Research Paper

A modelling framework for improving plant establishment during ecological restoration

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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 × 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) Á. 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

(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 × 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

$$z_i = \begin{cases} 1, & \text{if } d_i > T, \\ d_i/T, & \text{otherwise} \end{cases}. \tag{1}$$

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 $E\left(\sum_{j=1}^{J}\left(d_j - \bar{d}\right)^2\right)$, 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 × 2 seeding years × 3 states = 30 experiments) (Fig. 1). Sites were located