Restoration Ecology
THE JOURNAL OF THE SOCIETY FOR ECOLOGICAL RESTORATION

RESEARCH ARTICLE

Diminishing Returns from Higher Density Restoration Seedings Suggest Trade-offs in Pollinator Seed Mixes

Marit L. Wilkerson,[1,2] Kimiora L. Ward,[3] Neal M. Williams,[3] Katharina S. Ullmann,[3] and Truman P. Young[1]

Abstract

Native forbs have become a more central component of restoration programs, especially because of their role in supporting crop pollinators. This study evaluates the success of different native forb mixes and seeding rates using shared goals of restoration practitioners and agroecologists, namely percent native species cover, floral resources, native diversity, and cost-effectiveness. At 6 sites with hedgerows adjacent to agricultural lands in California's Central Valley, we planted 3 native forb seed mixes at 3 seeding rates and monitored germination, percent cover, and floral resources for 2 to 3 years. We also evaluated the cost of the mixes based on seeding rates and original seed prices. More than mix type, relative seeding rate strongly affected germination, cover, and floral resource success. The relative benefits of seeding with more species diminished at higher seeding rates, especially when cost was considered. Cover increased significantly over the years but diversity declined sharply after the first year. Increased cover of target species was mainly due to the effect of 1 dominant species *Grindelia camporum*, common gumplant. We summarize data from a similar forb restoration study showing that the species that dominated in our mix-and-rate experimental sites also attracted the greatest diversity and abundance of pollinators. These findings highlight trade-offs and balance-points within restoration and pollination services goals. We offer suggestions on how to weigh those trade-offs, given particular priorities and how native forb plantings can support combined goals of pollination services and restoration.

Key words: agroecology, cost-effectiveness, ecosystem services, native forbs, pollination services, seeding rates.

Introduction

Ecosystem services from pollinators have become increasingly important to agroecologists, restoration practitioners, and private landowners across the United States (Kremen et al. 2007; Ricketts et al. 2008) and worldwide (MEA 2003; Winfree 2010; Walsh 2013). Planting hedgerows along field margins has become a popular conservation action designed to attract native pollinators and service multifunctional restoration benefits (Kohler et al. 2008; Brodt et al. 2009; Hannon & Sisk 2009; Morandin et al. 2011). Revegetating field margins has often focused on native shrubs and grasses when establishing hedgerows. However, native forbs are increasingly used and evaluated in pollinator-focused restoration (Carreck & Williams 2002; Carvell et al. 2007; Dickson & Busby 2009; Lulow & Young 2009; Pywell et al. 2011; Scheper et al. 2013), and this practice has recently escalated in the Central Valley of California. The restoration paradigm for the Central Valley that historically focused on native grasslands is shifting to include the concept of mixed prairies (Hamilton 1997; Seabloom et al. 2003; Minnich 2008).

The intersection of restoration and pollination services goals raises several unanswered questions. Both restoration practitioners and agroecologists wish to know what mix of native forbs and which seeding rates will create a self-sustaining, multifunctional native community and will attract pollinators throughout the growing season. Knowing the cost-effectiveness of different native forb plantings also benefits both restoration and pollinator service goals (Holl & Howarth 2000; Sheley & Half 2006; Rowe 2010; Kettenring & Adams 2011). Cost-effectiveness also has important implications for private landowners who bear the brunt of financial and management costs (Bonnieux & LeGoffe 1997; Brodt et al. 2009).

In restoration, "best" seeding mixtures and rates for grasses and forbs are often based on professional judgment or practical considerations, such as seed availability or price (Rowe 2010). Relatively little is known about which seeding rates will ensure enough germination to create self-sustaining communities (Burton et al. 2006; Frances et al. 2010; Rowe 2010) or which species mix will maintain plant diversity to support a diverse pollinator community (Williams et al. in preparation). An increase in seeding rate should produce more germinants (Sheley & Half 2006), but the question remains whether the initial

[1]Department of Plant Sciences, University of California, Davis, Davis, CA 95616, U.S.A.
[2]Address correspondence to M. L. Wilkerson, email mlwilkerson@ucdavis.edu
[3]Department of Entomology and Nematology, University of California, Davis, Davis, CA 95616, U.S.A.

doi: 10.1111/rec.12141

Table 1. Description of each of the three seed mixes used in the mix-and-rate experiment organized by mix and flowering phenology.

Seed Mix	*Species*	*Common Name*	*Flowering Phenology*	*Life cycle*
Mix A	*Lupinus succulentus*	Arroyo lupine	Spring	Annual
	Eschscholzia californica	California poppy	Spring–summer	Annual/perennial
	Phacelia californica	California phacelia	Spring–summer	Perennial
	Lu. densiflorus	Chick lupine	Late spring–early summer	Annual
	Grindelia camporum	Gum plant	Summer–fall	Perennial
Mix B	*P. californica*	California phacelia	Spring–summer	Perennial
	Trifolium fucatum	Bull clover	Late spring	Annual
	Lu. formosus	Summer lupine	Late spring–summer	Perennial
	Trifolium obtusiflorum	Spiney clover	Late spring–summer	Annual
	Lotus purshianus	Spanish clover	Summer–fall	Annual
Mix AB	*Lu. succulentus*	Arroyo lupine	Spring	Annual
	E. californica	California poppy	Spring–summer	Annual/perennial
	P. californica	California phacelia	Spring–summer	Perennial
	T. fucatum	Bull clover	Late spring	Annual
	Lu. densiflorus	Chick lupine	Late spring–summer	Annual
	Lu. formosus	Summer lupine	Late spring–summer	Perennial
	T. obtusiflorum	Spiney clover	Late spring–summer	Annual
	G. camporum	Gum plant	Summer–fall	Perennial
	Lo. purshianus	Spanish clover	Summer–fall	Annual

germination flush and diversity will last through multiple years (Gilbert et al. 2003) or where the saturation point of diminishing returns lies for higher seeding rates (Burton et al. 2006).

For agroecologists and private landowners globally, ecosystem services are often a justifying factor behind hedgerow implementation and other agroconservation activities (Baudry et al. 2000; Brodt et al. 2009; Pywell et al. 2011; Scheper et al. 2013). Hedgerow plantings that include native forbs can attract a greater abundance and diversity of pollinators than unmanaged field margins (Kohler et al. 2008; Hannon & Sisk 2009; Pywell et al. 2011). As in restoration, emphasis lies on appropriate mixes with diverse species that bloom throughout the growing season (Vaughan et al. 2007; Winfree 2010). Winfree (2010) highlights the need for more rigorous research into determining "best" seed mixes for pollination services.

This project examined the relative success of three native forb seed mixes, each sown at three densities in hedgerows planted along replicated field margins, supported by data from separate investigations of pollinator attraction. Its purpose was to determine which type of seed mix and seeding rate is the most successful and cost-effective from the complementary perspectives of vegetation restoration and support of pollinators. Success was assessed based on (1) first year germination and cover, (2) multiyear (2–3 years) cover and floral resources, (3) diversity of forbs through time, (4) cost-effectiveness of each seed mix and seeding rate, and (5) ability of individual species to attract native pollinators. Success metrics were both short-term and longer-term to reflect varying goals that practitioners and landowners may have for their forb plantings.

Methods

Study Site and Design

All experimental plots were located on privately owned farms within Yolo County in the Northern Central Valley in California, which has a Mediterranean climate characterized by hot, dry summers and temperate, wet winters (Appendix S1A, Supporting Information for more detail). Our study area was chosen based on the fact that Yolo County has one of the highest densities of restored hedgerows in the United States (Brodt et al. 2009).

For the main study discussed here ("mix-and-rate" study hereafter), we compared three mixes. The mixes were drawn from a pool of nine species from six genera, all locally native to the study area (Hickman 1993). Mix A and B had five forb species each and Mix AB was a combination of the two with nine species (Table 1). *Phacelia californica* was present in all three mixes because it is a spring bloomer and hypothesized to be less aggressive than *Grindelia camporum*. The mixes were chosen to complement each other with roughly equal amounts of perennials and annuals and to flower throughout the growing season. All species were known or hypothesized to be attractive to pollinators. Seeding rates were calculated at the species-level (Appendix S1B) based on the recommendations of a local native forb and hedgerow expert (J. Anderson 2007, Hedgerow Farms, CA, personal communication). Seeding rates were relative (1×, 2×, and 4×) within a mix. Absolute seeding rates were not directly comparable across mixes; the baseline rate (1×) for Mix AB was higher than for the other mixes because it contained nearly twice as many species (Table 1 and Appendix S1B).

The six sites chosen for the mix-and-rate experiment had native shrub plantings installed using a consistent design in the preceding or same growing season as the first year of the experiment. Two sites also had native grass plantings. In winter 2008, three study sites were hand broadcast-seeded with forb mixes, followed by three more sites in winter 2009. Seeding areas were cleared and hoed before planting and were drip-line irrigated. All sites were seeded with three forb seed mixes at each of the three relative seeding rates, giving each site nine plots. The $1 \times 8\,m^2$ plots were located between planted shrubs and spaced evenly throughout the hedgerow.

To quantify pollinator use of different forbs, we examined data from an ongoing study on the ability of habitat enhancement in conventional agricultural settings to support wild pollinators (Williams et al. in preparation). Three sites ("pollinator plots," hereafter) were established in October 2009 to examine pollinator preference between five seed mixtures and their individual species. At each site, five $3 \times 15\,m^2$ pollinator plots were prepared with disking followed by successive glyphosate burn-downs or solarization. Plots were then hand broadcast-seeded with native forb mixes similar to those above but that included a total of 17 annual and perennial species (Appendix S1C). Irrigation was used during establishment and only once thereafter during July 2010.

Data Collection and Project Maintenance

Mix-and-Rate Plots. Plots were monitored for first year germination, cover, and floral resources and subsequently, where possible, for cover and floral resources. In 2008, the first three sites were monitored three times from May to August to capture seasonal changes. In 2009, all six sites (three second year sites and three first year sites) were monitored three times and same in 2010 across four sites (two third year sites and two second year sites). Two sites were excluded due to accidental herbicide treatment.

In May 2008 and 2009, the number of individual germinated seedlings, identified to species, was counted throughout each $8\,m^2$ plot. Cover and flower density was assessed during every sample. Cover was estimated visually and recorded as a percentage. Flower density of each species was estimated by counting the number of fresh open flowers. Overall, all six sites have one full year of data, five sites had 2 years of data, and two had 3 years. Each of the plots was regularly hand-weeded in the first 2 years after germination. We collected categorical cover data on weeds in October 2009; this supplementary analysis and results are detailed in Appendix S2.

Pollinator Plots. Pollinator plots were maintained in 2010–2011 with seasonal hand-weeding and fall/winter mowing. They were surveyed throughout the pollinator flight season at monthly intervals from April to September 2010 and 2011. During each sample, pollinators were netted at flowers during two 10-minute periods per plot and the specimens segregated according to the plant species they were visiting. Net collections were made on days with clear skies, temperatures above 16°C, and wind speed lower than 3.5 m/seconds averaged over 2 minutes.

Data Analysis

Mix-and-Rate Plots. The effects of seeding mix and relative seeding rate on each site's first spring germination counts and cover were examined with a mixed-model analysis of variance (ANOVA) using site as a random factor and mix, relative rate, and rate × mix as fixed factors. We then used a repeated measures multiple analysis of variance (MANOVA) time series analysis to examine the combined effect of mix and relative seeding rate on cover across 2 to 3 years. With repeated measures, site was included as a covariate, as was rate × mix. We ran these analyses for percent cover and floral resources of individual species and for whole mixes (aggregate values), each with separate MANOVAs, reporting Pillai's trace values (DasGupta 2005) for significant interactions between season and other independent variables. Floral resources were calculated by multiplying the corolla area (Hickman 1993) by the number of recorded flowers, providing an approximation of floral reward available to pollinators. Before analysis, germination counts (number of individual plants) and percent cover were log-transformed using the equation $\ln(Y + \varepsilon)$, with ε being a small, positive constant of 0.1.

To calculate cost-effectiveness, the cost per realized cover was calculated using either the species-specific seed costs divided by the percent cover of that species ($/cover) or for aggregate costs, the mix cost divided by the aggregate cover of that mix. Cost per cover values were log-transformed as above. We again used time series analysis to compare the effect of mix-and-rate on cost per cover over 2 and 3 years.

Pollinator Plots. To examine the ability of different target plant species to attract pollinators, we tested differences in mean per plot cumulative richness and abundance of visitors among target species and years using two-way ANOVA followed by pairwise comparisons among species (Tukey honestly significant difference [HSD]). The species by year interaction was not significant, so among-species comparisons were based on data pooled among years.

Results

Mix-and-Rate Plots

In the first spring, aggregate seedling counts were significantly positively correlated with percent cover ($df = 53$, $F = 313.09$, $p < 0.0001$, $R^2 = 0.86$). In each of the five surveys over the 3 years of data, aggregate cover strongly positively correlated with aggregate floral resources (all $p < 0.0001$). Site was always a significant factor in the repeated measures MANOVA, and there were often significant interactions between site and season. However, there were no significant interactions between mix and relative rate for any aggregate-level pattern or for the vast majority of individual species patterns. Therefore, we examined the main effects of mix and relative rate separately.

First Year Establishment in Mix-and-Rate Plots

Relative seeding rate ($p < 0.0001$) but not mixture significant affected the aggregate number of seedlings (Fig. 1a). Both relative rate and mix significantly affected aggregate aerial cover ($F = 7.04$, $p = 0.002$ and $F = 7.09$, $p = 0.002$, respectively; Fig. 1b).

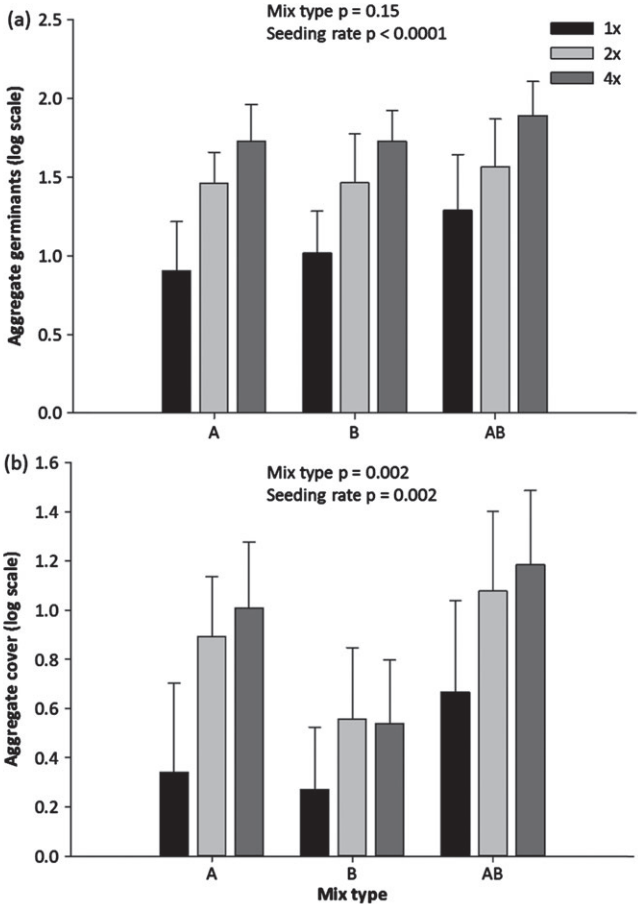

Figure 1. Effect of mix type and relative seeding rate on (a) aggregate number of germinant forbs and (b) aggregate forb cover in the first spring after planting. Each mix-and-rate combination is shown here with respective error bars for a more in-depth look at trends but analysis was conducted on mix-and-rate as separate independent factors in mixed ANOVA.

The effect of relative seeding rate and mix on number of germinants varied among individual species. For some species, neither factor significantly affected the number of germinants (Appendix S3A). For the aerial cover in the first spring after planting, only four of the nine species were significantly affected by relative seeding rate and/or mix (Appendix S3A).

Multiyear Cover and Floral Resources in Mix-and-Rate Plots

Over multiple seasons, mix type ceased to be as strong a factor as relative seeding rate for cover but both variables significantly affected floral resources. Relative seeding rate significantly affected aggregate species cover ($F = 4.52$, $p = 0.02$; Fig. 2), and season interacted significantly with rate × mix (Pillai's trace $p = 0.04$). Mix B produced significantly lower aggregate floral resources than either Mix A or AB ($F = 10.43$, $p = 0.0003$). Mix types differed in floral resources over the seasons (Pillai's trace $p = 0.005$; Fig. 3a). Relative rates 2× and 4× produced significantly higher floral resources than rate 1× but did not consistently differ from each other ($F = 3.41$, $p = 0.05$) (Fig. 3b). Both mix and seeding rate trends were strongly driven by *Grindelia camporum* (in Mix A and AB), which established quickly and at high density (Appendix S3B).

Mix and relative seeding rate significant affected percent cover and floral resources for only a few species, most often those found in Mix B and AB and those seemed to grow and flower best in Mix B over Mix AB (Appendix S3B). Season affected each species but in different ways. Four species peaked in cover and floral resources during the spring. Later-season bloomers, such as *G. camporum* and *Lotus purshianus*, peaked in cover and floral resources during the summer and fall. Aggregate and species-specific patterns for the third year were similar to those in the second year (Appendix S3C), but statistical analyses were not possible with only two sites. Several species had a marked initial bloom and cover increase in the first year followed by a steady decline in the subsequent 2 years (*Eschscholzia californica*, *Lupinus succulentus*, *Lo. purshianus*, *Trifolium obtusiflorum*, and *T. fucatum*).

Dominant Species and Biodiversity for Mix-and-Rate Plots

All nine species germinated, but only eight persisted for the second year and six species for the third year (Appendix S3D). Richness decreased, most strongly for rate 1× ($F = 4.32$, $p = 0.02$, Fig. 4). During the first spring, *Lu. densiflorus* was dominant in mixes in which it was sown (maximum average cover 16%), but later, *G. camporum* dominated with at least twice the cover of any other species (maximum 38% cover; Appendix S3D). In Mix B, the species with highest relative cover varied until the second fall when *Lu. formosus* became the dominant species (maximum average cover 16%; Appendix S3D). In the first fall, the cover of the two annual *Trifolium* species dropped to zero and afterward reached at most 0.05% average cover.

In the second spring, average native forb cover was at a 3-year peak with an average of 68% coverage across any given plot and site. Other cover consisted of bare ground, weed cover, and/or native grass cover. Mix B nearly always had the lowest native cover whereas Mix AB always had the highest, with 71% in the second spring (Appendix S3D). No one mix-and-rate combination was consistently the best in terms of average native forb cover.

Cost-Effectiveness

Mixes differed significantly in terms of aggregated costs ($F = 12.82$, $p < 0.0001$) after 2 years (Fig. 5) but relative seeding rate did not. The effect of time was also significant ($F = 7.46$, $p = 0.001$) and interacted significantly with seeding rate (Pillai's trace $p = 0.03$). Mixes B and AB were significantly less cost-effective than Mix A (i.e. had the highest cost per cover, \$/%; Fig. 5). By the third year (across the two sites monitored for all 3 years), Mix B was least cost-effective.

The highest seeding rate (relative rate 4×) was the least cost-effective for all individual species except for *G. camporum* (Appendix S3E). Overall, *Lu. formosus* was the least cost-effective species (per cover amount) at three to five times

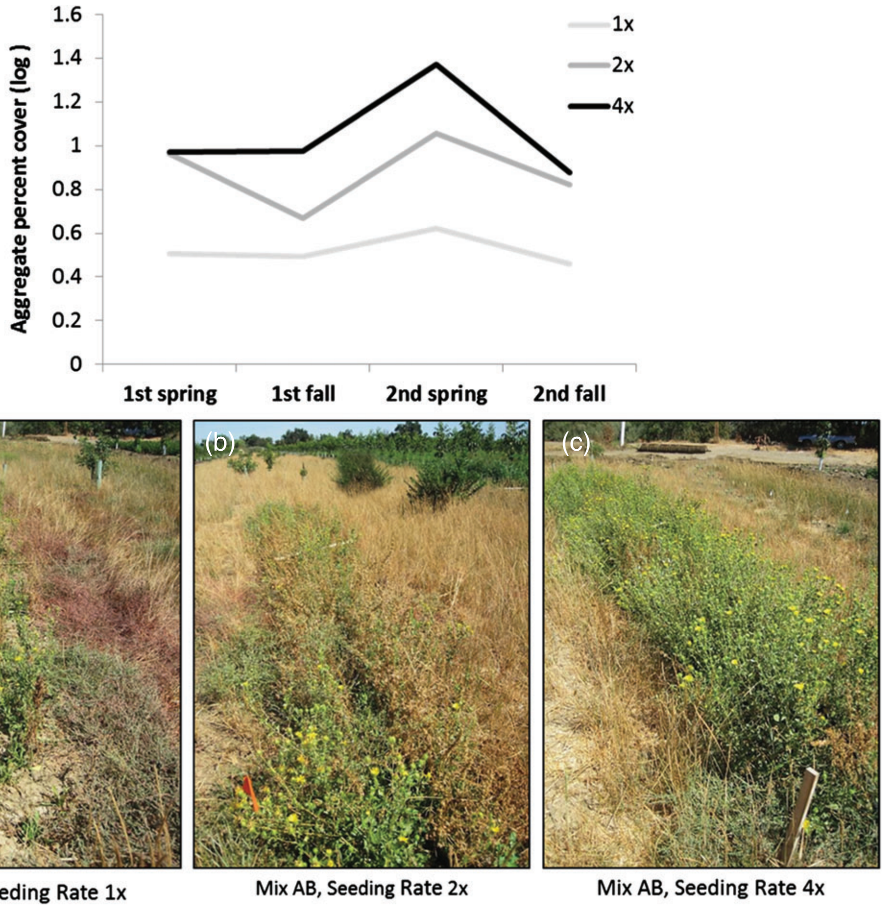

Figure 2. Effect of relative seeding rate ($p = 0.03$) and season ($p = 0.02$) on aggregate percent cover of forb plantings over 2 years (four collection seasons). Photos were taken at one site in the first fall after planting; letters represent statistically significant Tukey HSD groups. Mix type is not shown as it was not a significant factor for multiyear cover.

more than the next tier in cost (Appendix S3E). *Eschscholzia californica*, *Phacelia californica*, and *G. camporum* were the least expensive.

Pollinator Attractiveness in Pollinator Plots

Analysis here focused on the six overlapping species also found in the mix-and-rate plots (*Lu. succulentus*, *Lu. densiflorus*, *E. californica*, *G. camporum*, *Lu. formosus*, and *P. californica*). In the pollinator plots, plant species differed in their ability to attract native pollinators as shown by the average cumulative number of bee species or individuals collected over the whole season per plot from each plant species ($p < 0.01$, Tukey HSD tests) (Fig. 6). Plant species varied in the number of plots per site in which they were sown so averages were calculated per plot to standardize sampling effort. The perennial *G. camporum* attracted significantly more native bee individuals and higher diversity of bee species than other species (Fig. 6). The other forb species that had high germination, cover, and floral resources in mix-and-rate plots (*E. californica*, *P. californica*, and *Lu. formosus*), along with the lower-performing *Lu. densiflorus*, showed medium-high levels of attractiveness to pollinators and did not differ significantly from each other. Establishment for *Lu. succulentus* was too low in the pollinator plots to analyze.

Discussion

Overall, we found that increases in restoration expense and effort produced benefits but did so at diminishing rates. Increasing seeding rate produced strong benefits, but the highest relative rate provided little added benefit compared to the middle rate. Although the mix with the most species often had high germination, cover, and floral resources, it was not as cost-effective as another with roughly half the number of species. These nonlinearities in benefit mean that mix-and-rate combinations must be weighed for trade-offs between germination, cover, diversity, and cost-effectiveness. The "best" seed mix for a given restoration project will depend on that particular project's goals and time horizon (e.g. Burton et al. 2006). For example, the "best" seed mix differs depending on whether the goals were minimal cost and highest cover (Mix A at the rate 2×) or maximum floral diversity (Mix AB at rate 2×). We discuss the broader

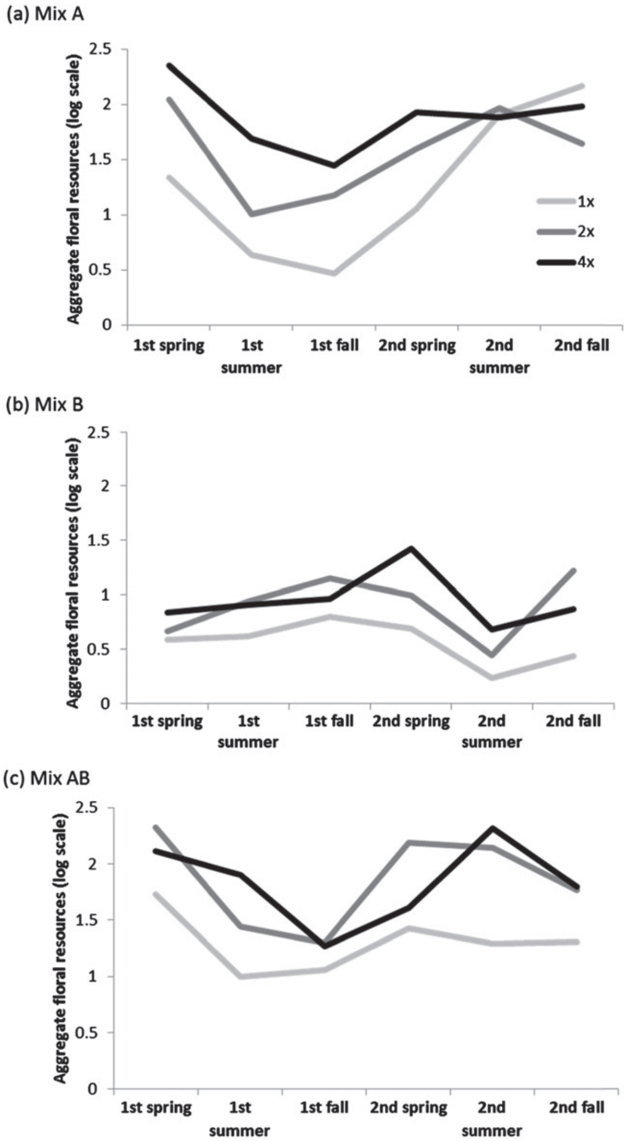

Figure 3. Effect of season ($p = 0.0003$), relative rate ($p = 0.05$), and mix type ($p = 0.0003$) on aggregate floral resources of native forbs, shown separately for (a) Mix A, (b) Mix B, and (c) Mix AB over 2 years (six collection seasons). Rate did not interact with season.

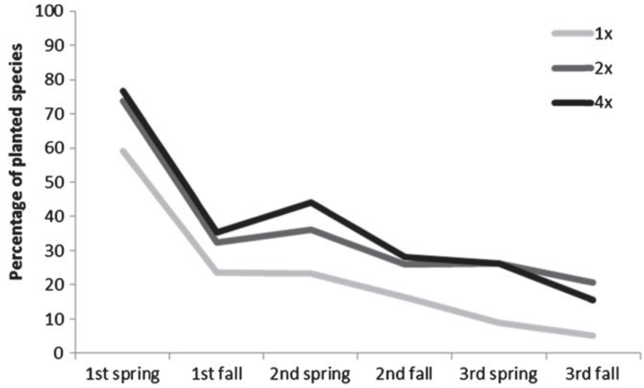

Figure 4. Percentage of planted forb species per mix that persisted (richness divided by number of species per mix) over time ($p < 0.001$) and split out by mix ($p = 0.02$). Statistical analysis was done only for first 2 years but patterns from third year after planting are also included to visualize longer-term patterns.

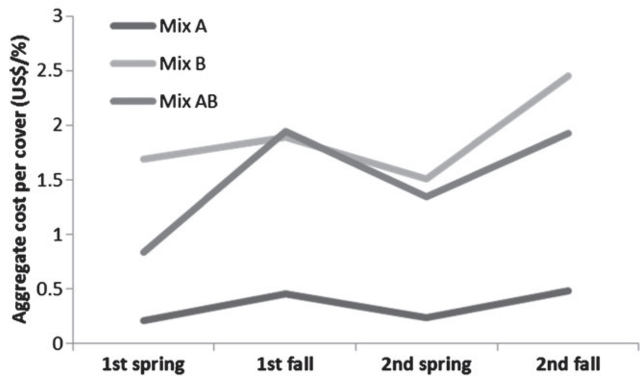

Figure 5. Average aggregate cost-effectiveness (cost per cover) of native forb mixes ($p < 0.0001$) over the first 2 years after planting (four seasons) ($p = 0.001$). There was no interaction with season.

implications of our results below in terms of differing goals and trade-offs for restoration practitioners and agroecologists.

More than mix type, relative seeding rate had a significant impact on establishment, growth, and floral resources. However, there was often little difference between the doubled and quadrupled seeding rates on the dependent variables, resulting in diminished returns. In a native grass and forb seeding study, Burton et al. (2006) found similar results of diminishing returns: lower rates produced greater cover than higher rates that suffered from density-dependent mortality. This phenomenon deserves to be explored further in scientific research as it has strong implications for resource-effective restoration practices. In our study, the 2× relative seeding rate is the best recommendation.

Mix type had more of an impact on cost-effectiveness, and this was likely due to the effect of absolute, rather than relative, seeding rates. Species-rich Mix AB had the highest absolute amount of seed at all relative seeding rates, and its cost-effectiveness was as low as that of Mix B, which consistently produced low cover. Thus, in terms of cost-effectiveness, Mix A is the better overall choice. Restoration practitioners should closely examine how differences in seeding rates impact project cost-effectiveness in addition to plant establishment and growth.

In our study, greater species diversity with lower cover changed to greater cover with lower diversity (Appendix S3D). The trade-off between cover and diversity has implications for both the restoration goal of plant diversity as well as for pollinator attractiveness. Low native species diversity and functional diversity have often been linked to a greater susceptibility to non-native invasion (Levine & D'Antonio 1999; Naeem et al. 2000; Pokorny et al. 2005). A diverse native plant community may likewise be important for supporting pollinator diversity (Carvell et al. 2007; Wratten et al. 2012; Scheper et al. 2013).

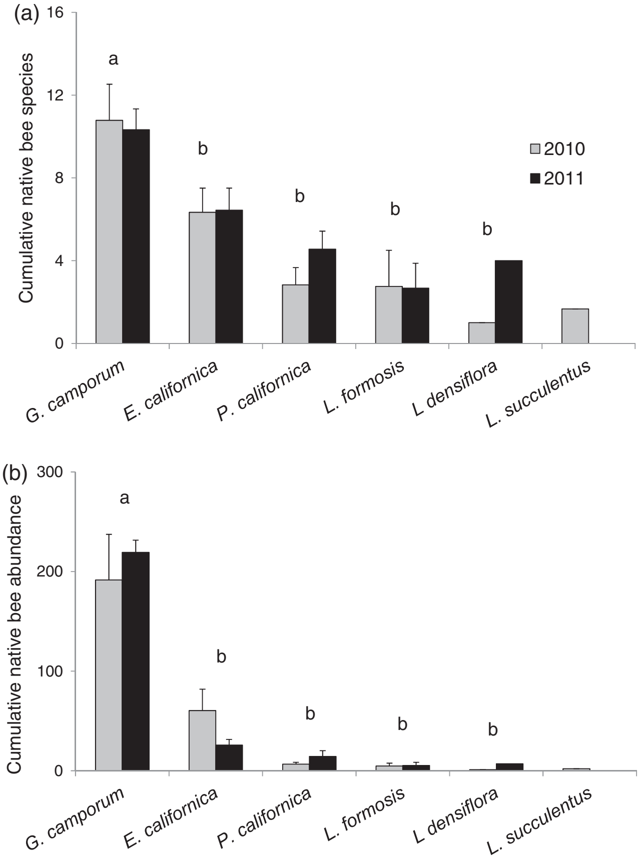

Figure 6. Mean ± standard error of (a) native bee richness and (b) abundance on target native forb species. Data are season-long totals for each plant species within each study plot averaged over the three study sites ($n = 3$ plots per site, three sites). Different letters above the bars indicate species that are significantly different from each other ($p < 0.01$ Tukey HSD, pooled between years). *Lupinus succulentus* was not included in testing because it did not establish successfully.

In our study, a large portion of the increased or sustained forb cover was due to one productive species (*Grindelia camporum*) that flowered the most in summer and fall. To compensate for decreased diversity and to complement the dominant species' flowering phenology (Kremen et al. 2007), mixes might include additional spring-blooming species and the original seeding rate of the dominant species could be decreased.

Weeds play a large factor in the success or failure of most restoration plantings, which is one of the reasons why the goal of high native cover is so common in restoration (Price & Weltzin 2003; Kettenring & Adams 2011). While our experimental forb plots were not designed to test efficacy against invasion, our results nonetheless indicate that seeding with native forbs at higher densities did not prevent weed encroachment (Appendix S2). Future native forb mix design might consider including species that persist in invasive-dominated areas (i.e. remnant forb species) (Lulow & Young 2009).

The longer-term decrease in cover we observed may be acceptable if a project's temporal goals are shorter-term. The impetus for this project was to assess native forb mixes that would provide continuous resources for pollinators only as long as it took for native shrubs to mature and to provide adequate resources (a relatively short-term goal). For forbs to play a more enduring role in the restored landscape, different species mixes, planting techniques, and/or weed control should be examined. We also note here that our results can be applied most appropriately toward small-scale restoration plantings. Our preparation, planting, and weeding techniques would not be feasible for larger-scale plantings.

With increased climate change impacts, understanding and managing pollination services inside and out of agroecological systems becomes increasingly imperative (Dixon 2009). Restoring them, and the important ecosystem services they provide, will require substantial and informed active management, particularly with respect to addition of forb seed. Yet there are also great rewards for these efforts, as forb restoration in agroecological systems can provide multiple ecosystem services beyond pollination services (Wratten et al. 2012). Using the take-home messages above, land managers and agriculturalists can move forward in restoring native forbs and the valuable services they provide.

Implications for Practice

- Higher seeding rates lead to diminishing returns for cover and floral resources.
- Potential trade-off between high cover, floral resources, and biodiversity goals.
- More species per mix may be less cost-effective than a native forb mix with fewer species.
- Seeding with native forbs, even at higher densities, may not relieve weed pressure.
- Clearly identify project goals, e.g. short versus long term goals.

Acknowledgments

We acknowledge the Xerces Society, C. Kremen, and lab from UC Berkeley, and J. Anderson of Hedgerow Farms for their role in instigating and/or supporting the mix-and-rate experiment. Special thanks to the farmers involved in the study, to E. Peffer, J. Stevens, K. Gravuer, J. Balachowski, and S. Sprenkle for manuscript comments and to the Young Lab from 2008 to 2010 for field assistance. Financial support was provided by the Xerces Society, UC Davis Plant Sciences Graduate Fellowship and Madson Scholarships (to M.W.). N. Pope, R. Glaeser, and M. Knoderbane helped collect data for the pollinator plantings supported through a National Fish and Wildlife Foundation grant (to N.W.).

LITERATURE CITED

Baudry, J., R. G. H. Bunce, and F. Burel. 2000. Hedgerows: an international perspective on their origin, function and management. Journal of Environmental Management **60:**7–22.

Bonnieux, F., and P. LeGoffe. 1997. Valuing the benefits of landscape restoration: a case study of the Cotentin in Lower-Normandy, France. Journal of Environmental Management **50:**321–333.

Brodt, S., K. Klonsky, L. Jackson, S. B. Brush, and S. Smukler. 2009. Factors affecting adoption of hedgerows and other biodiversity-enhancing features on farms in California, USA. Agroforestry Systems **76:**195–206.

Burton, C. M., P. J. Burton, R. Hebda, and N. J. Turner. 2006. Determining the optimal sowing density for a mixture of native plants used to revegetate degraded ecosystems. Restoration Ecology **14:**379–390.

Carreck, N. L., and I. H. Williams. 2002. Food for insect pollinators on farmland: insect visits to flowers of annual seed mixtures. Journal of Insect Conservation **6:**13–23.

Carvell, C., W. R. Meek, R. F. Pywell, D. Goulson, and M. Nowakowski. 2007. Comparing the efficacy of agri-environment schemes to enhance bumble bee abundance and diversity on arable field margins. Journal of Applied Ecology **44:**29–40.

DasGupta, S. 2005. Pillai's trace test. Encyclopedia of biostatistics. John Wiley & Sons, DOI: 10.1002/0470011815.b2a13067 (online only).

Dickson, T. L., and W. H. Busby. 2009. Forb species establishment increases with decreased grass seeding density and with increased forb seeding density in a northeast Kansas, USA, experimental prairie restoration. Restoration Ecology **17:**597–605.

Dixon, K. W. 2009. Pollination and restoration. Science **325:**571–573.

Frances, A. L., C. R. Adams, and J. G. Norcini. 2010. Importance of seed and microsite limitation: native wildflower establishment in non-native pasture. Restoration Ecology **18:**944–953.

Gilbert, J. C., D. J. G. Gowing, and R. J. Bullock. 2003. Influence of seed mixture and hydrological regime on the establishment of a diverse grassland sward at a site with high phosphorus availability. Restoration Ecology **11:**424–435.

Hamilton, J. G. 1997. Changing perceptions of pre-European grasslands in California. Madrono **44:**311–333.

Hannon, L. E., and T. D. Sisk. 2009. Hedgerows in an agri-natural landscape: potential habitat value for native bees. Biological Conservation **142:** 2140–2154.

Hickman, J. C., editor. 1993. The Jepson manual: higher plants of California. University of California Press, Berkeley.

Holl, K. D., and R. B. Howarth. 2000. Paying for restoration. Restoration Ecology **8:**260–267.

Kettenring, K. M., and C. R. Adams. 2011. Lessons learned from invasive plant control experiments: a systematic review and meta-analysis. Journal of Applied Ecology **48:**970–979.

Kohler, F., J. Verhulst, R. vanKlink, and D. Kleijn. 2008. At what spatial scale do high-quality habitats enhance the diversity of forbs and pollinators in intensively farmed landscapes? Journal of Applied Ecology **45:**753–762.

Kremen, C., N. M. Williams, M. A. Aizen, B. Gemmill-Herren, G. LeBuhn, R. Minckley, et al. 2007. Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land-use change. Ecology Letters **10:**299–314.

Levine, J. M., and C. M. D'Antonio. 1999. Elton revisited: a review of evidence linking diversity and invasibility. Oikos **87:**15–26.

Lulow, M. E., and T. P. Young. 2009. High native forb richness in Central Valley "Grassland" sites in the Western Sacramento Valley and adjacent foothills. Grasslands **19:**7–11.

Millenium Ecosystem Assessment (MEA). 2003. Ecosystems and human well-being: a report of the Conceptual Framework Working Group of the Millenium Ecosystem Assessment. Island Press, Washington, D.C. (available from http://pdf.wri.org/ecosystems_human_wellbeing.pdf).

Minnich, R. A. 2008. California's fading wildflowers: lost legacy and biological invasions. University of California Press, Berkeley.

Morandin, L., R. F. Long, C. Pease, and C. Kremen. 2011. Hedgerows enhance beneficial insects on farms in California's Central Valley. California Agriculture **65:**197–201.

Naeem, S., J. M. H. Knops, D. Tilman, K. M. Howe, T. Kennedy, and S. Gale. 2000. Plant diversity increases resistance to invasion in the absence of covarying extrinsic factors. Oikos **91:**97–108.

Pokorny, M. L., R. L. Sheley, C. A. Zabinski, R. E. Engel, T. J. Svejcar, and J. J. Borkowski. 2005. Plant functional group diversity as a mechanism for invasion resistance. Restoration Ecology **13:**448–459.

Price, C. A., and J. F. Weltzin. 2003. Managing non-native plant populations through intensive community restoration in Cades Cove, Great Smoky Mountains National Park, USA. Restoration Ecology **11:**351–358.

Pywell, R. F., W. R. Meek, R. G. Loxton, M. Nowakowski, C. Carvell, and B. Woodcock. 2011. Ecological restoration on farmland can drive beneficial functional responses in plant and invertebrate communities. Agriculture, Ecosystems & Environment **140:**62–67.

Ricketts, T. H., J. Regetz, I. Steffan-Dewenter, S. A. Cunningham, C. Kremen, A. Bogdanski, et al. 2008. Landscape effects on crop pollination services: are there general patterns? Ecology Letters **11:**499–515.

Rowe, H. I. 2010. Tricks of the trade: techniques and opinions from 38 experts in tallgrass prairie restoration. Restoration Ecology **18:**253–262.

Scheper, J., A. Holzschuh, M. Kuussaari, S. G. Potts, M. Rundlof, H. G. Smith, and D. Kleijn. 2013. Environmental factors driving the effectiveness of European agri-environmental measures in mitigating pollinator loss - a meta-analysis. Ecology Letters **16:**912–920.

Seabloom, E. W., E. T. Borer, V. L. Boucher, R. S. Burton, K. L. Cottingham, L. Goldwasser, W. K. Gram, B. E. Kendall, and F. Micheli. 2003. Competition, seed limitation, disturbance, and reestablishment of California native annual forbs. Ecological Applications **13:**575–592.

Sheley, R. L., and M. L. Half. 2006. Enhancing native forb establishment and persistence using a rich seed mixture. Restoration Ecology **14:**627–635.

Vaughan, M., M. Shepherd, C. Kremen, and S. H. Black. 2007. Farming for bees: guidelines for providing native bee habitat on farms. 2nd edition. Xerces Society for Invertebrate Conservation, Portland, Oregon.

Walsh, B. 2013. The trouble with beekeeping in the anthropocene. TIME. Time Inc., 9 August 2013. (available from http://science.time.com/2013/08/09/the-trouble-with-beekeeping-in-the-anthropocene/) [accessed on 18 December 2013].

Winfree, R. 2010. The conservation and restoration of wild bees. Pages 169–197 in R. S. Ostfeld and W. H. Schlesinger, editors. Year in ecology and conservation biology 2010. Wiley-Blackwell, Malden, Massachusetts.

Wratten, S. D., M. Gillespie, A. Decourtye, E. Mader, and N. Desneux. 2012. Pollinator habitat enhancement: benefits to other ecosystem services. Agriculture, Ecosystems and Environment **159:**112–122.

Supporting Information

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

Appendix S1. Additional seeding rates and design details.
Appendix S2. Costs of weeds.
Appendix S3. Species-specific results.