 (usually *Themeda triandra* Forssk.) to C_3 grasses (McIntyre & Lavorel, 2007; Moore, 1970), shifting grass resource use to the cooler months when virtually all forbs are also actively growing (Ehleringer & Monson, 1993). This may cause forb exclusion, although experimental results have been equivocal (Chesson, 2000; Prober, Thiele, & Lunt, 2002; Symstad, 2000). Altogether, increased soil fertility, exotic abundance

and a shift from C_4 to C_3 dominance create novel abiotic and biotic conditions for native forb re-establishment. Re-establishment of the dominant C_4 grass is possible (Cole, Lunt, & Koen, 2004) but expensive.

We investigate whether the removal of some of the most immediately tractable barriers (seed limitation, grazing pressure and lack of disturbance), allows native forbs to re-establish in novel grassland, without removing the more intractable barriers (nutrient enrichment, exotic species invasion, shifted species dominance). In other words, we test whether we can manage for a single component (forb richness), in a novel system, because restoring the whole system may be prohibitively expensive at large scales.

We removed seed limitation by sowing seed at a site that has been grazed, nutrified, invaded by exotics, shifted from C_4 to C_3 native grass dominance and that is also devoid of most native forb species. The site is no longer grazed and is now burnt with a 2–3-year fire interval as part of its management regime. We tracked population dynamics over a period of 3 years and assessed community composition after 3 years, examining the population and community-level response since some specific species are the focus of conservation attention and the entire ecological community is federally listed. With a view to guiding management we asked the following questions:

1. Can native forb species establish and survive in a novel grassland with high fertility, abundant exotics and C_3 grass dominance (native and exotic), when seeded at a time of low vegetation cover?
2. To what degree does soil disturbance enhance establishment of added native forb seeds?

2 | MATERIALS AND METHODS

2.1 | Study site

The study was conducted in a grassland in Victoria, Australia (37.83° S, 144.52° E), about 40 km south-west of Melbourne. The grassland is a degraded example of Natural Temperate Grassland of the Victorian Volcanic Plains, an ecological community listed as Critically Endangered under the Australian Government's *Environment Protection and Biodiversity Conservation Act 1999* (Threatened Species Scientific Committee, 2008).

The study site was grazed by stock (sheep from European settlement (~1835) until 2003, then cattle) at low densities until the site came under conservation management in 2012. The site was aerially fertilized with single superphosphate at a rate of 100 kg/ha, applied every 2–3 years for at least a decade prior to 2012. Prior to European settlement, the grassland was likely dominated by the native C_4 grass *T. triandra*, with a high native forb diversity (Sinclair & Atchinson, 2012; Stuwe & Parsons, 1977).

The experimental site has essentially lost its C_4 grass component and is dominated by C_3 grasses, including native perennial tussock grasses (*Austrostipa bigeniculata* (Hughes) S.W.L. Jacobs & J. Everett, *Rytidosperma* spp., and *Poa usieberiana* Spreng.) along with exotic annual grasses (*Lolium rigidum* Gaudich and *Vulpia bromoides* (L.) Gray

(DELWP, 2015). Native forbs, especially those sensitive to grazing, are sparse and richness is low with soil nutrients elevated (detailed comparison in Appendix S1).

2.2 | Species selection

We selected 10 native forb species from the ecological community that are no longer present at the site, but which all occur in similar remnant grasslands within a 25-km radius. The species are from a range of families, with a diversity of life-history traits (Table 1). All seed was initially sourced from the wild in the same grassland community within 50 km of the study site; it was then grown for one generation in open nursery conditions to provide sufficient seed to conduct the experiment.

2.3 | Experimental design

A wildfire occurred at the site on 24 January 2013. Experimental plots were established within the burnt patch in April 2013; 60 plots were established using a randomized block design, with the 1.44-m² plots each 1 m apart (Fig. S1 in Appendix S1). Experimental plots consisted of the following treatments: seeding alone ($n = 20$), soil disturbance and seeding ($n = 20$), and control ($n = 20$). To enable evaluation of maximum establishment potential, the plots were fenced to exclude rabbits and discourage kangaroos.

Seed of the 10 native forb species was applied to the seed addition plots on 25–26 April 2013. Application rates were predominantly determined by seed availability informed by a target of

100 germinable seeds per species per m² with germinability based on the literature (Gibson-Roy, Delpratt, & Moore, 2007a; Morgan, 1998b), although the seed used in this experiment had not been cleaned, making comparisons difficult. The goal was to ensure that seed was not limiting balanced against competition from the other planted species. Subsequent seed weight assessments and germination tests indicated that the amount of germinable seed sown varied between species (Table 1). Seeds for all 10 species were sown together in each plot, using a forb sowing density comparable to sowing rates in grassland reconstructions in the region which sow between 0.5 and 1.0 g/m² of mixed forb seed (Greening Australia, personal communication).

Immediately prior to sowing, seeds were mixed with a fixed volume (750 ml) of damp coarse sand to facilitate even spread of the seed and reduce wind dispersal during application. The seed-sand mixture was applied evenly by hand to each 1.44-m² seeded-only, and soil disturbance and seeded plot within a temporary windbreak 1.2 × 1.2 × 0.3 m high. For the soil disturbance treatment, plots were raked prior to seed addition with sufficient force to break up the dry soil surface but not to remove the re-growing grass tussocks. Sand alone was applied to the control plots. All plots were watered with 7 L of water shortly after seed addition, similar to previous successful forb restoration treatments (Gibson-Roy, Delpratt, & Moore, 2007b).

The experimental plots were not exposed to any management interventions between April 2013 and March 2015. In April 2015 (autumn), a prescribed burn was conducted as part of the management regime for the grassland. This occurred before the growing season between the second and third year of monitoring.

TABLE 1 Seed characteristics of the native forb species re-introduced into novel temperate grassland in south-eastern Australia. Seed mass and germination fraction (mean of 6 replicates of 10–50 seeds (depending on species) at 20°C, 12 hr light per day for 35 days) were measured approximately 12 months after sowing. Life-forms relevant to disturbance responses are based on the observations of the authors, and follow Raunkiær (1934): G = Geophyte, species which retreat below-ground, H = Hemicyptophyte, species which retain buds at soil level, T = Therophyte, annual species. All species except *Wahlenbergia victoriensis* are capable of re-sprouting after fire

Species	Family	Life span	Life-form	Mass (mg) per individual seed (SE)	Mass of seed sown (g/m ²)	Mean number seeds sown per m ²	Germination fraction (SE)
<i>Arthropodium minus</i> R. Br.	Asparagaceae	Perennial	G	1.06 (0.04)	0.144	137	0.23 (0.07)
<i>Brachyscome dentata</i> Gaudich.	Asteraceae	Perennial	H	0.40 (0.03)	0.087	218	0.48 (0.05)
<i>Chysocephalum</i> sp. 1 sensu Fl. Victoria	Asteraceae	Perennial	H	0.11 (0.03)	0.042	372	0.21 (0.06)
<i>Craspedia variabilis</i> J. Everett & Doust	Asteraceae	Perennial	H	0.76 (0.06)	0.208	274	0.46 (0.02)
<i>Leptorhyncos squamatus</i> (Labill.) Less.	Asteraceae	Perennial	H	0.14 (0.01)	0.042	304	0.11 (0.03)
<i>Podolepis linearifolia</i> Jeanes	Asteraceae	Perennial	H	0.79 (0.03)	0.181	228	0.04 (0.01)
<i>Senecio macrocarpus</i> Belcher	Asteraceae	Perennial	H	0.28 (0.008)	0.521	1,839	0.19 (0.04)
<i>Solenogyne gunnii</i> (Hook.f.) Cabrera	Asteraceae	Perennial	H	0.37 (0.007)	0.052	140	1.0 (na)
<i>Velleia paradoxa</i> R.Br.	Goodeniaceae	Perennial	H	10.75 (1.4)	0.785	73	0.81 (0.06)
<i>W. victoriensis</i> P.J.Sm.	Campanulaceae	Annual	T	0.01 (0.0002)	0.007	724	0.80 (0.06)

2.4 | Data collection

The experiment was monitored for 3 years to determine seedling establishment, survival and reproduction in association with the soil disturbance treatment and plant cover.

2.4.1 | Demographic monitoring

The number of individuals per species in central 1 m² of each plot was recorded at monthly intervals throughout the first spring after the seeds were sown (August–December 2013) and once in each of the second and third springs (October 2014; October 2015).

We used “establishment” to describe plants that grew in the first year, since many of these were flowering, and measured establishment as the maximum number of individuals for each species in each plot across the spring 2013 monitoring period (August–December). *Chrysocephalum* sp. 1 established, but was not monitored in the first year because germinants could not be reliably distinguished from another species germinating in the plots, *Helichrysum luteoalbum* L. Rchb. (Asteraceae).

Reproductive effort was measured in the first year as the maximum proportion of individuals flowering over the August–December monitoring periods. In the second and third years, reproductive effort was measured as the proportion flowering at the October monitoring period.

2.4.2 | Total plant cover

The extent of live plant cover was determined by applying colour-thresholding analysis of quadrat digital images (Kendal et al., 2013). Plant cover was calculated as the proportion of pixels classified as containing green vegetation (See Appendix S1 for details).

We recorded two different measures of community structure.

2.4.3 | Community dominance

In the first year, we recorded the identity of the three most dominant species in each plot, based on visual cover estimates (6 December 2013). Dominant species were then categorized as native or exotic to create a dominant species origin co-variate for analysis (there was insufficient sample size for analysis at the species level).

2.4.4 | Community composition

In spring of the third year (19 October 2015), we recorded visual cover estimates of species-level plant cover (including sown species), as well as bare ground, litter and rock estimated to the nearest 1%, by agreement among two experienced assessors (Daubenmire, 1959). This species-level data enabled analysis of treatment and composition effects on seeded forb cover, to supplement the previous analyses on counts.

2.5 | Data analysis

Establishment, survival and reproduction were analysed for each year separately, using treatment (soil disturbance), total plant cover

(derived from colour thresholding) and dominance (native or exotic) as predictors. Broad patterns across all of the species were assessed using generalized linear mixed models (GLMM) with plot and species as random factors (Table S1 in Appendix S1). Individual species responses were analysed using generalized linear models (GLM). Species-level analyses of survival and reproductive effort could only be performed on a subset of four and three species, as listed below. All analyses were run in R version 3.1.2 (R Core Team, 2015) and used the following packages for data synthesis (doBy, lattice, plotrix, plyr) and analysis (lme4, MASS, hglm). Model distributions and link functions were chosen based on model diagnostics with data evaluated to ensure they met statistical assumptions. Goodness-of-fit was measured as the R^2 of a linear regression of the observed vs. fitted values for GLMs and GLMMs (Piñeiro, Perelman, Guerschman, & Paruelo, 2008). We approximated the contribution of the fixed variables in the GLMM by calculating the R^2 of a linear regression of the observed vs. fitted values for the corresponding GLM model (i.e. excluding random effects).

2.5.1 | Establishment

Establishment was analysed using a negative binomial distribution with a log link (Table S1 in Appendix S1). There was one outlier for *Senecio macrocarpus* with over 100 individuals consistently recorded in one treatment plot throughout the first spring, and peaking at 310 individuals. This outlier had high leverage in the analysis of establishment, and therefore this analysis was repeated with the outlier removed with both versions presented. Total plant cover at the time of seeding (April 2013) was used as a co-variate for all establishment models.

2.5.2 | Survival

Survival to the second and third years was analysed as the proportion of individuals that had survived from the previous year (except for *Wahlenbergia victorensis*, an annual). Proportion survival was analysed using a beta-binomial distribution (logit link) and a quasibinomial distribution (logit link) for the GLMMs and GLMs respectively (Table S1 in Appendix S1). Abundance in the third year was analysed as the count of individuals in October 2015 using a quasipoisson distribution with a square root link. Abundance in the third year was only analysed at the species level, as a mixed model with all species included could not be fit. In the third year, only 1 of the 40 plots was dominated by exotics and so exotic dominance was not used as a co-variate. All survival and reproductive effort models (see below) used total plant cover derived from images taken in October of the corresponding year (Table S1 in Appendix S1).

2.5.3 | Reproductive effort

Reproductive effort was analysed as the proportion of individuals that were flowering in each year. In the first year, this was the maximum proportion flowering over the August–December monitoring periods.

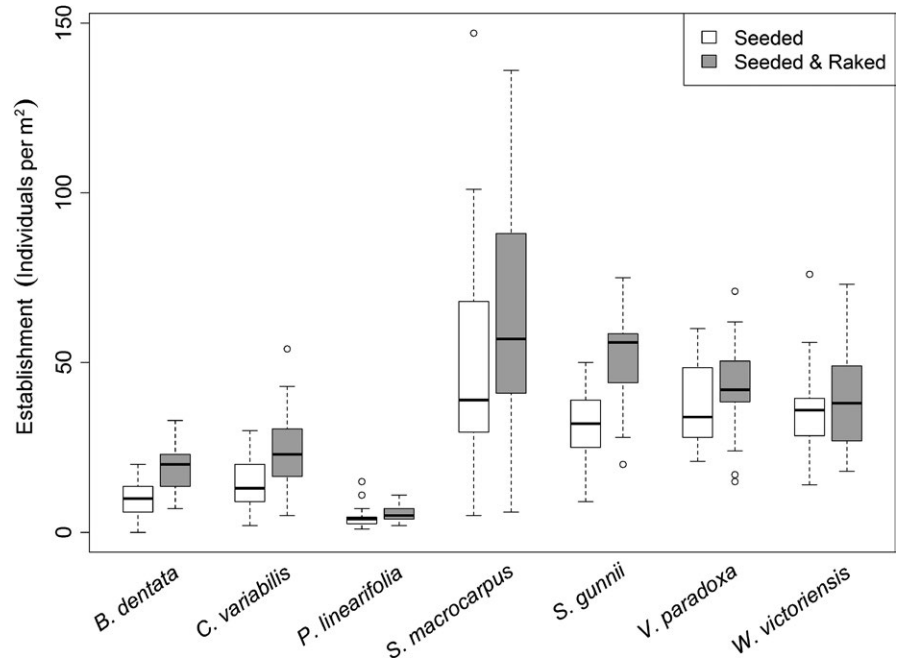


FIGURE 1 Effect of soil disturbance treatment (raking) on seedling establishment at the end of the first year of the experiment (bold line shows median, box edges show first and third quartile, whiskers show minimum and maximum value and outliers exceed $\pm 3 \times$ IQR.) The *Senecio macrocarpus* outlier (individuals per $m^2 = 320$) is not shown

In the second and third years, reproduction was measured as the proportion flowering at the October monitoring period. Reproductive effort was analysed using a beta-binomial distribution (logit link) and a quasibinomial distribution (logit link) for the GLMMs and GLMs respectively (Table S1 in Appendix S1).

2.5.4 | Plant community analysis

The effect of plant community composition on seeded forb cover after 3 years was analysed with a GLM using a quasibinomial distribution (logit link; Table S1 in Appendix S1). Plant community cover was aggregated into cover class categories: native grass, exotic grass, seeded native forb, non-seeded native forb and exotic forb.

3 | RESULTS

3.1 | Establishment and survival

Eight of the species sown established in the first year: *Brachyscome dentata*, *Craspedia variabilis*, *Chyrsocephalum* sp. 1, *Podolepis linearifolia*, *Senecio macrocarpus*, *Solenogyne gunnii*, *Velleia paradoxa* and *Wahlenbergia victoriensis* (Figure 1). *Arthropodium minus* and *Leptorhynchus squamatus* did not establish. Establishment rates were 1%–7% of total seeds sown for *B. dentata*, *C. variabilis*, *P. linearifolia*, *S. macrocarpus* and *W. victoriensis*, and higher at 22%–60% of seeds sown for *S. gunnii* and *V. paradoxa*, (Table S2 in Appendix S1).

Six of the eight species were observed in the second and third year (Table 2). By the third year, abundance had declined markedly for all six species, with low survival from the first to second year, but higher survival to the third year (Table 2). Two species that established did not persist. *Wahlenbergia victoriensis*, the only obligate annual among the seeded species, and *C. variabilis* were not observed after the first year (Table 2).

3.2 | Factors influencing establishment and survival

Soil disturbance increased establishment in the first year by 50% overall (Figures 1 and 2a; Table S3 in Appendix S1; all statistical test results presented in referenced tables), with significant increases in *B. dentata*, *C. variabilis* and *S. gunnii*, and positive but not significant effects on the remaining species (Figure 2b). Total live plant cover ranged from 2% to 13% at the time of seeding, and strongly influenced establishment (Figure 2a; Table S3 in Appendix S1). Overall, an increase in initial plant cover of 10% reduced establishment by 47%, and while the effects were negative for all species, cover significantly reduced establishment in only *S. gunnii* and the annual *W. victoriensis* (Figure 2c; Table S4 in Appendix S1). Similarly, dominance by exotic species substantially reduced establishment by 24% (Figure 2a; Table S3 in Appendix S1), significantly negatively affecting *B. dentata*, *S. gunnii*, *V. paradoxa* and *W. victoriensis* (Figure 2d; Table S4 in Appendix S1). Goodness-of-fit measures indicated that the multi-species model fit reasonably well with predicted values explaining approximately 50% of the observed variation (Table S3 in Appendix S1). This was predominantly due to the model accounting for differences between species with predictions using only the fixed effects explaining 7% of the observed variation (Table S3 in Appendix S1) consistent with the low goodness-of-fit values of the single species models (Table S4 in Appendix S1).

Survival to the second year was weakly positively associated with total plant cover in the second spring, with a 10% increase in plant cover increasing the odds of survival by 34% (Table S3 in Appendix S1). Although the soil disturbance treatment did not affect survival to the second year across all species (Table S3 in Appendix S1), there were legacy effects of soil disturbance for some species, enhancing the odds of survival by about two-fold in *B. dentata*, *S. gunnii* and *V. paradoxa* (Table S4 in Appendix S1). Survival from the second to third year was

TABLE 2 Mean (standard error) establishment (Year 1) and abundance (Years 2 and 3) of the 10 experimentally seeded species. Undist. = seeded treatment, Disturbed = soil disturbance and seeded treatment, $n = 20$ per treatment

Species	Establishment Y1 (individuals per m ²)		Abundance Y2 (individuals per m ²)		Abundance Y3 (individuals per m ²)	
	Undist.	Disturbed	Undist.	Disturbed	Undist.	Disturbed
<i>Arthropodium minus</i>	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
<i>Brachyscome dentata</i>	10 (1)	19 (2)	1 (0.3)	4 (1.0)	2 (0.5)	6 (1)
<i>Chrysocephalum</i> sp. 1	NA	NA	2 (0.3)	2 (0.4)	1 (0.2)	1 (0.2)
<i>Craspedia variabilis</i>	14 (8)	25 (12)	0 (0)	0 (0)	0 (0)	0 (0)
<i>Leptorhynchos squamatus</i>	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
<i>Podolepis linearifolia</i>	5 (1)	5 (1)	0.3 (0.1)	0.3 (0.1)	0.1 (0.1)	0.1 (0.1)
<i>Senecio macrocarpus</i>	49 (7)	78 (14)	19 (4)	29 (5)	7 (2)	12 (3)
<i>Solenogyne gunnii</i>	31 (2)	51 (4)	1 (0.4)	3 (0.8)	1 (0.3)	1 (0.3)
<i>Velleia paradoxa</i>	38 (3)	43 (3)	1 (0.3)	2 (0.4)	0.3 (0.1)	0.3 (0.1)
<i>Wahlenbergia victoriensis</i>	37 (14)	39 (16)	0 (0)	0 (0)	0 (0)	0 (0)

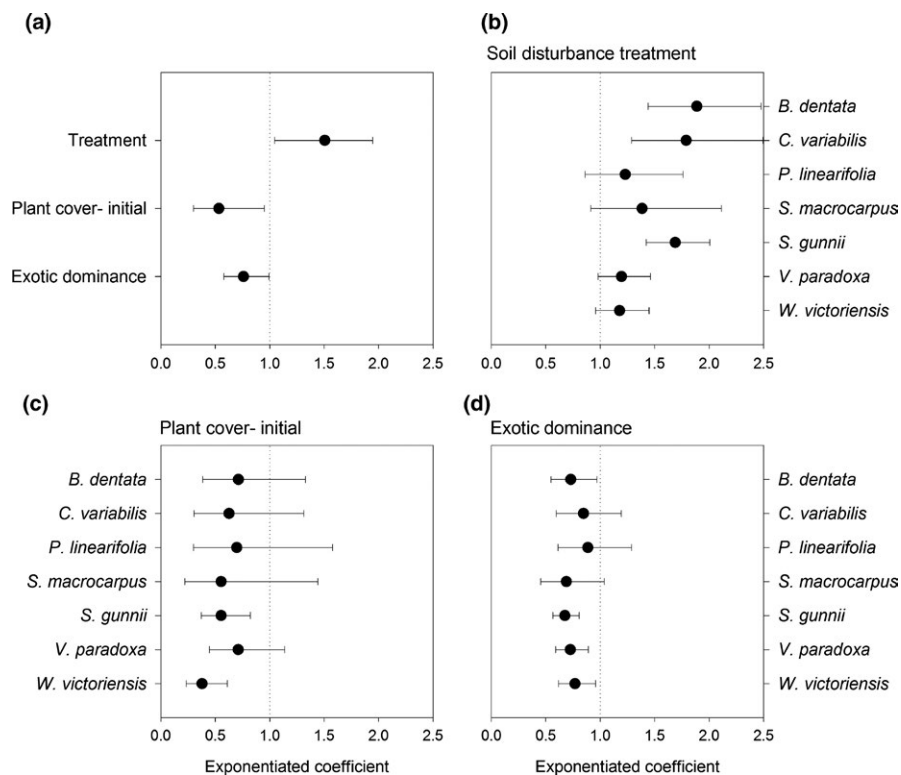


FIGURE 2 Effect of soil disturbance treatment, initial plant cover and exotic dominance on establishment success from model with all species included (a), and from individual species models (b–d). Exponentiated model coefficients and 95% confidence intervals are shown, such that a coefficient of 1.0 indicates no effect, coefficients <1.0 indicate that predictor decreased establishment, and coefficients >1.0 indicates that predictor increased establishment (i.e. coefficient of 1.2 = 20% increase; coefficient of 0.8 = 20% decrease). Effects are statistically significant ($\alpha = 0.05$) when the 95% confidence interval does not cross 1.0. All corresponding p -values are listed in Tables S3 and S4 in Appendix S1. Plant cover coefficients correspond to the effect with an increase in plant cover of 10%. *Senecio macrocarpus* results in b–d are for the model with outlier removed; results of models with and without the outlier are in Table S4 in Appendix S1

not significantly affected by either soil disturbance or spring plant cover (Table S3 in Appendix S1). However, the effect of soil disturbance on abundance persisted to the third year for *B. dentata*; with abundance 2.5-fold higher in the disturbed than undisturbed plots (Table S4 in Appendix S1).

3.3 | Reproductive effort

Five of the eight established species flowered within the first year: *B. dentata*, *S. macrocarpus*, *S. gunnii*, *V. paradoxa* and *W. victoriensis* (Table S5 in Appendix S1). The proportion of plants that were

flowering in the first year was high for *W. victoriensis* (69%; Table S5 in Appendix S1), as expected for an obligate annual. In contrast, 1%–14% of plants flowered in the longer lived *B. dentata*, *S. macrocarpus* and *S. gunnii*, and <1% in *V. paradoxa* (Table S5 in Appendix S1). Overall, flowering in the first year was unaffected by soil disturbance, spring plant cover or exotic dominance (Table S3 in Appendix S1), with weak evidence that *S. gunnii* flowering was negatively associated with plant cover (Table S4 in Appendix S1). In the second year, only *Chrysocephalum* sp. 1, *P. linearifolia* and *S. macrocarpus* flowered (Table S5 in Appendix S1).

Five of the six species present flowered in the third year. Reproductive effort increased from the previous year, with 22% of *B. dentata* and *V. paradoxa*, and 60%–70% of *Chrysocephalum* sp. 1, *P. linearifolia* and *S. macrocarpus* individuals flowering. Reproductive effort in the third year was unaffected by treatment or spring plant cover overall (Table S3 in Appendix S1), with weak evidence that *B. dentata* reproductive effort was positively associated with plant cover (Table S4 in Appendix S1).

3.4 | Community composition

By the third spring, the seeded forbs collectively comprised around $2.0\% \pm 0.5\%$ (standard error) cover in the seeded-only plots and $2.8\% \pm 0.6\%$ in the soil disturbance and seeded plots. There was not a clear legacy effect of the soil disturbance treatment on seeded forb cover although there was a positive but insignificant association (Figure 3; Table S6 in Appendix S1). Seeded forb cover was negatively associated with exotic grass cover (Figure 3, Table S6 in Appendix S1). There was no evidence of association between planted forb cover and either bare ground cover or native grass cover.

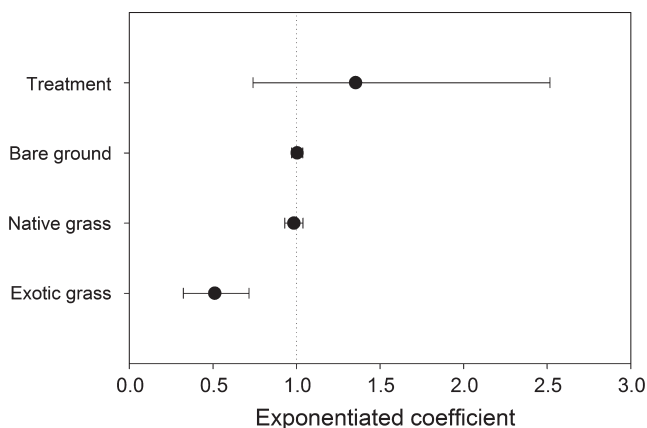


FIGURE 3 Effect of soil disturbance treatment and cover class on seeded forb cover 3 years after seeding. Exponentiated model coefficients and 95% confidence intervals for data with outlier removed are shown, such that a coefficient of 1.0 indicates no effect, coefficients <1.0 indicate that the predictor decreased the odds ($p/(1-p)$, where p is seeded cover and coefficients >1.0 indicate that the predictor increased the odds ($p/(1-p)$) of cover. Coefficients correspond to the effect with an increase in cover of 1%. Full model results, including p -values, and estimates from the model with the outlier are listed in Table S6 in Appendix S1

4 | DISCUSSION

This study indicates that component-wise management of novel ecosystems can be feasible. Seed addition resulted in new forb populations that have persisted for 3 years for 6 of the 10 seeded species, including the nationally threatened *S. macrocarpus* (Department of the Environment, 2016). This demonstrates that the establishment and survival of these native forb species was not restricted by the novel abiotic and biotic conditions encountered in this highly modified grassland. Two species in this experiment did not establish at all (*A. minus*, *L. squamatus*) and two species established but did not persist after the first year (*W. victoriensis*, *C. variabilis*), indicating that these species may not be able to persist under the novel conditions that they experienced, although other explanations are also plausible. The species that failed to establish have low germination capacity (Gibson-Roy et al., 2007a; Morgan, 1998a), and have also failed to establish when there was low nutrient availability and no exotic competitors (Gibson-Roy et al., 2007b). The failure after the first year of the annual *W. victoriensis* occurred across the region and was presumably due to the dry spring (S. Sinclair, pers. obs.). This annual species re-appeared in nearby natural populations the subsequent spring (S. Sinclair, pers. obs.), but did not re-appear at our study site, suggesting that 1 year of flowering did not create sufficient seed bank for persistence of this species. While not ubiquitously successful, this experiment suggests it is possible to enhance the conservation value of a novel ecosystem by increasing forb richness.

Eight of the 10 species were established in the first year, indicating that these species were seed limited. This seed limitation was not surprising given the severe regional population declines and intense fragmentation of grasslands in the study region since European settlement. These results support previous work that seed limitation often limits recruitment opportunities (Clark, Poulsen, Levey, & Osenberg, 2007; Seabloom et al., 2003; Turnbull, Crawley, & Rees, 2000). However, microsite characteristics such as seed-soil contact are also important for enhancing seedling establishment (Maron et al., 2014; Turnbull et al., 2000) and were shown to be important here. Soil disturbance increased establishment by 50%, showing that microsite availability also limited establishment in this system. Hence, establishment was co-limited by seed and microsite availability as has been shown elsewhere (Aicher, Larios & Suding 2011; Turnbull et al., 2000).

Surprisingly, there was little evidence of a legacy effect of the disturbance treatment on population size in the second and third year, with the effect persisting through the following 2 years only for *B. dentata*. There was also little evidence that the disturbance treatment increased cover of the seeded species after 3 years, contrasting with seed addition experiments in Germany and the US that found cover of seeded non-N-fixing forbs was higher in disturbed than undisturbed plots 3 years post-treatment (Maron et al., 2014). This lack of disturbance treatment legacy may be because, despite high initial establishment, subsequent processes (e.g. competition, resource availability, environmental stress) ultimately limited population size (Godefroid et al., 2011). This explanation is supported by

high mortality rates between the first and second years, although the second year of the experiment was also dry and this may also have contributed to high mortality. These results suggest that soil disturbance may not be necessary if sowing at these densities into regions of very low plant cover.

Our results indicate that the elevated soil fertility associated with extensive fertilization may not always be a barrier to restoration of native forbs. Low establishment success of native perennials in nutrient-enriched grassland has been previously reported in association with dominance of exotic species better adapted to exploit high-nutrient conditions (Prober, Lunt et al., 2002, 2005). In this study, we also observed negative associations between exotic species dominance and establishment (but not survival) and between seeded forb cover and exotic grass cover, suggesting that competition from exotics may have negatively affected native forb establishment and growth. Mean bare ground cover exceeded 30% in all spring (October) monitoring sessions suggesting that competition may have been mitigated in this experiment by disturbances (drought and fire) that limited above-ground biomass and maintained ground-level light availability during the course of the experiment.

The experiment was established in grassland burnt a few months previously and was subject to a prescribed fire between the second and third spring. Fire is considered a key structuring process in these grasslands and has been shown to maintain diversity in Australian temperate grasslands by preventing native grasses from competitively excluding other species (Morgan, 1998b), although opposing effects have been shown elsewhere (Larios, Aicher, & Suding, 2013). Fire also maintains ground-level light availability in this grasslands (Morgan, 1998b) which has been shown to be a key determinant of grassland diversity (Borer et al., 2014) and forb recruitment (Morgan, 1998b). In these grasslands, fire may also minimize competitive exclusion by exotics due to adaptations of perennial native forbs that can escape fire by retreating below-ground or re-shooting from the base (Morgan, 1999a; Table 1), compared to annual exotics or some native C_3 grasses for which fire mortality may be high (Sinclair, Duncan, & Bruce, 2014). Furthermore, fire may alter competitive interactions to favour natives through impacts on soil nutrient availability (Bennett, Judd, & Adams, 2003) and soil biota (Egidi et al., 2016). Therefore, the management burn may have helped to reduce competition with exotic species.

Drought may also have reduced competition with exotics. The second spring following seed addition was dry (BOM, 2016). The effect of drought on the relative abundance of native and exotic plants depends on the system, species and context, with drought favouring exotics in some cases (Jimenez et al., 2011; Larios et al., 2013), and natives in others (Meisner, De Deyn, de Boer, & van der Putten, 2013). In this experiment, the low above-ground biomass associated with drought probably favoured the seeded species by limiting above-ground competition. Altogether, these results suggest elevated nutrients themselves are not a barrier but rather, their indirect impacts via competition can be a barrier, and this may be mitigated by disturbance including managed fire.

The establishment of native forb species in the novel C_3 grass matrix suggests that the shifted dominance profile of the grassland

from C_4 - to C_3 -dominance is not a barrier to re-introducing these native forbs. Most grassland forbs, including all those seeded here, use C_3 photosynthesis and grow in the cooler seasons (Ehleringer & Monson, 1993). In remnant grasslands, they occur alongside the dominant C_4 *T. triandra*. Theory suggests a seasonal partitioning of resources between the C_4 and C_3 species based on timing of maximum growth (Chesson, 2000; Ehleringer & Monson, 1993). This temporal differentiation in maximum growth has been empirically shown for *T. triandra* with C_3 grasses but not clearly with forbs (Groves, 1965). Given the abundance of novel C_3 -dominated grasslands in need of restoration in southeast Australia (Department of Sustainability, Environment, Water, Population and Communities, 2011), these results suggest that transitioning back to C_4 grass dominance and low soil nutrients may not be necessary for increasing native forb diversity, provided biomass management maintains ground-level light availability. The effect of exotic competition documented above is different to C_3 vs. C_4 dominance as the dominant C_3 species are a mix of natives and exotics.

While native forb establishment and survival in these novel conditions is clearly possible, continued monitoring and evidence of recruitment is needed to demonstrate population persistence. Re-introduced populations often suffer gradual declines after initial establishment (Godefroid et al., 2011; Morgan, 1999b), such that short-term monitoring sometimes leads to overconfident reporting of success (Godefroid et al., 2011). We planted at high densities and saw high post-establishment mortality between the first and second spring, with a smaller decline between the second and third spring. Planted forb densities are now comparable to, or somewhat higher than, those observed in native grasslands (Patton, 1935). It is too soon to tell if planted forb population sizes will stabilize at near-natural levels, or continue to decline. Encouragingly, second-generation recruits were observed for two species during the experiment: two plants of *B. dentata* and two of *S. macrocarpus* were noted in the third year in control plots that were unoccupied in years 1 and 2.

This study suggests that biodiversity and conservation value can be enhanced in novel ecosystems through simple and low-intensity measures. We have shown that seed addition to a novel grassland can improve forb diversity, a key conservation value for these grasslands (Sinclair et al., 2015), without restoring all components of the original community (native dominance, soil nutrient profile, C_4 dominance). Altogether these results highlight the need to think beyond the baseline and re-imagine ecosystems to identify management activities that can enhance biodiversity without necessarily attempting a return to a historic state.

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AUTHORS' CONTRIBUTIONS

J.L.M and S.S. conceived the idea; J.L.M., A.J., J.M. and S.S. designed the experiment; all authors collected the data; T.Z. and A.J. analysed the data; T.Z. and J.L.M. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data supporting the results of this paper are archived in Dryad Digital Depository <https://doi.org/10.5061/dryad.3913b> (Zamin et al., 2017).

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SUPPORTING INFORMATION

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