



## Research Paper

# A modelling framework for improving plant establishment during ecological restoration



Matthew J. Rinella<sup>a,\*</sup>, Jeremy J. James<sup>b</sup>

<sup>a</sup> USDA-Agricultural Research Service, Fort Keogh Livestock and Range Research Laboratory, Miles City, MT, 59301, USA

<sup>b</sup> University of California, Sierra Foothill Research and Extension Center, Browns Valley, CA, USA

## ARTICLE INFO

## Article history:

Received 2 May 2017

Received in revised form 14 July 2017

Accepted 8 August 2017

Available online 29 August 2017

## Keywords:

Biodiversity  
Ecological restoration  
Grassland  
Plant establishment  
Seedling survival  
Trait

## ABSTRACT

Plants seeded during ecological restoration sometimes persist but more often fail to establish. Biodiversity has been shown to stabilize a number of ecological processes, suggesting biodiverse seed mixes could be designed to stabilize plant establishment outcomes. In particular, it may be possible to design seed mixes to increase chances at least some seeded species will be adapted to whatever environmental conditions arise during establishment. To explore this possibility, we developed a modelling framework and applied it to data from 30 field experiments (15 sites  $\times$  2 seeding years) conducted in a big sagebrush (*Artemisia tridentata* Nutt.) ecosystem. In each experiment, three native and one nonnative grass were sown (600 seeds  $m^{-2}$ ) in separate plots, and we estimated the probability each species germinated and survived through two growing seasons post-seeding. Applying an optimization algorithm to these survival probabilities allowed us to assign species identities to 600 seeds  $m^{-2}$  in a manner maximizing the number of experimental conditions yielding  $\geq 5$  plants  $m^{-2}$ , a common plant density goal in grassland restoration. Allocating 353 (216, 555) [point estimate (95% CI)] seeds to *Poa secunda* J. Presl and 247 (11, 378) seeds to *Pseudoroegneria spicata* (Pursh) Å. Löve maximized our native plant density goal (goal achieved in 12 (10, 14) of 30 experiments), and the allocation to  $>1$  species supports the hypothesis biodiverse seed mixes could be designed to reduce establishment failures. Averaged over experiments, *P. spicata* survival was roughly half of *P. secunda* survival, but *P. spicata* nevertheless contributed to the density goal by compensating for low *P. secunda* survival in certain experiments. Strategically combining species with different seed/seedling traits can increase chances of achieving adequate plant establishment during ecological restoration.

Published by Elsevier B.V.

## 1. Introduction

Terrestrial ecosystems have become increasingly degraded (United Nations Environment Programme, GRID-Arendal, 2010), making the restoration of plant communities capable of providing for society's needs a major 21st century challenge (Millennium Ecosystem Assessment, 2005). Attempts to establish desired flora regularly involve introducing plants as seeds (Merritt and Dixon, 2011), but seeding outcomes are notoriously variable, with the sown species often failing to establish (Fehmi et al., 2014; MacDougall et al., 2008; Merritt and Dixon, 2011; Rinella et al., 2012; e.g. Wilson et al., 2004). Considerable research is focused on reducing establishment failures, with one branch of the research

aimed at discovering traits regulating plant survival during critical, early post-seeding periods (i.e.  $>0$ –4 years) when mortality rates are routinely 95–100% (Davalos et al., 2015; Fansler and Mangold, 2011; e.g. Westbury et al., 2006). Studies have identified traits (e.g. coleoptile densities, germination rates, germplasm provenances) correlated with young plant survival and growth in small numbers of seeding years and sites (Atwater et al., 2015; Baughman et al., 2016; but see, Larson et al., 2016; Pywell et al., 2003; e.g. Roberts et al., 2010). However, plant establishment varies dramatically across seeding years because of weather variation (e.g. Bakker et al., 2003; Wilson, 2015) and across sites within ecosystems because of abiotic and biotic variation (e.g. Bakker et al., 2003; Young et al., 2015), and it is unclear if any particular traits are consistently beneficial or if different traits are favored under different environmental conditions. It is easy to conceive of different conditions favoring different traits. For example, rapid germination can be deleterious in years when brief favorable periods stimulate germination just before hazardous events (e.g. freezing temperatures)

\* Corresponding author.

E-mail addresses: [matt.rinella@ars.usda.gov](mailto:matt.rinella@ars.usda.gov), [sue.bellows@ars.usda.gov](mailto:sue.bellows@ars.usda.gov) (M.J. Rinella), [jjjames@ucanr.edu](mailto:jjjames@ucanr.edu) (J.J. James).

(Fenner, 1987), but rapid germination might be beneficial in years when benign conditions endure following germination (Nagahama et al., 2016). Although temporal replication is rare in restoration research (Vaughn and Young, 2010), and those studies that do replicate temporally or spatially rarely compare species performances across sites or seeding years, a few studies have suggested the species/variety with the greatest establishment can vary by site within ecosystems (Gallagher and Wagenius, 2016; Lym and Tober, 1997) and seeding year within sites (James et al., 2011), providing evidence that different conditions favor different traits.

One way to account for fitness variation would be to seed diverse seed mixes to help ensure at least some species, varieties or populations will be adapted to future, unknown plant establishment conditions. To date, no research has tested if plant establishment goals can be more consistently achieved with more diverse seed mixes, which is surprising given the stabilizing effect biodiversity is known to have on a suite of ecological variables/ecosystem services, such as crop yield, invasion resistance and pollinator forage availability (e.g. Dorado and Vázquez, 2014; Downing et al., 2014; Hautier et al., 2015; Isbell et al., 2017). Of particular relevance are studies showing biodiversity can stabilize plant community responses to weather extremes (Isbell et al., 2015), the most-cited cause of plant establishment failures during ecological restoration (e.g. Foroughbakhch et al., 2006; Hardegree et al., 2016). The most studied variable has been biomass production, and it has become increasingly clear that growth responses to precipitation and temperature regimes vary by species, and this allows biodiversity to buffer biomass production against inter-annual weather variation (e.g. Craven et al., 2016; Elst et al., 2017). Similarly, there is some evidence seedling survival responses to precipitation and temperature regimes vary by species (e.g. Fay and Schultz, 2009), so biodiversity may promote consistent seedling establishment in the same way it promotes consistent biomass production.

In this paper, we develop a framework for assessing seed mix biodiversity as a tool for achieving plant establishment goals, and we illustrate the framework using survival data on four grass species from 30 western U.S. seeding experiments (2 seeding years  $\times$  15 sites). We begin by estimating probabilities individuals of each species survived each experiment. Then we use these probabilities in functions stipulating explicit plant establishment goals. We use optimization algorithms to allocate species identities to fixed numbers of seeds (i.e. 600 seeds  $m^{-2}$ ) in a manner maximizing achievement of the goals across our 30 sets of environmental conditions (i.e. 30 experiments). Because we sowed only one species per plot, we assume reallocating seeds from one species to another species would not have altered density-dependent mortality rates. A willingness to operate under this assumption reduces the empirical burden by avoiding the need to sow species in mixture at multiple rates to estimate competitive effects on survival. We devote careful attention to examining how violations of this assumption would affect our conclusions.

The first goal we consider pertains strictly to the density of established plants, without reference to numbers of species. For example, a stand averaging, say, 10 plants  $m^{-2}$  satisfies the goal equally well regardless of the number of species in the stand. Examining how our analysis assigns species identities to seeds provides insight into the value of biodiversity for meeting the density goal. In particular, if the goal is best met by assigning the same species identity to all seeds, this is counterevidence to the hypothesis biodiversity improves plant establishment. On the other hand, if the goal is best met by allocating seeds to multiple species, this is evidence biodiverse seed mixes could be designed to reduce establishment failures. A goal based strictly on plant density without reference to the number of species is not inconsistent with common practice. Because seeding is expensive and failure-prone, it is often infeasible to restore diverse native plant communities, so managers often

sow relatively inexpensive, widely available seed of one or a few species in hopes of restoring certain functions to degraded sites (e.g. Knutson et al., 2014; Liu et al., 2015; Lym and Tober, 1997). Our study system, for example, is extensively invaded by the invasive annual grass *Bromus tectorum* L., and a common objective is to establish small numbers of grasses that will provide forage and reduce erosion and wildfire risks posed by *B. tectorum* (Boyd and Davies, 2012; Boyd and Lemos, 2016; Knapp, 1996). Often, in order to reduce risks of establishment failures, aggressive non-native grasses such as *Agropyron desertorum* (Fisch. ex Link) Schult. are sown alone or included in seed mixes. A downside to these species is they can prevent other, more desired species from establishing (Davies et al., 2013).

We turn next toward specifying a density goal. Superficially, it seems a rational density goal would be to maximize long run average densities, with the average being over seeded sites (i.e. maximize  $E(D)$ , with  $E$  being the expected value function and  $D$  being plants  $m^{-2}$ ). However, setting maximum mean density as the goal could lead to erratic outcomes; i.e. high densities at some sites and low or zero densities at others. Moreover, setting maximum mean density as the goal guarantees all seeds will be assigned to the single species with the greatest mean survival rate. To improve on  $E(D)$ , we assign species identities to seeds in a manner maximizing  $E(Z)$ , where

$$z_i = \begin{cases} 1, & \text{if } d_i > T, \\ d_i/T, & \text{otherwise} \end{cases} \quad (1)$$

This says  $z_i$  equals mean plant density at site  $i$ , i.e.  $d_i$ , divided by target density, i.e.  $T$ , except if  $d_i$  is greater than  $T$ , in which case  $z_i$  equals 1. As such, sites with densities equaling or exceeding the target density are scored as complete “successes,” i.e. 1s, and sites with lower densities are scored proportional to complete successes. This new goal realistically assumes that, because of growth, reproduction and density-dependence, boosting young plant densities above a threshold value does not provide better long-term restoration outcomes (Pyke and Archer, 1991; Weiner and Freckleton, 2010). The value  $T$  represents an estimate of the young plant density needed to achieve long-term restoration objectives. With maximum  $E(Z)$  as the goal, the optimal number of seed mix species is no longer assured to be one. Instead, it can theoretically be as high as  $S/T$  species, where  $S$  is total seed rate. Maximizing  $E(Z)$  requires setting  $T$ , and heuristic values used for deciding if young plant densities are sufficient to meet long-term restoration goals are logical candidates for  $T$  (Boyd and Davies, 2012; e.g. Ogle et al., 2011).

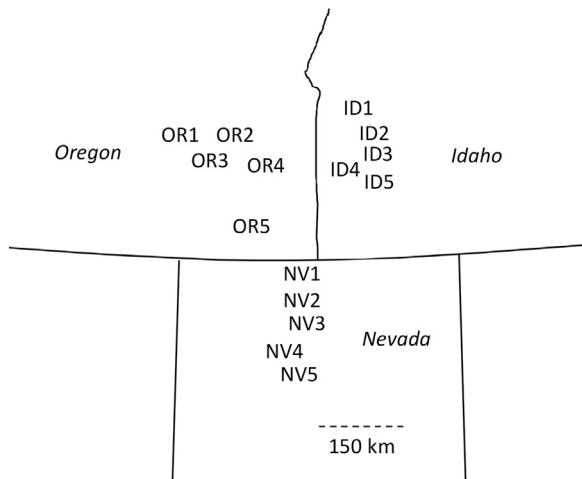
Besides goals pertaining strictly to plant densities, managers might choose to pursue a variety of other goals. To illustrate how our approach could be used in pursuing a range of goals, we examine a species evenness goal. Loosely, this goal is to establish similar numbers of individuals of each species within any given site. More formally, the goal is to assign species identities to seeds in a manner

minimizing  $E\left(\sum_{j=1}^J (d_j - \bar{d})^2\right)$ , with  $J$  being the number of sown species,  $d_j$  being mean density of species  $j$  and  $\bar{d}$  being the mean density of all sown species. Analyzing this goal allows us to evaluate tradeoffs between density and evenness.

## 2. Materials and methods

### 2.1. Site descriptions

In 2012 and 2013, we initiated 5 experiments in Idaho, Nevada and Oregon, three states in the northwestern U.S. (5 sites  $\times$  2 seeding years  $\times$  3 states = 30 experiments) (Fig. 1). Sites were located



**Fig. 1.** Sites where survival probabilities of four grass species were estimated following seeding in 2012 and 2013.

within big sagebrush (*Artemisia tridentata* Nutt.) habitats differing widely in long-term average precipitation (ranging from 150 to 280 mm per year), elevation (920–1470 m) and soil texture [sand (19–76%), silt (20–70%) and clay (4–24%)]. Though historically supporting diverse mixtures of perennial grasses, forbs and sagebrush, the sites were highly degraded at the time of study, with *B. tectorum* comprising >90% of total plant cover.

## 2.2. Experimental methods and vegetation sampling

We seeded one exotic perennial bunchgrass (*A. desertorum*) and three native perennial bunchgrasses [*Elymus elymoides* (Raf.) Swezey, *Poa secunda* J. Presl and *Pseudoroegneria spicata* (Pursh) Å. Löve] in each experiment. Seeds were acquired from Granite Seed (Leigh UT, U.S.A), and seed from the same seed lot were used in all experiments. In each experiment, one grass species was sown to four randomly selected 10 × 10-m plots (4 grass species × 4 plots = 16 plots per experiment) at a rate of 600 live seeds m<sup>-2</sup>. Pure live seed was determined by quantifying the fraction of total material that was seed and assessing the portion of viable seed using lab germination and cut tests on seeds to determine seed fill.

Plots were sown between October 21 and November 28 each year, and glyphosate was applied the spring prior to seeding to reduce *B. tectorum* seed production. Plots were lightly tilled the fall of seeding, and seeds were mixed with rice hulls and broadcasted with a hand-powered spreader. Plots were gently packed with a roller to improve soil-seed contact. In each plot, a 2.0 × 0.5-m quadrat was permanently marked and censused monthly during the first growing season (February to June) for new seedlings, live plants and dead plants. In the second growing season, surviving plant densities and tiller counts were measured end of May.

## 2.3. Analysis

The probability individual *i* germinated and survived to the second growing season after seeding [i.e. Pr(*y<sub>i</sub>* = 1)] was assumed to follow a Probit model (Albert and Chib, 1993):

$$\Pr(y_i = 1) = \Phi(\beta_{1j(i)} + \beta_{2k(i)} + \beta_{3l(i)} + \beta_{4m(i)} + \beta_{5n(i)} + \beta_{6o(i)}), \quad (2)$$

where  $\Phi$  denotes the cumulative distribution function of the standard normal distribution and  $\beta_1$  through  $\beta_6$  are parameter vectors. Indicator functions,  $j(i)$  through  $o(i)$ , map individuals to species, seeding year, site, plot, site × seeding year, and site × species × seeding year parameters, respectively. Priors on elements of  $\beta_1$  and  $\beta_2$  were uniform with support on the whole

real line and priors on elements of  $\beta_3, \beta_4, \beta_5,$  and  $\beta_6$  were normal with mean 0 and standard deviation  $\tau_3, \tau_4, \tau_5,$  and  $\tau_6,$  respectively. The prior on each  $\tau$  was uniform over the positive real line. We constructed a Gibbs sampling algorithm to simulate the posterior distribution (Gelman et al., 2014).

For our density goal (Eq. (1)), each of  $x = 1, 2, 3, \dots, 20,000$  posterior simulations was used to compute a 30 × 4 (# of experiments × # of species) matrix of survival probability estimates,  $P_x$ , and for each  $P_x$  we used a numerical maximization algorithm to compute

$$\operatorname{argmax}_{s_{x1}+s_{x2}+s_{x3}+s_{x4}=600} \sum_{i=1}^{30} \begin{cases} 1, & \text{if } d_i > T, \\ d_i/T, & \text{otherwise} \end{cases}, \quad (3)$$

where the  $s_x$  are seed rates of the four grasses and  $d_i = \sum_{j=1}^4 s_{xj} P_{xij}$

(Wolfram Research, 2016). Eq. (3) reflects assigning species identities to seeds in a manner maximizing  $\sum_{i=1}^{30} \begin{cases} 1, & \text{if } d_i > T, \\ d_i/T, & \text{otherwise} \end{cases}$

subject to the constraint total seed rate is 600 m<sup>-2</sup>. We set  $T = 5$ , a common benchmark for assessing perennial grass seeding success in our study region (Boyd and Davies, 2012). We repeated the maximization with the  $s_x$  corresponding to *A. desertorum* set to zero to investigate diversity effects among exclusively native species.

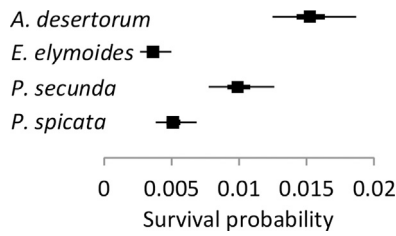
For our evenness goal, we used a minimization algorithm to compute

$$\operatorname{argmin}_{s_{x1}+s_{x2}+s_{x3}+s_{x4}=600} \sum_{i=1}^{30} \operatorname{Var}(s_{x1} P_{xi1}, s_{x2} P_{xi2}, s_{x3} P_{xi3}, s_{x4} P_{xi4}), \quad (4)$$

where Var is the variance function. Eq. (4) reflects assigning species identities to seeds in a manner minimizing the sum of plant density variances. We base all inferences on confidence intervals and Bayesian *P*-values calculated from the posterior distributions (Gelman et al., 2014).

The {*A. desertorum*, *E. elymoides*, *P. secunda*, *P. spicata*} seed mixes sown in field experiments were {600, 0, 0, 0}, {0, 600, 0, 0}, {0, 0, 600, 0}, and {0, 0, 0, 600}, and we used Eqs. (3) and (4) to estimate plant densities that would have resulted from all other possible seed mixes sown at 600 seeds m<sup>-2</sup>, such as {55, 45, 150, 350}. The assumption in using Eqs. (3) and (4) for this purpose is that replacing seeds of one species with seeds of another species would not have altered density-dependent mortality rates. We believe this assumption is justified because seeded plants were too small and sparsely distributed to cause appreciable density-dependent mortality. At study's end, average plant heights and tillers per plant were 4–10 and 3–6 cm, respectively, depending on site and species, and >90% of plots supported <20 plants m<sup>-2</sup>. *A. desertorum* densities approaching 200 m<sup>-2</sup> have been observed the second growing season after planting at another site in our study ecosystem (James et al., 2011), suggesting our plots could have supported appreciably more plants without density-dependent mortality. Finally, regressions of final versus emerged densities showed no evidence of density-dependent mortality (i.e. saturation).

Although we believe density-dependent mortality was likely negligible, we nevertheless analyzed how the presence of this mortality would have influenced our conclusions (see Appendix S1 in Supplementary material). According to our analysis, low density-dependent mortality would not have altered our conclusions and high density-dependent mortality would have led us to underestimate the value of biodiversity; i.e. underestimate the number of species needed to maximize Eq. (3) (see Appendix S1 in Supplementary material). There is an intuitive explanation for this result. In each experiment, the seed mix most likely to generate density dependent mortality would be one devoted entirely to the best-



**Fig. 2.** Point estimates (squares), 75% CI (thick lines) and 95% CI (thin lines) estimating probabilities seeded species germinated and survived until the second growing season after seeding. Estimates are of means over 30 seeding efforts (i.e. 2 seeding years at 15 sites). Differences between all species are significant ( $P \leq 0.03$ ).

surviving species, and our field experiments included those seed mixes. As such, if density dependent mortality occurred, it likely caused us to overestimate the number of seeds of the best-surviving species needed to achieve a given density. Logic similar to that used in analyzing Eq. (3) led us to conclude density dependent mortality would cause Eq. (4) to underestimate maximum evenness. In summary, our estimates should be viewed as conservative in that they may underestimate the value of biodiversity for meeting plant establishment goals.

**3. Results**

Averaged over sites and seeding years, survival probabilities differed widely by species ( $P=0.001$  to  $P=0.03$ ) (Fig. 2). Average *A. desertorum*, *E. elymoides*, *P. secunda*, and *P. spicata* densities were 8.5 (7.5, 9.2), 2.0 (1.6, 2.2), 5.5 (4.6, 6.0), and 2.8 (2.3, 3.1) plants  $m^{-2}$ , respectively. Survival of the nonnative *A. desertorum* was similar to or greater than survival of other species in all but a very few experiments (data not shown). Conversely, different native species had greater survival rates in different experiments (Fig. 3).

Because *A. desertorum* almost always had the greatest survival, the Eq. (3) density goal was best achieved by assigning no seeds to *E.*

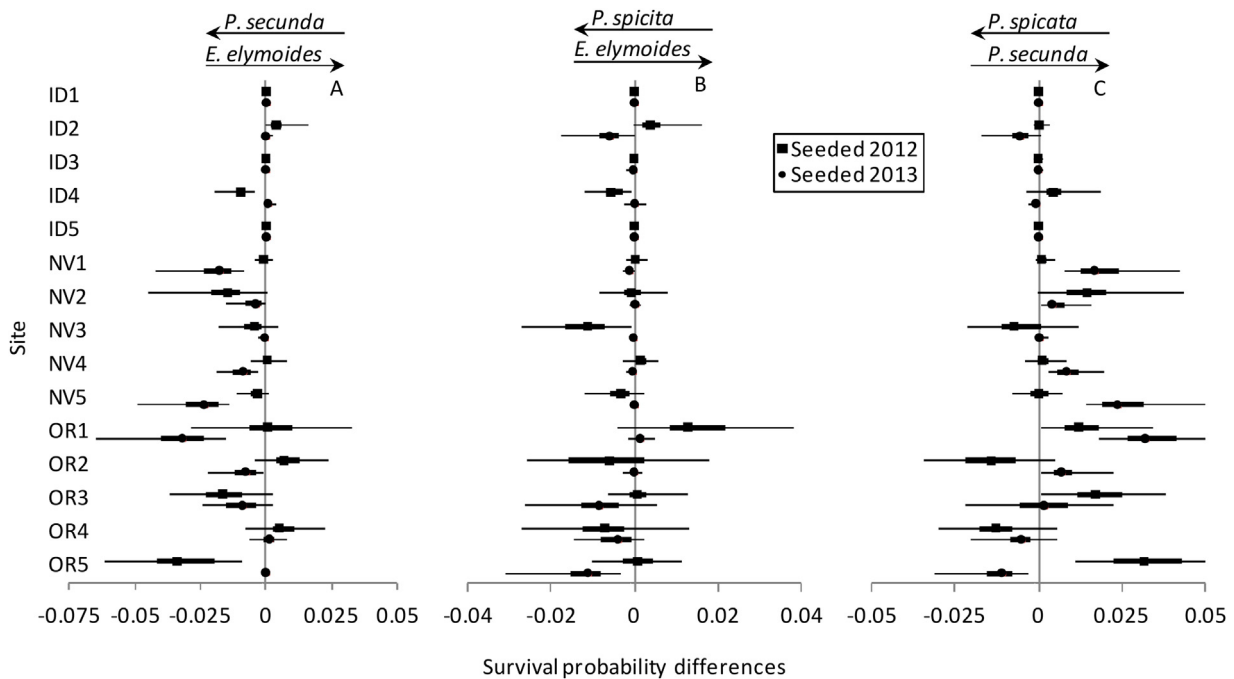
*elymoides* ( $P > 0.99$ ), *P. secunda* ( $P = 0.40$ ) and *P. spicata* ( $P > 0.99$ ) and instead assigning all 600 seeds  $m^{-2}$  to *A. desertorum*. With all seeds assigned to *A. desertorum*, 60% (46%, 70%) of seeding efforts were “successful” (i.e. supported  $>T = 5$  plants  $m^{-2}$ ), and density averaged over experiments was 9.8 (6.8, 12.8) plant  $m^{-2}$  (Fig. 4B1). No plants of any species survived at ID1 and ID5, which is why estimated densities at these sites were zero regardless of how seeds were allocated to achieve restoration goals (Fig. 4C1–C3).

When the exotic *A. desertorum* was excluded from analysis to explore native seed mixes, the  $\{E. elymoides, P. secunda, P. spicata\}$  seed mix that maximized Eq. (3) had  $\{0 (0, 40), 353 (216, 555), 247 (11, 378)\}$  seeds  $m^{-2}$  (Fig. 4A2). When seed numbers were set at  $\{0, 353, 247\}$  (i.e. point estimates of maximizing values), plants  $m^{-2}$  averaged  $\{0 (0, 0.2), 1.2 (0.05, 2.1), 3.5 (2.1, 5.6)\}$  (Fig. 4B2), and 40% (30%, 46%) of experiments supported  $>T = 5$  plants  $m^{-2}$ , which is lower than when the analysis included *A. desertorum* and all seeds were allocated to this species ( $P < 0.001$ ).

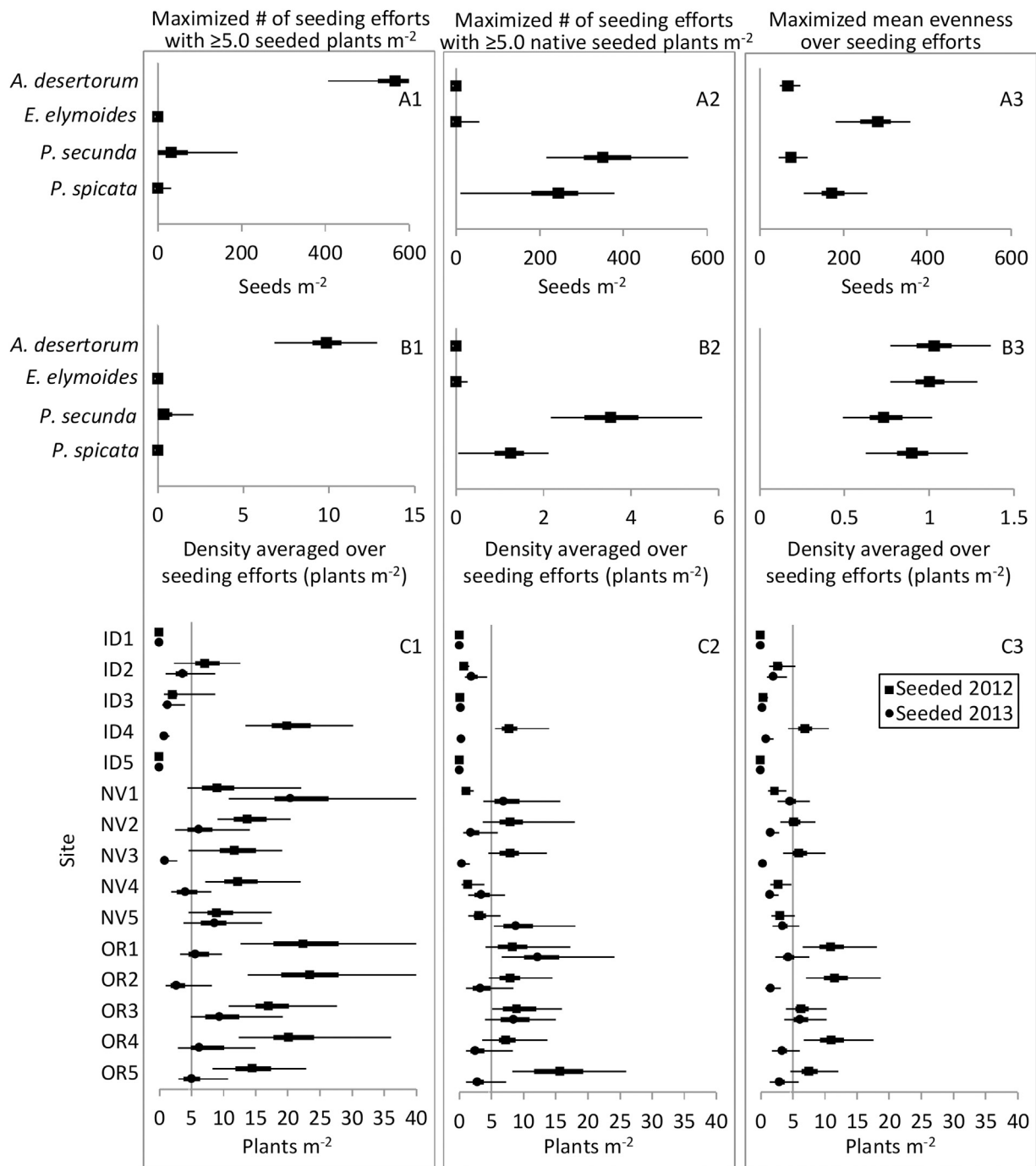
As should be expected, the  $\{A. desertorum, E. elymoides, P. secunda, P. spicata\}$  seed mix that maximized evenness (i.e. Eq. (4)) had fewer than average seeds devoted to species with greater than average survival probabilities:  $\{68 (48, 97), 284 (181, 360), 76 (45, 114), 172 (105, 257)\}$  (Figs. 2 and 4A3). When seed numbers were set at  $\{68, 284, 76, 172\}$  (i.e. point estimates of minimizing values), plants  $m^{-2}$  averaged  $\{1.0 (0.8, 1.4), 1.0 (0.8, 1.3), 0.7 (0.5, 1.0), 0.9 (0.6, 1.2)\}$  (Fig. 4B3), and 30% (20%, 37%) of experiments supported  $>T = 5$  plants  $m^{-2}$ , which is lower than when the goal was maximizing the Eq. (3) density goal using all species ( $P < 0.001$ ) or just natives ( $P = 0.05$ ).

**4. Discussion**

When all seed mix candidates were native, the plant density goal (i.e. Eq. (3)) was best met by allocating seeds to both *P. secunda* and *P. spicata* (Fig. 4A2), and the allocation to  $>1$  species provides evidence biodiversity could be used to limit plant establishment failures. Averaged over experiments, the survival rate of *P. spicata*



**Fig. 3.** Point estimates (squares and circles), 75% CI (thick lines) and 95% CI (thin lines) estimating differences between seeded species' survival probabilities in 30 seeding efforts (i.e. 2 seeding years at 15 sites). Arrows indicate directions of increasing survival rates for listed species. For example, the second-to-bottom point estimate in Panel A indicates *P. secunda* survival exceeded *P. spicata* survival by  $\sim 0.03$  at OR5 in 2012, and the bottom estimate in this panel indicates *P. spicata* survival exceeded *P. secunda* survival by  $\sim 0.01$  at this same site in 2013. CIs not overlapping zero line are significant ( $P \leq 0.025$ ).



**Fig. 4.** Point estimates (squares and circles), 75% CI (thick lines) and 95% CI (thin lines) estimating effects of allocating 600 seeds  $m^{-2}$  among four grass species three different ways to achieve three different restoration goals. In the first column, the goal was maximizing partial and complete “successes” among 30 seeding efforts (i.e. 2 seeding years at 15 sites), with a complete success being a seeding effort giving  $\geq 5.0$  plants  $m^{-2}$  the second growing season after seeding. In the middle column, the goal was the same but the seed rate of *A. desertorum*, the only exotic grass, was fixed at zero. In the third column, the goal was maximizing species evenness averaged over seeding efforts. When *A. desertorum* was included, there was little evidence allocating any of the 600 seeds to native grasses increased success (A1). When *A. desertorum* was excluded, a mix of *P. secunda* and *P. spicata* maximized success (A2). Maximizing evenness substantially reduced numbers of successes (C3 versus C1).

was roughly half that of *P. secunda* (Fig. 2), but *P. spicata* nevertheless contributed to the density goal by compensating for low *P. secunda* survival in certain experiments (i.e. Fig. 3C, ID2 2013 and OR5 2013 and likely OR2 2012 and OR4 2013). Although allocating seeds to two instead of one species better met the density goal, the improvement was modest: Allocating all seeds to *P. secunda* instead of a mix of *P. secunda* and *P. spicata* reduced Eq. (3) by 1.1 (0.1, 2.4) units, implying including *P. spicata* increased chances of attaining the density goal by  $\sim 4\% = 100 \times 1.1/30$ . While this differ-

ence is modest, the two-species seed mix has the added benefit of providing greater biodiversity.

When the nonnative *A. desertorum* was included as a seed mix candidate, the density goal was best met by allocating all seeds to this one species (Fig. 4A1). This was not entirely unexpected as *A. desertorum* is known to have higher mean survival rates than natives of the region (James et al., 2011; Waldron et al., 2005). It stands to reason biodiversity will be of most value for achieving density goals when the species being sown share similar mean sur-

vival rates (and low survival covariances), because this increases chances species experiencing higher-than-average survival will compensate for species experiencing lower-than-average survival. In addition to *A. desertorum*, other nonnatives with comparatively high survival rates have also been used to restore functions and services (e.g. forage production) to degraded systems, such as *Agropyron fragile* (Roth) P. Candargy and *Agropyron trichophorum* (Link) Richter, (Ferrell et al., 1998; Waldron et al., 2005). When seeded into degraded systems, individual nonnative species often fail to establish (e.g. Rinella et al., 2012; Stonecipher et al., 2017), and it may be possible to design biodiverse, nonnative seed mixes reduce establishment failures.

Densities were sharply reduced when seeds were distributed to maximize evenness instead of the density goal (Fig. 4C1 versus C3). The main reason for the evenness analysis was to illustrate the applicability of our approach to a variety of restoration goals. For example, features of Eqs. (3) and (4) could be combined into new goals reflecting compromises between density and evenness, such as

$$\operatorname{argmax}_{s_{x1}+s_{x2}+s_{x3}+s_{x4}=600} \sum_{i=1}^{30} \begin{cases} T - \operatorname{Var}(s_{x1}P_{xi1}, s_{x2}P_{xi2}, s_{x3}P_{xi3}, s_{x4}P_{xi4}), & \text{if } d_i > T, \\ d_i - \operatorname{Var}(s_{x1}P_{xi1}, s_{x2}P_{xi2}, s_{x3}P_{xi3}, s_{x4}P_{xi4}), & \text{otherwise} \end{cases}$$

In this case, perfectly even sites with densities  $\geq T$  would best meet the goal. Also, our approach could be easily extended to variables other than plant and seed densities. For example, with no additional assumptions or field research, it would be straightforward to rerun our analysis fixing seed cost instead of seed rate. Extensions integrating plant size information (e.g. cover, biomass) are also possible. Finally, although seedling establishment is critical to restoration success, short-term data can poorly predict long-term seeding outcomes (Rinella et al., 2012), so extending our approach to longer time frames could be valuable. However, longer studies may face greater empirical demands: Depending on the long-term restoration goal being studied, it may be necessary to sow species in mixture at multiple rates to estimate how species interactions shape plant community compositions over the long-term.

Our conceptual and analytical framework and preliminary results could inspire a productive new area of research focused on using biodiversity as a tool for attaining plant establishment goals during ecological restoration. The research would seek species/varieties/populations exhibiting variation in fitness (e.g. survival, growth) rankings across seeding environments (e.g. Fig. 3C), because this fitness rank variation is what allows multi-species seed mixes to buffer against establishment failures. Currently, aside from the initial estimates we provide here (Fig. 3), next to nothing is known about typical magnitudes of fitness rank variation in any given system. With only four species, our study had limited ability to identify this variation, and future studies with more species may reveal greater variation. Also, benefits of biodiversity tend to strengthen with increasing environmental variability (Dimitrakopoulos and Schmid, 2004; Griffin et al., 2009), and our study had limited environmental variability because it consisted of only two seeding years and a cluster of sites confined to a small fraction of our study species' native range. Future studies including greater environmental variation and more genotypes may reveal stronger benefits of biodiversity to plant establishment.

If traits responsible for fitness rank variation could be identified, our approach could be retooled to operate on those traits instead of species, which would facilitate extending our approach to other systems and genotypes. However, identifying these traits would require extensive research. For example, identifying seed and coleoptile traits linked to young plant survival in just one seeding environment in our system required Larson et al. (2016) to measure traits and vital rates of our four study species plus 43

others. Identifying traits regulating fitness rank variation would require repeating laborious vital rate measurements like those of Larson et al. (2016) under a large number of seeding environments (i.e. site-year combinations). Moreover, relationships between traits and environmental conditions are likely nuanced, making it difficult to know which variables to isolate and study. For example, precipitation from seeding to final measurement critically regulates young plant survival during grassland restoration (e.g. Bakker et al., 2003), and this variable varied appreciably in our study, with means of experiments seeded 2012 and 2013 being 291 and 348 mm, respectively. Yet, survival rankings were inconsistent among different experiments seeded the same year (e.g. Fig. 3C OR2 vs. OR5), suggesting total precipitation did not drive survival rank variation. Instead of total precipitation or other coarse variables, subtle variables such as precipitation and temperature during short post-germination intervals likely determine relative species performances. Differential susceptibility of species to idiosyncratic, site-specific factors such as granivory (Gurney et al., 2015) and soil crusting (Romao and Escudero, 2005) likely also contribute to fitness rank variation.

Whether or not it proves feasible to discover traits regulating fitness rank variation, our study illustrates means for capitalizing on this variation to improve restoration outcomes. It should be possible to seek and strategically combine ensembles of genotypes that exhibit fitness rank variation to increase chances at least some seed mix members will be adapted to whatever plant establishment conditions happen to arise.

## Funding

This work was supported by the USDI-Bureau of Land Management and USDA-National Institute of Food and Agriculture.

## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecolmodel.2017.08.005>.

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