Using strip seeding to test how restoration design affects randomness of community assembly

Running head: Restoration and randomness

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Author contributions: ‘EG conceived and designed the research; EG, JS, BG performed the experiments; EG analyzed the data; EG, JS, BG wrote and edited the manuscript’.

ABSTRACT

The re-establishment and enhancement of plant diversity is typically a priority for restoration practitioners. Since diversity and stability can be affected by the magnitude to which randomness drives community dynamics, modifying randomness (via habitat heterogeneity) could provide utility for vegetation managers. We investigated the value of using strip seeding to manipulate the magnitude to which randomness structures plant communities across a grassland in Davis, CA. Five years after restoring portions of a degraded site (0%, 33%, 50%, 66%, and 100% of an area) to create patches of seeded and unseeded strips, we assessed the amount of Jaccard dissimilarity across quadrats within strips and estimated the magnitude to which randomness contributed to community assembly (termed the nugget). We found higher nuggets in the 66% and 33% seeding treatment levels compared to the 0%, 50%, and 100% seeding treatment levels. In the 33% and 66% level of the seeding treatment, we also found that unseeded strips, which are regularly exposed to random events of dispersal from seeded strips, had a higher nugget than seeded strips. This work suggests that strategic seeding techniques that enhance habitat heterogeneity can increase the role of randomness in community dynamics. Strip seeding strategies appear to provide utility as a tool to indirectly enhance diversity across a degraded site.

KEYWORDS: Assembly rules; Grassland; Restoration; Revegetation; Strip seeding

Implications for Practice:

- Many plant communities are randomly assembled and higher rates of randomness often lead to greater species diversity and community stability
- Managers can manipulate the role of randomness in structuring communities by using a strip seeding approach to increase habitat heterogeneity
- Seeding 33% or 66% of a degraded area in strips appears to be a useful strategy for enhancing randomness within a restoration plant community

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65 INTRODUCTION

66 Vegetation managers employ a variety of strategies to address the effects of recent large-scale
67 land conversion associated with changing agricultural practices and climate change. Ecological
68 restoration is a commonly used approach to mitigate the negative effects of habitat degradation
69 in an attempt to re-establish a variety of ecosystem services. Due to the difficulty in successfully
70 restoring natural systems (particularly semi-arid and arid habitats; Hardegree et al. 2011),
71 managers typically use all available tools to deploy effective restoration strategies. This can
72 include the direct or indirect integration of ecological theory into restoration design (Wainwright
73 et al. 2018). For example, theory that describes processes driving community assembly is
74 expected to provide critical direction for planning restoration efforts (Young et al. 2001;
75 Temperton et al. 2004).

76 Assembly rules generally describe the process through which species assemble into
77 communities given a common pool of species (Diamond 1975). There are two dominant theories
78 as to how communities develop. Classical tradeoff-based niche models predict a process of
79 community development where species differ in traits and existing species at a site will more
80 strongly inhibit the establishment of species with similar resource requirements, due to strong
81 competition (e.g. Tilman 1982). This model is largely drive by priority effects or the order and
82 timing of species arrival to a site (Fukami 2015). Conversely, neutral models predict that
83 regional propagule abundances drive assembly and that once a species has arrived to a site, its
84 ability to establish is independent of its traits and the traits of existing species at the site (Hubbell
85 2001). Studies have identified factors that can be useful for predicting which model might
86 dominate in a particular system, including patterns of trait divergence (de Bello et al. 2012),

nutrient availability (Conradi et al. 2017), ecosystem size (Fukami 2004), diversity (Wilson & Watkins 1994), and the frequency and intensity of disturbance (Püttker et al. 2015).

The process of plant community assembly is expected to be contingent on several factors which might have different levels of influence. These include biotic drivers such as inhibition and facilitation (Connell & Slatyer 1977), and abiotic factors, or environmental filters such as soil type or annual precipitation (Bazzaz 1991). Although reliant on a considerable amount of understanding of local dynamics (e.g. Prach et al. 2001), the incorporation of community assembly theory into restoration can enhance management outcomes. For example, theory describing assembly rules can be leveraged by restoration practitioners to identify appropriate species traits to achieve management goals (Lockwood 1997; Young et al. 2001), create a hierarchy of abiotic filters for survival and establishment of restoration species (Keddy 1999), predict invasion dynamics (Fargione et al. 2003), and enhance aboveground biomass (Weidlich et al. 2017).

Despite the acknowledgment that community assemblages are likely the product of a mix of different biotic and abiotic factors, the contribution of stochastic events to community structure should not be ignored. Randomness is largely driven by chance seed production, dispersal and establishment events. Randomness is also driven by environmental heterogeneity (Ågren & Fagerström 1984), which can operate at different scales, from large, such as the presence of small wetlands (Freestone & Inouye 2006) , to small, such as ~~the preseneepatterns~~ of soil resources (Armas & Pugnaire 2005). Although identifying the magnitude to which randomness might structure a community is difficult because it can be scale dependent and interact with deterministic factors (Karst et al. 2005; Cavender-Bares et al. 2006), studies have

demonstrated that random processes often contribute (at least in part) to community assembly in many systems (Gotzenberger et al. 2011; Marteinsdottir et al. 2018).

At local scales, the role of randomness in structuring communities is relevant to restoration practitioners because this relationship can be related to important ecological dynamics. For example, higher rates of randomness in a community often result in higher species diversity (Pool 1989; Hurtt & Pacala 1995) due to greater functional trait redundancy. This could ultimately enhance the stability of communities, especially those made up of a small number of species (Song & Saavedra 2018). Randomness can also modify competitive outcomes (Law and Dieckmann 2000) or promote the coexistence of competitors (Chesson 1985), ultimately resulting in changes to invasion dynamics.

Because randomness can modify community assembly and, therefore, management goals and restoration outcomes, restoration practitioners might benefit from actively manipulating randomness. For example, because randomness is affected by environmental heterogeneity (Ågren & Fagerström 1984), managers can explore ways to enhance heterogeneity within restoration designs. Although random effects might be expected to play a larger role in structuring communities early on during the successional process (i.e., right after seeding, Herben et al 1999), patterns of randomness are expected to be maintained through time (Thórhallsdóttir 1990). Therefore, successful manipulation of randomness early on in a restoration project is expected to confer long term benefits. Evidence for effective ways to manipulate randomness in a restoration design, however, is essentially absent.

Strip seeding, which has recently been proposed as a low-cost method to restore native plant communities (Rayburn & Laca 2013), provides an opportunity for investigating the utility of enhancing randomness within a restoration program. The method involves seeding species

132 mixtures into dense patches that cover a fraction of the target area, creating a series of alternating
133 seeded and unseeded strips. The seeded species are then expected to naturally disperse into
134 adjacent unseeded areas. The method results in higher initial patchiness than traditional
135 broadcast seeding methods, and is therefore expected to enhance randomness by facilitating
136 heterogeneity in space and time across a landscape (Chesson 1981). The initial size and
137 configuration of the strips or the patch size and landscape position may also be a key determinant
138 in the role of randomness in community assembly through their influence on dispersal limitation
139 (Ord et al. 2017; Cook et al. 2005).

140 There has not yet been an investigation into the value of strip seeding to enhance
141 heterogeneity and, subsequently, randomness for community assembly. In the first ~~of its kind~~
142 study of its kind, we explored the utility of a strip seeding approach to affect the magnitude of
143 randomness that contributes to small-scale community assembly in a restoration framework. On
144 a large experiment where percentage of an area restored was manipulated using strips (from 0%
145 restored to 100% restored), we investigated how treatment type (percent of area restored)
146 affected the magnitude to which randomness was calculated to contribute to community
147 assembly. We also investigated if a variety of soil and plant community properties contribute to
148 differences in randomness across plots. We expected that plant communities in strip seeding
149 treatment levels with the highest amounts of heterogeneity (greater differences in the presence of
150 seeded sites across a plot) would be characterized by the highest amounts of randomness. We
151 also expected the community pool to have a positive relationship with randomness because
152 chance can play a larger role in species-rich areas (Lieberman & Lieberman 2007).

153 METHODS

154 *Experimental site*

The study was conducted at the University of California, Davis Agricultural Research Fields in Davis, California. The site has a Mediterranean climate with a mean annual precipitation of 445.77 mm and a mean average temperature high of 23.72 °C and low of 7.78 °C (1893 - 2016 averages; Western Regional Climate Center 2018). Precipitation has high intra-annual variation with approximately 95% of precipitation falling in the winter and spring months (Oct - April).

The study site is surrounded by a temporally changing mix of plant types ~~from on~~ experimental fields.

In November 2011, after mowing the field site, a mixture of six native perennial bunchgrass species and one native annual grass species were seeded in strips at varying seed coverage rates on 0.13 ~~hectare~~^{ha} plots (Supplemental Table 1). The majority of non-seeded species are annual non-native grasses that dominate grassland habitats in the area, and some non-native forbs commonly found in agricultural fields and grasslands. The five seeding treatments (0%, 33%, 50%, 66%, and 100%) created different sized areas of native grassland separated by different sized unseeded areas (Rayburn & Laca 2013; Supplemental Figure 1). Each plot was made up of 18 strips, and each strip was 2.4m wide and 25m long. Each plot was separated by a 5m interspace that was mowed annually. Plots were randomly assigned within blocks. Blocks were replicated 4 times, for a total of 20 plots. Because of the way the strips are aligned, the 66% and 33% levels of the treatment are considered to have the greatest heterogeneity (e.g. three contiguous strips must have both seeded and unseeded strips), followed by the 50% level (e.g. three contiguous strips might have both seeded and unseeded strips) and then the 0% and 100% levels (three contiguous strips never have both seeded and unseeded strips). The plots were mowed annually starting in 2012 to reduce invasive annual grass cover.

Data collection

For each plot, one seeded and one contiguous unseeded strip were randomly chosen for data collection in 2016. In plots treated with 0% or 100% seeding (i.e. the plot has all unseeded strips or all seeded strips), one strip in each plot was randomly chosen as the ‘seeded strip’ and a contiguous strip was then identified as the ‘unseeded strip’. In each strip, we sampled the plant community in 25cm x 25cm quadrats on a 2.4m transect (the width of an individual strip) that started at the border of the seeded and unseeded strip, in the middle of the plot. We chose this quadrat size based on the small spatial scale at which processes in the experimental plant communities are likely taking place (Dieckmann et al. 2000). Moreover, this is the scale at which variation in local soil properties important for driving plant interactions is accurately captured (Schlesinger et al. 1996). Although these transects exist on short spatial scales, they are relevant for two reasons. First, these are spatial scales that are of interest to managers using strip seeding approaches. Second, on larger spatial scales, randomness might not be related to transect extent (Brownstein et al. 2012).

In each strip, quadrats were placed on the transect at different distances from a border of a seeded and unseeded strip (at 0m, 0.15m, 0.6m, 0.9m, 1.5m, 2.1m, and 2.25m away from the border). This approach provided us with a variety of distances between quadrats (i.e. a variety of expected dissimilarities in plant communities between ~~quadrats~~~~plots~~). In April 2017 (peak biomass), we conducted a visual survey of aerial cover of all plant species found in each quadrat. We also recorded cover of litter and bare ground. After the plant survey was completed, we measured soil pH and temperature in the field using a hand-held meter (Hanna Instruments, Carrollton TX) in the field. We also collected a soil sample from the top 5 cm of soil in each plot using a ~~2.54 cm 1”~~-diameter soil core. Soil samples were sieved in the field into paper bags and

transferred directly to the University of California, Davis Analytical Lab where they were processed for percent soil moisture and total organic carbon.

Analysis

A separate analysis was conducted for quadrats in unseeded and seeded strips in each treatment level (0%, 33%, 50%, 66%, and 100% seeding). Dissimilarities (Jaccard) in species composition were identified between all seven quadrats in each transect in each strip type (unseeded and seeded). To fit a relationship between quadrat distance and Jaccard dissimilarities, we used a Gompertz asymptotic equation (Mistral et al. 2000). From the fitted curves, we identified the nugget (the y-intercept): conceptually, the dissimilarity at zero distance between quadrats and the measure of the amount of randomness in a community (Brownstein et al. 2012). The basis for using the nugget as an estimation of randomness is that two quadrats at zero distance from one another will experience the same environmental effects and be subjected to comparable dispersal events; therefore, any variation in dissimilarity can be attributed to local random effects. As the nugget gets bigger, random effects are expected to have a larger role in driving community dynamics. We also identified the asymptote for each fitted curve, which is the highest average dissimilarity across patches (Meyers et al. 2014) – essentially, it broadly describes variability across sampled plots. We used ANOVA to identify significant differences in the contribution of fixed factors treatment level, strip type and quadrat distance, and random factor quadrat nested within replicate, on Jaccard dissimilarity values.

We also investigated Pearson correlations between pooled quadrat-level characteristics per treatment (community pool [total number of species found in quadrats in each plot], mean species richness, mean litter cover, mean bare ground cover, mean soil pH, mean soil temperature, mean soil moisture and mean soil total organic carbon) and the nugget across all

quadrats to identify any potential drivers of randomness at our site. All analyses were conducted in R version 3.4.2 (R Development Core Team, 2017).

RESULTS

We found high spread in dissimilarity in 0% seeded plots. The nugget in the 0% seeding plots was 0.11 and the asymptote was 5.55 (Fig 1a; SE = 0.13, p = 0.41). Dissimilarity values in the 0% plots were significantly lower than those found in plots for all other treatment levels ($F = 29.7$, $p < 0.001$). Dissimilarity values were also significantly higher in seeded strips compared to unseeded strips across treatment levels ($F = 8.72$, $p = 0.003$). We found lower spread in dissimilarity values in seeded strips in 33% seeded plots compared to unseeded strips. The nugget for unseeded strips in 33% seeded plots was 0.55 and the asymptote was 7.10 (Fig 1b; SE = 0.18, $p = 0.003$), and the nugget in seeded strips in 33% seeded plots was 0.35 and the asymptote was 8.53 (Fig 1b; SE = 0.19, $p = 0.07$). The nugget was extremely low for both unseeded (nugget = 0, SE = 0.18, $p = 0.99$; Fig. 1c), and seeded strips (nugget = 0, SE = 0.18, $p = 0.02$; Fig. 1c) in the 50% seeded plots. However, the asymptote for the unseeded strips (8.44) was lower than for the seeded strips (> 1.00). The nugget for unseeded strips in 66% seeded plots was 0.75, and the asymptote was 6.98 (Fig 1d; SE = 0.15, $p < 0.001$), and the nugget in seeded strips in 66% seeded plots was 0.31, with an asymptote of 8.41 (Fig 1d; SE = 0.15, $p = 0.04$). The nugget in the 100% seeding plots was 0.19, and the asymptote was 8.50 (Fig 1e; SE = 0.11, $p = 0.09$).

The nugget was negatively correlated to soil pH (correlation = -0.75, $p = 0.03$; Fig 2). No other significant correlations were found between the nugget and soil or plant community properties (Supplemental Table 2).

DISCUSSION

The maintenance, re-establishment, and enhancement of plant diversity is typically a dominant goal of restoration practitioners. Since diversity ~~can be~~ is affected by the structure and heterogeneity of local landscapes (Gardner & Engelhardt 2008), modifying these habitat characteristics can be considered a tool for vegetation managers (Baer et al. 2005). We attempted to identify the utility of using strip seeding to manipulate heterogeneity (and therefore, randomness) across a restored landscape in order to potentially enhance plant community stability (Song and Saavedra 2018) and species richness (Tilman & Pacala 1993).

As expected, we found higher nuggets in the 66% and 33% seeding treatment levels compared to the 0%, 50%, and 100% seeding treatment levels, suggesting that strategic seeding strategies that enhance habitat heterogeneity can increase the role of randomness in community dynamics. Strip seeding approaches that enhance heterogeneity of a landscape can increase biodiversity across a landscape by leveraging suitable habitat in unseeded areas (Franklin & Lindenmayer 2009). For example, unseeded habitat that requires restoration might not be suitable for native plant establishment due to (among other things) a lack of adequate propagule pressure. Once strip seeding is employed, the unseeded matrix can then serve as habitat that can be managed for the biodiversity changes that occur in response to dispersal from the seeded sites. Moreover, seeded strips areas are characterized by greater variability in species identity, as demonstrated by higher asymptotes than those found in unseeded strips. So, seed dispersed from these areas are more likely to find safe sites for germination and establishment in unseeded strips due to a greater range in niche space occupied by individuals across the seeded sites.

We also found that unseeded strips in the 33% and 66% level of the seeding treatment had ~~a higher nugget~~ higher fine-scale heterogeneity than seeded strips, a pattern that was absent in the

other levels of the seeding treatment. Unseeded strips are regularly exposed to random events of dispersal from a more variable community across the seeded strips, which can enhance the magnitude to which randomness structures community composition in these areas. This dynamic is particularly important for smaller sized patches (Debinski et al. 2001), suggesting that managers hoping to use strip seeding to enhance heterogeneity and diversity should be considerate of seeding strip sizes. Alternatively, the way in which the experiment was implemented could be driving these patterns (Grman et al. 2013). For example, seeded strips were drill seeded with a mix that likely resulted in a regular pattern of germinating and establishing individuals, reducing random effects on communities across the strips.

We unexpectedly found that the community pool did not demonstrate any relationship with randomness. In fact, out of all measured variables, only pH showed any relationship with randomness. Perhaps we should have expected as much. Plants can affect the spatial distribution of a variety of soil properties (Zuo et al. 2008), and soil properties are often not randomly distributed across a site (Maestre & Cortina 2002). However, despite studies that have shown recorded low spatial variability of pH in soil (Röver & Kaiser 1999)~~Moreover~~, management activities ~~can have been shown to~~ affect the variability of soil properties in unexpected directions (Bruland & Richardson 2005). Moreover, the presence of perennial plants can strongly modify spatial variability of soil pH on small scales (Jackson & Caldwell 1993). Ultimately, effects of individual biotic or abiotic components on randomness contributions to plant community assembly are likely largely mediated by a complex network of interacting factors, diluting the measurable direct effect. Moreover, some resources might be distributed in such a way as its heterogeneity is at too fine a scale to actually affect plant dynamics (Purves & Law 2002).

Although we found evidence that strip seeding increased the relevance of random effects in the assembly of plant communities through the enhancement of heterogeneity, it is possible that the experimental treatments had other effects on the system to ultimately augment the types of plant species found across our plots. For example, seeding native species into our freshly mowed site dictates the first species to ‘arrive’, ultimately leveraging priority effects. Priority effects can significantly transform community structure by providing an advantage to species that arrive and establish early (Belyea & Lancaster 1999). Priority effects can drive successional processes (Connell & Slatyer 1977) – a slow, non-random development to a particular community – through the inhibition of later arrivals. Clearly, a strip seeding approach can create differences in community assembly in restored areas through a variety of mechanisms (Young et al. 2001). Because community assembly can be driven by processes that affect other management priorities (such as productivity, e.g. Weidlich et al. 2018), it is important for practitioners to understand how restoration techniques might interact with community dynamics.

Enhancing heterogeneity of a site is not a silver bullet for managers (Palmer et al. 2010). For example, effects of heterogeneity may be swamped by dominance of a single species (Baer et al. 2005; Tang et al. 2013) or growth form (Herben et al. 1999). Moreover, despite the clear importance of randomness for structuring communities (Cottenie 2005), there is no agreed upon magnitude of ‘randomness’ that appears to be particularly useful for managers. Finally, assembly ‘rules’ not be flexible enough to accommodate the complexity associated with natural systems. However, managers have noted the need for more research that provides science-based recommendations to enhance restoration goal achievement (Gornish et al. 2016). The use of strip seeding to lower restoration costs while also enhancing biodiversity through increased site heterogeneity appears to be a powerful potential tool for restoration practitioners. The paucity of

assessments of this approach, however, limits its utility. Since patch size can directly modify community-level (Debinski et al. 2001) and ecosystem-level (Bowker et al. 2013) management goals, researchers should focus on conducting experiments that can provide insight into strip seeding design effects on management outcomes.

ACKNOWLEDGEMENTS

We thank Gretchen Brownstein for code.

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Figure 1. Dissimograms and best fit lines for unseeded (open circles and full line) and seeded

475 (filled circles and dotted line) strips across percent seeded treatment: (A) 0% seeded; (B) 33%
476 seeded; (C) 50% seeded; (D) 66% seeded; and (E) 100% seeded. The x-axis is the distance
477 between each possible pair of plots, the y-axis is the complement of the Jaccard coefficient,
478 $D_{Jaccard}$.

479 **Figure 2.** The relationship between nugget values and soil pH, with best fit linear regression line.