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Toward Improving Pollinator Habitat: Reconstructing Prairies with High Forb Diversity

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ABSTRACT

Reconstructed prairies can provide habitat for pollinating insects, an important ecosystem service. To optimize reconstructions for pollinators, goals may include enhancing flowering plant cover and richness and increasing bloom availability early and late in the growing season. Resistance to invasive exotic species must also be a goal in any reconstruction, but it is unclear how increasing forb richness and dominance may affect susceptibility to invasion. We compared planted forb richness and cover, cover of planted grasses, and persistence of exotic species 10 y post-planting of reconstructions with 58 species (extra-high richness), 34 species (high), 20 species (medium), and 10 species (low) planted at the same time in the same fields, and using the same methods and overall seeding rate at Neal Smith National Wildlife Refuge in Iowa, USA. Planted forb richness and cover were higher and planted warm-season, but not cool-season, grass cover was lower in the extra-high richness plots. Mean Coefficient of Conservatism was higher and there was less cover of exotic forbs in the extra-high richness plots. Cover of exotic cool-season grasses was greater in the extra-high richness plots than in the lower-richness plots and this trend was still increasing at the last sample date. Our results are encouraging in that we increased cover of pollinator-friendly habitat, but invasive grasses are a concern as they may reduce forb cover and opportunities for ground-nesting bees in the long term.

Index terms: ecosystem services; flowering plants; pollinator habitat; restoration; tallgrass prairie

INTRODUCTION

Prairie reconstruction, by which native prairie plants are sown on former agricultural fields, or restoration, in which remnant prairies are managed to improve prairie characteristics, are increasingly being regarded as methods by which ecosystem services can be reinstated on degraded or unproductive lands (e.g., Gerla et al. 2012). These methods increase biodiversity directly via the diversity of the planted species as well as indirectly via the support of higher trophic levels by the planted species. While biodiversity is itself valuable, one of the ecosystem services often targeted in reconstructions and restorations in an agricultural matrix is pollination (Pywell et al. 2011; Korpela et al. 2013; Morandin and Kremen 2013; M'Gonigle et al. 2015). Restoration and reconstruction can provide habitat for native pollinators (Tonietto and Larkin 2018) and pollinator diversity and abundance can be similar between remnant and reconstructed prairies (Denning and Foster 2018a). Wild bees and other flower-dependent insects that use reconstructions have been shown to improve crop and native plant fruit set (Garibaldi et al. 2013; Rader et al. 2016; Kaiser-Bunbury et al. 2017), providing strong evidence that this ecosystem service can, in fact, be restored.

The value of prairie reconstruction for pollinators resides primarily in the floral resources provided by the planted species (Roulston and Goodell 2011). Richness and abundance of forbs that mature throughout the growing season and collectively

provide season-long bloom are key to supporting the greatest variety of pollinating insects as well as for reducing opportunities for exotic plant invasion. To achieve this high level of forb diversity, more “conservative” (Freyman et al. 2016) species, i.e., those with occurrences restricted to high-quality native prairie, as well as later successional species, need to be included in seed mixes. This need for high season-long plant richness presents two major challenges to prairie reconstruction. First, practitioners must be able to facilitate the establishment of conservative species in highly disturbed, formerly cultivated soil. Many studies have documented difficulties encountered when planting high-diversity prairie reconstructions (Kindscher and Tieszen 1998; Barak et al. 2017) and the disappointing return on investment in seed (Larson et al. 2018a). Enhancing forb diversity in seed mixes may ultimately and conversely risk reduction in forb cover in the reconstructions if seed mixes contain more seeds of many species with narrow germination and establishment requirements that fail to thrive, and fewer seeds of the robust species that typically make up the majority of the forb component in less diverse mixes. Second, practitioners must reduce the relative abundance of highly competitive warm-season grasses in the seed mix to reduce pressure on the slowly establishing or poorly competitive forbs, with the collateral result of reducing pressure on nonnative and undesirable plant species that would be outcompeted by the grasses if they were more abundant. Prairie grasses can be highly competitive and can reduce

invasion by potentially invasive plants, but also can prevent establishment of desired prairie forb species (Dickson and Busby 2009; Török et al. 2010; Valko et al. 2016). On the other hand, poor establishment of some forbs may be exacerbated by an overly dense seeding that increases competition among planted species (Burton et al. 2006; Wilkerson et al. 2014). If invaders of concern are ecologically similar to the planted forbs, limiting similarity may reduce invasion, although evidence is mixed (e.g., Emery 2007). Despite these challenges, evidence that prairie reconstructions support pollinators and other flower-dependent insects is encouraging (Tonietto and Larkin 2018); the goal now is to reduce uncertainty in outcomes of high forb diversity plantings.

Previous studies of the effects of planting methods (dormant season broadcasted, growing season broadcasted, growing season drilled) on establishment and persistence of the planted species in reconstructed tallgrass prairies have shown that, at 10 y post-planting, variation in timing and method of planting did not influence the resulting planted species cover or presence of invasive species (Larson et al. 2011; Larson et al. 2017), although Applestein et al. (2018) found that planting method affects results in other prairies. These reconstructions (Larson et al. 2011, 2017) used a typical ratio of 50% warm-season grasses, 20% cool-season grasses, 20% perennial forbs, and 10% legumes, but varied richness levels (low, 10 species; medium, 20 species; high, 34 species). Here, we report on additional treatments planted concurrently with these earlier studies (Larson et al. 2017) at the Neal Smith National Wildlife Refuge study sites in Iowa using the same three planting methods, but with a higher (58 species) seed mix richness to achieve the following objectives. First, we wanted to compare effects of planting method on forb cover among seed richness levels, to determine if increasing forb richness interacted with planting methods or season of planting compared to less forb-rich seed mixes. The second objective was to compare planted forb and cool- and warm-season grass cover between the less species-rich plantings and the extra-high forb richness planting (hereafter called “extra-high” plots) to see if the greater proportion of forb seeds and lower proportion of grass seeds planted were reflected in the observed vegetation 10 y after planting. Third, we aimed to determine if observed forb richness was in fact higher in the extra-high plots. Fourth, we compared mean Coefficient of Conservatism (C; Freyman et al. 2016) between less diverse plantings and the extra-high plots to determine if planting more forbs resulted in proportionately greater presence of conservative species 10 y post-planting. Finally, we compared exotic species cover among the four diversity levels to see if extra-high forb richness resulted in greater vulnerability to invasion.

METHODS

Study Sites

This study was conducted on three fields formerly in a corn-soybean cropping rotation on US Fish and Wildlife Service property at Neal Smith National Wildlife Refuge (NWR), Iowa. The refuge was established in 1990 with a vision to reconstruct the ecosystems that occurred there historically, predominantly

tallgrass prairie. Growing-season precipitation (May–September) was variable, but generally below the long-term average during the early establishment period 2006–2009; mean annual temperature near Neal Smith NWR was 10 °C (50 °F) (see figure S1 in Larson et al. [2017]). No effort was made to exclude herbivores. The distance between fields was approximately 1–2 km. Primary soil types and slopes in the three fields were silty clay loam (0–2% slope), silty clay loam (9–14% slope), and loam (14–18% slope), formed from fine-textured loess and glacial till deposits.

Study Design and Data Collection

Planting method and seed mix richness treatments are described in detail in Larson et al. (2011), but a fourth, extra-high seed mix richness was planted for this study. Planting methods ($n = 3$) and seed richness ($n = 4$) were fully crossed in a completely randomized design with replication of 12 in each of three fields with a total of 144 plots per field. Planting methods included dormant- and growing-season broadcasted and growing-season drilled seed applications. These were fully crossed with low-, medium-, high-, and extra-high richness mixes of 10, 20, 34, and 58 species, respectively. Each planting method-by-richness treatment was applied to twelve 12.2×12.2 m “treatment cells” on three fields at Neal Smith NWR. A 2×6 m plot, in which we counted all species present, was placed in the center of each treatment cell, and a 0.25×4 m subplot for cover measurements (see below) was randomly placed within the 2×6 m plots. All the species in the low richness mix were included in the medium richness mix, all the species in the medium richness mix were included in the high richness mix, and all the species in the high richness mix were included in the extra-high richness mix. Each low-, medium-, and high-richness seed mix contained species from four functional groups (“guilds” as defined by Brown [2004]): cool-season grasses (20%), warm-season grasses (50%), legumes (10%), and non-legume perennial forbs (20%); the extra-high seed mix comprised 14% warm-season grasses, 5% cool-season grasses, 68% perennial forbs, and 13% legumes (percentages by seed number). Total number of seeds planted ($430/\text{m}^2$) did not vary among treatments (Table 1). Because we did not randomly assign species to richness levels, tests of effects of richness are not independent of species composition. We planted approximately 430 seeds/ m^2 , regardless of richness of the mix, so the higher richness mixes generally had fewer seeds of each species, although the extra-high mix distributed seeds evenly among species (Table 1). Mean Coefficient of Conservatism (C) of the species planted was 4.7 (low richness), 5.1 (medium), 4.8 (high), and 5.1 (extra-high). Species planted, their C values and functional groups, and the relative density of seeds by species in each mix can be found in Table 1. All fields were mowed (cut vegetation was not removed) once in early summer in 2005 and 2006 for control of annual weeds and were burned prior to green-up in spring 2009 and again in the dormant season prior to the 2015 survey.

We visually estimated plant cover to the nearest 1% of each species (total cover could therefore exceed 100%), once during the period from mid-June through early July in 2005, 2006, 2007, 2010, and 2015 in the 0.25×4 m subplot. Species richness

Table 1.—Planting locations, establishment as of 2015, and seed and seed mix characteristics. Nomenclature follows <http://plants.usda.gov> (accessed 28 September 2018). Species recorded in Low, Medium, and High plots that were not planted there presumably dispersed from plots in which they had been planted.

Planted ^b	Species	C ^c	Establishment (%) ^a				Seeds/oz	Guild ^d	Ratio of seeds in extra-high mix to seeds in other mixes		
			Low	Medium	High	Extra-high			E:Low	E:Medium	E:High
lmhe	<i>Elymus canadensis</i>	3	24.1	13	11.1	21.3	4200	coolgr	0.11	0.11	0.37
lmhe	<i>Dalea purpurea</i>	8	22.2	9.26	9.26	3.7	19,000	legume	0.28	0.85	1.67
lmhe	<i>Helianthus occidentalis</i>	8	0	0.93	0	17.6	14,000	lforb	0.30	0.89	1.78
lmhe	<i>Monarda fistulosa</i>	2	85.2	86.1	76.9	86.1	70,000	mforb	0.30	0.89	1.79
lmhe	<i>Symphotrichum novae-angliae</i>	3	13	8.33	6.48	3.7	66,000	lforb	0.30	0.91	0.91
lmhe	<i>Verbena hastata</i>	3	0.01	0.01	0	0.01	93,000	mforb	0.30	0.91	1.79
lmhe	<i>Andropogon gerardii</i>	4	98.1	94.4	99.1	84.3	10,000	warmgr	0.09	0.12	0.12
lmhe	<i>Bouteloua curtipendula</i>	6	27.8	27.8	18.5	24.1	6000	warmgr	0.18	0.26	0.26
lmhe	<i>Schizachyrium scoparium</i>	5	23.1	10.2	25	18.5	15,000	warmgr	0.18	0.26	0.26
lmhe	<i>Sorghastrum nutans</i>	4	89.8	88	88	92.6	12,000	warmgr	0.18	0.26	0.26
mhe	<i>Dalea candida</i>	10	3.7	13.9	22.2	3.7	18,000	legume		0.94	1.91
mhe	<i>Lespedeza capitata</i>	3	33.3	73.1	69.4	39.8	8000	legume		0.26	0.26
mhe	<i>Artemisia ludoviciana</i>	2	0	18.5	5.56	0	250,000	lforb		0.89	1.78
mhe	<i>Coreopsis palmata</i>	7	0	2.78	1.85	0	10,000	mforb		0.89	1.78
mhe	<i>Heliopsis helianthoides</i>	4	16.7	71.3	77.8	49.1	6300	mforb		0.89	1.79
mhe	<i>Potentilla arguta</i>	8	0.93	11.1	8.33	3.7	230,000	mforb		0.90	2.11
mhe	<i>Solidago rigida</i>	4	40.7	57.4	35.2	40.7	41,000	lforb		0.91	1.77
mhe	<i>Zizia aurea</i>	6	28.7	87	91.7	83.3	11,000	eforb		1.78	1.78
mhe	<i>Panicum virgatum</i>	5	13	13	14.8	10.2	14,000	warmgr		0.26	0.26
mhe	<i>Sporobolus asper</i>	3	0.93	0	0.93	0	30,000	warmgr		0.26	0.26
he	<i>Elymus virginicus</i>	5	0	0	0.93	0	5200	coolgr			3.82
he	<i>Asclepias verticillata</i>	0	7.41	2.78	60.2	38	11,000	mforb			1.78
he	<i>Echinacea pallida</i>	7	9.26	3.7	73.1	57.4	5200	mforb			1.78
he	<i>Liatis aspera</i>	8	0	0	0.93	0	12,000	lforb			2.38
he	<i>Phlox pilosa</i>	7	1.85	0.93	9.26	6.48	19,000	eforb			1.80
he	<i>Pycnanthemum virginianum</i>	4	3.7	0	6.48	13	220,000	mforb			2.11
he	<i>Ratibida pinnata</i>	4	88	81.5	89.8	88	30,000	mforb			1.77
he	<i>Rudbeckia hirta</i>	2	47.2	30.6	63.9	65.7	92,000	mforb			1.86
he	<i>Symphotrichum ericoides</i>	3	3.7	3.7	1.85	0.93	200,000	lforb			1.75
he	<i>Symphotrichum laeve</i>	7	0	0.93	0	0	55,000	lforb			1.79
he	<i>Tradescantia ohioensis</i>	4	10.2	6.48	77.8	70.4	8000	eforb			1.79
he	<i>Vernonia fasciculata</i>	1	0.93	0	7.41	7.41	24,000	mforb			1.78
e	<i>Stipa spartea</i>	6	0	0	0	0.93	680	coolgr			
e	<i>Amorpha canescens</i>	8	0	0	0	0	16,000	legume			
e	<i>Astragalus canadensis</i>	4	0	0	0	2.78	17,000	legume			
e	<i>Baptisia alba</i>	6	0.93	2.78	3.7	57.4	1700	legume			
e	<i>Chamaecrista fasciculata</i>	1	84.3	74.1	72.2	83.3	2700	legume			
e	<i>Desmodium canadense</i>	6	13	14.8	12	34.3	5500	legume			
e	<i>Anemone cylindrica</i>	7	0.93	0	4.63	2.78	26,000	mforb			
e	<i>Asclepias tuberosa</i>	6	4.63	2.78	4.63	47.2	4300	mforb			
e	<i>Coreopsis tripteris</i>	4	0	4.63	4.63	13	14,000	lforb			
e	<i>Delphinium carolinianum</i>	7	1.85	0	0	7.41	60,000	mforb			
e	<i>Eryngium yuccifolium</i>	8	0	0	0	6.48	7500	mforb			
e	<i>Gentiana alba</i>	4	1.85	3.7	5.56	5.56	140,000	lforb			
e	<i>Helenium autumnale</i>	4	0	0	0	0	130,000	lforb			
e	<i>Heuchera richardsonii</i>	8	0	0	0	0.93	700,000	eforb			
e	<i>Liatis pycnostachya</i>	6	0	0	0.93	0.93	16,000	mforb			
e	<i>Parthenium integrifolium</i>	9	1.85	3.7	0.93	63	7000	mforb			
e	<i>Penstemon digitalis</i>	4	0	0.93	0	7.41	130,000	eforb			
e	<i>Ruellia humilis</i>	3	0.93	2.78	0.93	19.4	5200	mforb			
e	<i>Solidago speciosa</i>	7	0	0	0	0	95,000	lforb			
e	<i>Symphotrichum oolentangiense</i>	7	0	0	0	0	80,000	lforb			
e	<i>Thalictrum dasycarpum</i>	4	0	0	0	35.2	11,000	eforb			
e	<i>Tradescantia bracteata</i>	4	0	0	0	0	10,000	eforb			
e	<i>Veronicastrum virginicum</i>	5	0	0	0	0	800,000	mforb			
e	<i>Viola pedatifida</i>	8	0	0	0.93	0	28,000	eforb			
e	<i>Sporobolus heterolepis</i>	9	0	0	0	0	16,000	warmgr			
e	<i>Tridens flavus</i>	0	0	0	0	0	26,000	warmgr			

^a Establishment is expressed as a percentage of the total plots (summed across all three study sites) planted to the diversity level noted in the column head.

^b l = low richness plots; m = medium richness plots; h = high richness plots; e = extra-high richness plots.

^c Coefficient of Conservatism.

^d Functional group: coolgr = cool-season grass; forb = perennial forb (e = early-blooming, m = mid-season blooming, l = late-season blooming); legume = leguminous forb or shrub (all bloom mid-season except late-blooming *L. capitata*); warmgr = warm-season grass.

was evaluated in the 2×6 m plot by counting all species encountered in the plot in 2007, 2010, and 2015. In this paper, we primarily focus on the results of the 2015 surveys, 10 y after planting, except for evaluation of change over time in forbs and selected exotic species (see below). We used the C values from the Iowa database in the online Universal Floristic Quality Assessment Calculator (<https://universalfqa.org/about>, accessed 24 September 2018) to calculate mean C. The data used in the analyses are available in Drobney et al. (2020).

Statistical Analysis

We used generalized linear mixed models (Proc GLMM in SAS 9.4; SAS Institute Inc. 2015) to evaluate the role of planting method, seed mix richness, and their interaction on cover of forbs, cool-season, and warm-season grasses, forb richness, total exotic cover, and mean C. These factors were also evaluated for cover of forbs and particular noxious or problematic exotic species, but with year as a repeated measure to examine change over time. The analysis was a randomized block design; each field was a random block and plots were subsamples nested within each field, planting method, and seed mix richness. Means within significant treatment effects were separated with Fisher's Least Significant Difference (Milliken and Johnson 2002). Cover was expressed as a proportion of total live cover to standardize effects of growing conditions that varied by year. We assumed a beta distribution for proportion response data, normal for all other response variables. To better characterize individual species' responses, the proportion of plots in which each species was planted and established and the proportion of plots in which each species was not planted but to which it spread, were also calculated (Table 1).

RESULTS

By 2015, eight of the species planted only in the extra-high plots (i.e., they could not have dispersed from other plots) were not observed (one legume, six forbs, and one warm-season grass; Table 1). Six additional species that were planted in extra-high treatments, as well as other richness treatments, did not occur in extra-high plots but did occur in other plots (one cool-season grass, four forbs, and one warm-season grass; Table 1). Overall, low-richness plots accumulated 35 species (26 of which dispersed from other plots), medium-richness plots 36 species (17 from high- and extra-high plots), high-richness plots 40 species (11 from extra-high plots), and extra-high plots 43 species, as measured 10 y post-planting. The observed forb species, including those that dispersed from other plots, have collective flowering phenologies that span the April–October growing season in all plots, regardless of planted richness (Figure S1).

Planted Species

Cover of forbs as a proportion of total live cover in the extra-high plots increased from 0.0015 ± 0.0019 in 2005 to 0.27 ± 0.041 (least square mean \pm SE) in 2015 and did not differ among planting methods ($F_{2, 4} = 3.20$, $P = 0.1479$) in 2015. Increases in forb cover over time were seen in the other

seed mix richness plots, but differences among planting methods persisted into 2015 for these lower richness plots (see figure S2b in Larson et al. 2017). Forb cover was similar in high- and extra-high richness plots, but lower on medium-richness and lower still on low-richness plots (Figure 1b). There was an interaction between planting method and year ($F_{8, 96} = 2.5$, $P = 0.0165$; Figure 1a) such that extra-high forb cover was higher in the dormant-season broadcasted plots in 2005–2007, but all planting methods produced similar forb cover thereafter. By 2015, forb cover varied among seed mix richness ($F_{3, 22} = 45.4$, $P < 0.0001$; Figure 1b) but not among planting methods ($F_{2, 22} = 0.06$, $P = 0.9381$) and there was no interaction between seed mix richness and planting method ($F_{6, 22} = 0.65$, $P = 0.6927$). Cover of warm-season grasses in 2015 was substantially lower in the extra-high plots than in the lower richness plots ($F_{3, 22} = 13.77$, $P < 0.0001$; Figure 2a). Warm-season grass cover also varied with planting method, with higher cover in the growing-season drilled than dormant-broadcasted plots ($F_{2, 22} = 3.82$, $P = 0.0377$; Figure 2b) but no interaction between method and seed mix richness ($F_{6, 22} = 0.36$, $P = 0.899$). Ten years after planting, presence of planted cool-season grasses at our study fields was negligible (mean cover as a proportion of total live cover = 0.0027 ± 0.01) and did not vary among seed mix richness ($F_{3, 22} = 1.27$, $P = 0.31$) or planting method ($F_{2, 22} = 0.29$, $P = 0.2711$). Observed forb richness in 2015 increased with seed mix richness ($F_{3, 22} = 291.58$, $P < 0.0001$; Figure 3) but was unaffected by planting method ($F_{2, 22} = 0.5$, $P = 0.6126$) and the two factors did not interact ($F_{6, 22} = 0.87$, $P = 0.5289$).

Although mean C was the same in medium and extra-high seed mixes, established species in extra-high plots had 20% higher mean C than did established species in the medium richness plots ($F_{3, 22} = 37.81$, $P < 0.0001$; Figure 4a). Mean C varied slightly with planting method ($F_{2, 22} = 4.06$, $P = 0.0317$, Figure 4b) but there was no interaction between seed mix richness and planting method ($F_{6, 22} = 1.31$, $P = 0.2959$).

Exotic Species

No differences in exotic cover were found among seed mix richness levels ($F_{3, 22} = 1.78$, $P = 0.1794$) but growing-season drilled plots had marginally less cover of exotics than did dormant-season broadcasted plots ($F_{2, 22} = 3.3$, $P = 0.0559$; Figure 5); there was no interaction between the two factors ($F_{6, 22} = 1.13$, $P = 0.3774$). With respect to the most troublesome exotic species, it was the cool-season invasive grasses, *Bromus inermis* and *Poa pratensis*, that continued to increase in cover over the duration of the study, most notably in the extra-high plots (Table 2, Figure 6). Interestingly, *P. pratensis* cover on the growing-season drilled plots was only about half that on the broadcasted plots (0.84 ± 0.37 , 1.66 ± 0.37 , and 1.65 ± 0.37 , mean \pm SE, proportion of total live cover for growing-season drilled, dormant-season broadcasted, and growing-season broadcasted, respectively) in 2015. The invasive forbs, *Cirsium arvense*, *Daucus carota*, *Carduus nutans*, and *Rumex crispus*, had largely disappeared from the extra-high plots by the end of the study (Figure 6).

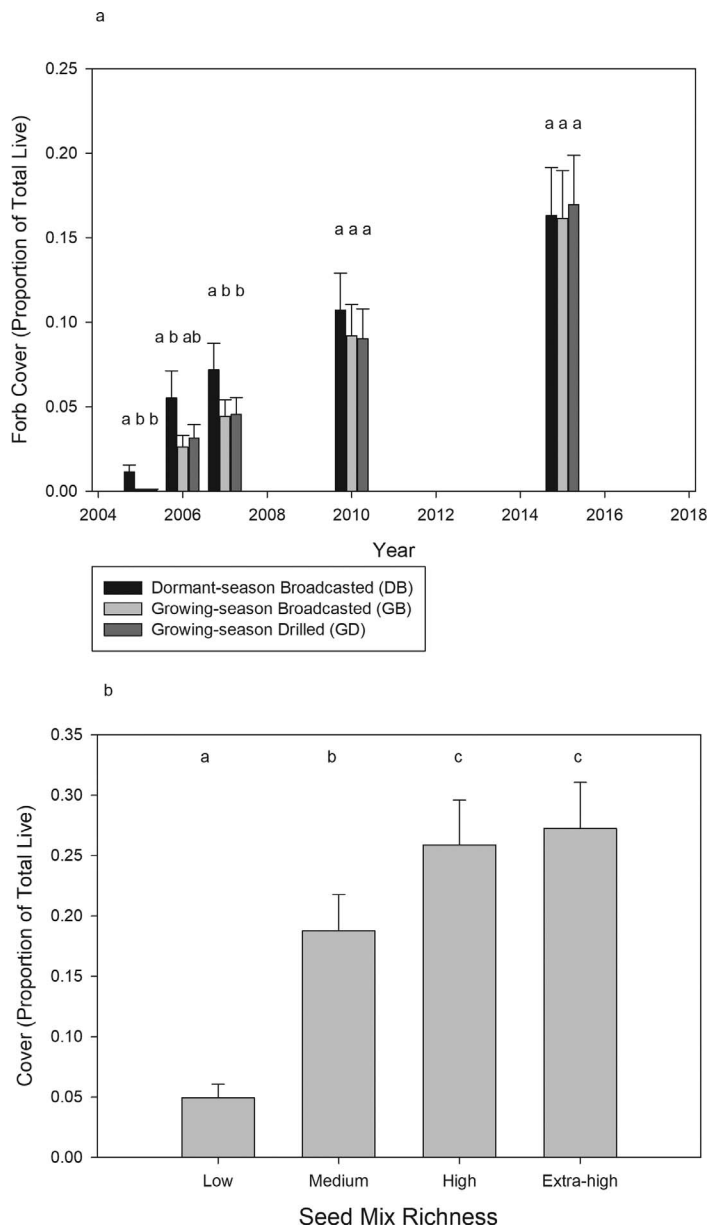


Figure 1.—Forb cover by sowing method and time, and by richness levels. (a) Cover of forb species as a proportion of total live cover over time in plots planted with one of three planting methods: dormant-season broadcasted (DB), growing-season broadcasted (GB), and growing-season drilled (GD). Shown are means plus standard errors. Bars with the same letters within a year do not differ. (b) Cover of planted perennial forbs as a proportion of total live cover 10 y after planting on plots with low (10 species), medium (20 species), high (34 species), and extra-high (58 species) seed mixes. Shown are least square means plus 1 standard error. Means of bars with the same letter do not differ significantly.

DISCUSSION

Our goal in this study was to compare prairie reconstruction outcomes (e.g., cover and richness of forbs, mean C, and exotic invasion) of an extra-high (58 species) seed mix with outcomes of lower richness mixes. We found no evidence that extra-high

forb richness responded differently to planting methods compared with lower richness seed mixes. By 2015 all three planting methods produced similar cover of forbs in the extra-high richness plots as was observed previously in the lower richness plots (Larson et al. 2017). That said, forb cover was slightly higher at earlier sample dates in the dormant-season broadcasted plots, suggesting that this technique can result in more pollinator-supporting habitat sooner after planting than the growing-season planting methods we tested. Planted forbs had somewhat higher cover than warm-season grasses (27.25% forbs vs. 21% warm-season grasses) in the established vegetation 10 y after planting in the extra-high plots. This result suggests that despite their competitive advantage, warm-season grasses do not usurp resources quickly enough to thwart some of the forbs that establish more slowly, at least if their seed density is less than about one-quarter that of forbs. Forb richness was also higher in the extra-high plots than in the lower-richness plots in 2015. Higher planted forb richness along with higher mean C in extra-high than other plots indicate that some of the more conservative species were better able to establish in the extra-high plots. Together, these results suggest that planting a diverse mix of variously conservative species simultaneously can be a successful strategy to increasing forb richness. The biological significance of the modest increase in mean C that we observed can only be determined in the context of the goals for the reconstruction. Nonetheless, there is value in taking a long view when assessing the success or failure of a planting. As observed by Spyreas et al. (2012) for old fields in New Jersey that were naturally revegetating, mean C followed a predictable, increasing pattern over time, similar to that seen in the extra-high plots. That mean C was higher in the extra-high plots suggests the value of redundancy: despite failure of some species to establish and/or persist to 2015, others were present to take their place.

Competitive grasses are often implicated in low establishment of subordinate taxa, including most forbs, in prairie restorations and reconstructions (Howe 1999; McLachlan and Knispel 2005; McCain et al. 2010). For example, when Klopff et al. (2014) varied native grass dominance from 20% to 97%, the highest forb diversity was found in the two lowest planted grass dominance categories. Although we cannot show cause-and-effect with our study design, the extra-high plots, where fewer warm-season grass seeds were planted, and where grasses were seeded at the same rate per species as the forbs, supported greater forb cover. We note that because number of seeds planted per species was confounded with richness of the seed mix in our study, we cannot formally test for effects of seed number per species.

Although cover of certain exotic species we tracked was higher in the extra-high than the lower richness plots soon after planting, by the 10th year seed mix richness did not influence total exotic cover. Total exotic cover alone does not tell the whole story, however. Although invasive forbs had declined as the extra-high plantings matured, the two most problematic exotic grasses, *Poa pratensis* and *Bromus inermis*, continued to increase, and at rates higher than those observed in the lower-richness plots. The lower density of strongly competitive grasses and/or the lack of established cool-season grasses may have allowed expansion of cool-season exotic

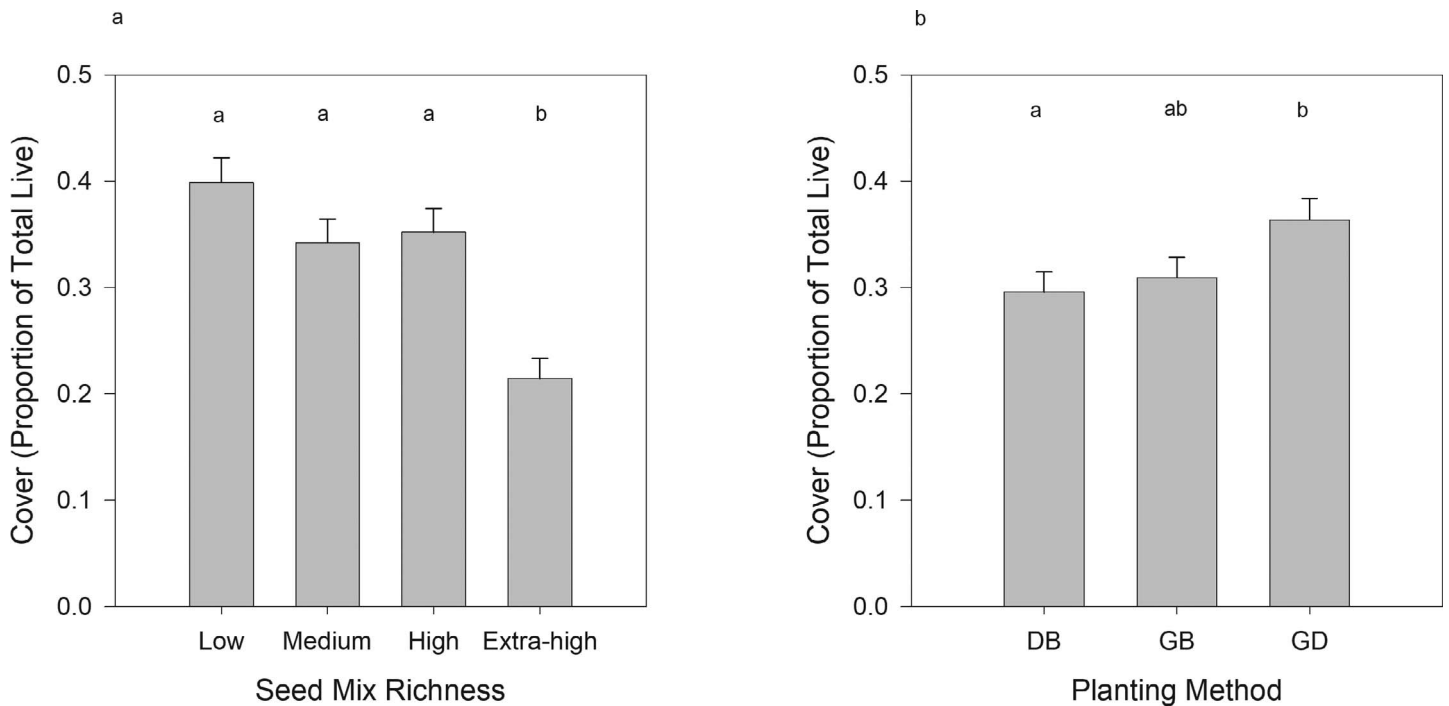


Figure 2.—Cover of planted warm-season grasses as a proportion of total live cover 10 y after planting on (a) plots with low (10 species), medium (20 species), high (34 species), and extra-high (58 species) seed mixes; and (b) on plots planted by dormant-season broadcasted (DB), growing-season broadcasted (GB), and growing-season drilled (GD). Shown are least square means plus 1 standard error. Means of bars with the same letter do not differ significantly.

grasses (Symstad 2000). Canada wild rye (*Elymus canadensis*) was the primary planted cool-season grass species that successfully established, however, and it is particularly sensitive to burning and declined precipitously after the 2009 prescribed fire (Larson et al. 2017). Although unrelated to seed mix richness, the growing season drilled method had slightly less cover of *P. pratensis* than did the other two methods. By

2015 cover of warm-season grasses in the drilled plots had surpassed that in the broadcasted plots, a response others have observed (Ambrose and Wilson 2003; Larson et al. 2011), and may, over time, suppress *P. pratensis*.

A central question, which we address only indirectly, is whether the additional forbs in the extra-high richness plots support more pollinators than lower-richness plots. Several lines of evidence suggest that they can. Season-long bloom is an important consideration (Blaauw and Isaacs 2014), and not only did our extra-high plots achieve this, but dispersal of both early- and late-season forbs into other plots resulted in a forb composition capable of season-long bloom throughout the plots. Floristic Quality Assessment score explained 31% of the variation in butterfly abundance across a diverse group of grassland reconstructions in Ohio (Peters et al. 2016). The increase we document in mean C in higher-richness plots suggests these also may improve habitat for butterflies and other pollinating insects. Denning and Foster (2018b) observed a correlation between forb and bee diversity on their tallgrass prairie study sites, so the greater forb richness we observed in our extra-high plots may prove attractive to bees, which are arguably among the most important pollinating insects (Larson et al. 2018b). Adding forb species was effective in our study, in that these species established, persisted, and even dispersed to other plots during the 10 y since planting. Grygiel et al. (2014) similarly found that forbs could disperse to adjacent disturbed areas from central planting locations, suggesting that with patience, forb richness can increase across a site via seed dispersal and improve pollinator habitat at the same time.

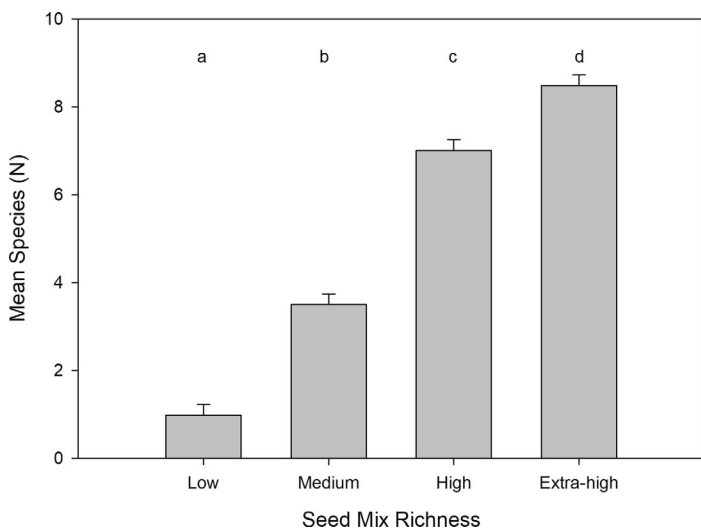


Figure 3.—Richness of planted perennial forbs 10 y after planting on plots with low (10 species), medium (20 species), high (34 species), and extra-high (58 species) seed mixes. Shown are least square means plus their standard errors. Means of bars with the same letter do not differ significantly.

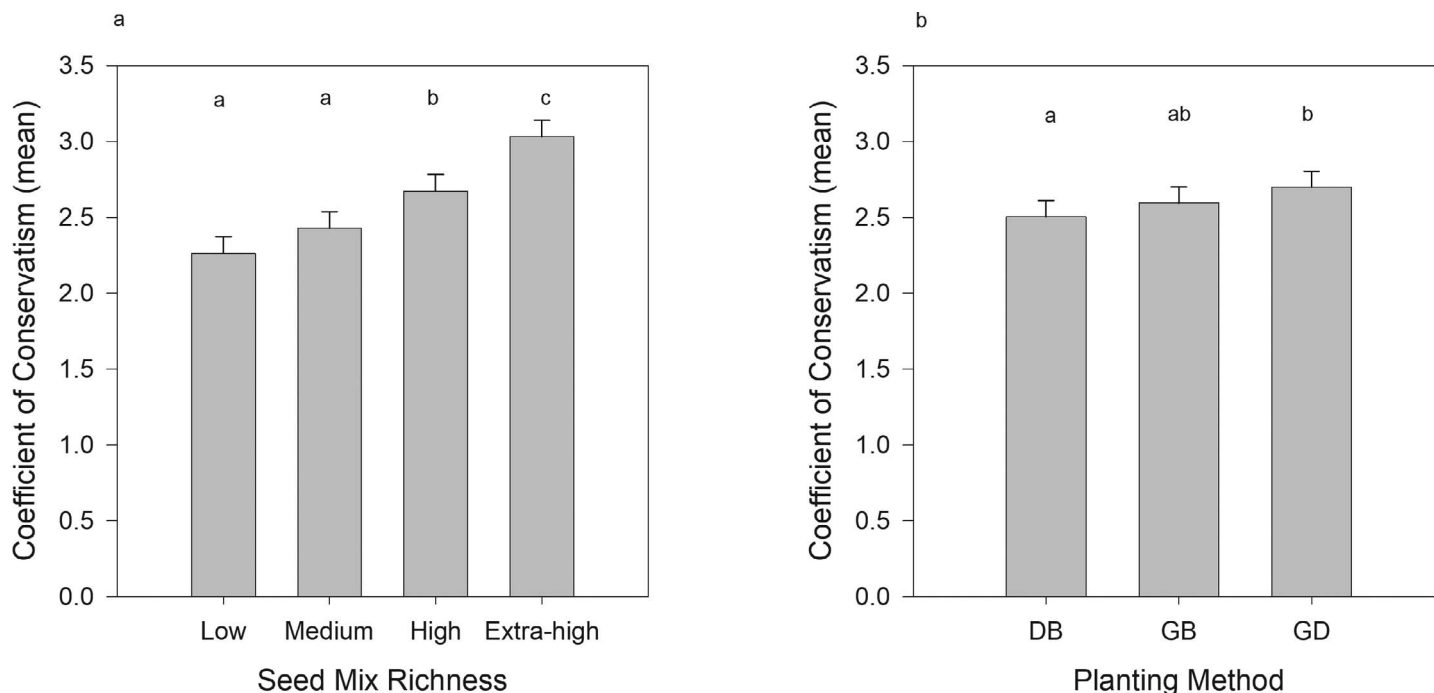


Figure 4.—Mean Coefficient of Conservatism 10 y after planting on (a) plots with low (10 species), medium (20 species), high (34 species), and extra-high (58 species) seed mixes; and (b) on plots planted by dormant-season broadcasted (DB), growing-season broadcasted (GB), and growing-season drilled (GD). Shown are least square means plus 1 standard error. Means of bars with the same letter do not differ significantly.

In conclusion, we urge restoration practitioners and land stewards to carefully evaluate their objectives when planning a forb-rich planting to support pollinators. It is not necessary to adopt a particular planting method when using a seed mix high in forbs; after 10 y, species richness was similar regardless of the planting method. Nonetheless, we observed a slight tradeoff between earlier establishment of forbs in the dormant

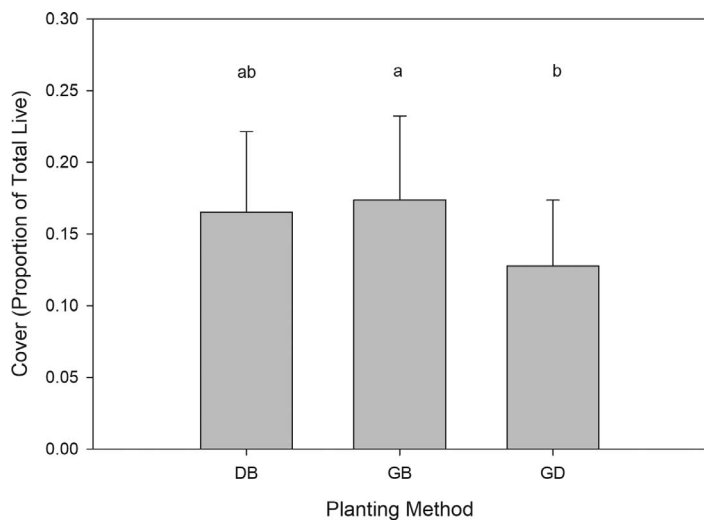


Figure 5.—Cover of exotic species as a proportion of total live cover on plots planted by dormant-season broadcast (DB), growing-season broadcast (GB), and growing-season drill (GD). Shown are least square means plus 1 standard error. Means of bars with the same letter do not differ significantly.

broadcasted planting method vs. somewhat greater establishment of warm-season grasses in the growing season drilled planting method, which also had slightly less cover of the exotic grass *P. pratensis* (but not of *B. inermis*). Unlike exotic forbs, these two cool-season grasses were still increasing as of the 10 y survey and may put the entire restoration in jeopardy in the long term. However, the degree that cool-season exotic species threaten plantings also may be influenced by burn frequency and timing (Willson and Stubbendieck 1997), which were held constant in this study. Ecological restoration must increasingly serve many functions (Guo et al. 2018); reducing invasion by exotic species must be part of plans to enhance pollinator habitat. Our results are but a first step toward developing methods for resilient and diverse prairie reconstructions.

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Table 2.—Results of statistical tests for individual invasive or problematic species at Neal Smith National Wildlife Refuge, Iowa. Method refers to planting method/season (dormant-season broadcasted, growing-season broadcasted, growing season drilled); diversity is the richness level of the seed mix (low, medium, high, extra-high); year is the year in which sampling occurred (2005–2007, 2010, and 2015).

Variable	Type III tests of fixed effects				
	Effect	Num DF	Den DF	F	Pr > F
Cover of <i>Cirsium arvense</i>	Year	4	96	6.67	<0.0001
	Method	2	22	0.72	0.4978
	Diversity	3	22	0.27	0.8445
	Method*Year	8	96	0.84	0.5683
	Diversity*Year	12	96	0.64	0.8075
	Method*Diversity	6	22	0.97	0.4693
	Method*Diversity*Year	24	96	0.66	0.8815
Cover of <i>Bromus inermis</i>	Effect	Num DF	Den DF	F	Pr > F
	Year	4	96	16.71	<0.0001
	Method	2	22	0.42	0.6633
	Diversity	3	22	3.83	0.024
	Method*Year	8	96	0.34	0.9482
	Diversity*Year	12	96	2.98	0.0014
	Method*Diversity	6	22	0.32	0.918
Method*Diversity*Year	24	96	0.6	0.9233	
Cover of <i>Poa pratensis</i>	Effect	Num DF	Den DF	F	Pr > F
	Year	4	96	69.09	<0.0001
	Method	2	22	4.2	0.0284
	Diversity	3	22	4.76	0.0105
	Method*Year	8	96	2.81	0.0076
	Diversity*Year	12	96	4.51	<0.0001
	Method*Diversity	6	22	1.27	0.311
Method*Diversity*Year	24	96	1.17	0.2907	
Cover of <i>Daucus carota</i>	Effect	Num DF	Den DF	F	Pr > F
	Year	4	96	137.12	<0.0001
	Method	2	22	2.89	0.0771
	Diversity	3	22	9.77	0.0003
	Method*Year	8	96	2.69	0.0103
	Diversity*Year	12	96	8.94	<0.0001
	Method*Diversity	6	22	1.07	0.4072
Method*Diversity*Year	24	96	0.98	0.5014	
Cover of <i>Carduus nutans</i>	Effect	Num DF	Den DF	F	Pr > F
	Year	4	96	9.14	<0.0001
	Method	2	22	2.28	0.1263
	Diversity	3	22	2.92	0.0566
	Method*Year	8	96	2.72	0.0095
	Diversity*Year	12	96	2.76	0.0029
	Method*Diversity	6	22	0.71	0.6455
Method*Diversity*Year	24	96	1	0.4787	
Cover of <i>Rumex crispus</i>	Effect	Num DF	Den DF	F	Pr > F
	Year	4	96	2.26	0.068
	Method	2	22	0.65	0.5302
	Diversity	3	22	0.91	0.4499
	Method*Year	8	96	0.86	0.5511
	Diversity*Year	12	96	1.59	0.1079
	Method*Diversity	6	22	0.71	0.6444
Method*Diversity*Year	24	96	1.08	0.3851	

product names is for descriptive purposes only and does not imply endorsement by the US Government.

The findings and conclusions in this article are those of the authors and do not necessarily represent the views of the US Fish and Wildlife Service.

Author contributions: PD and DLL conceived and designed the research; PD planted the reconstructions; KVS managed the reconstructions and supported data collection; JLL supervised data collection; DLL analyzed the data; DLL, PD wrote and JLL, KVS edited the manuscript.

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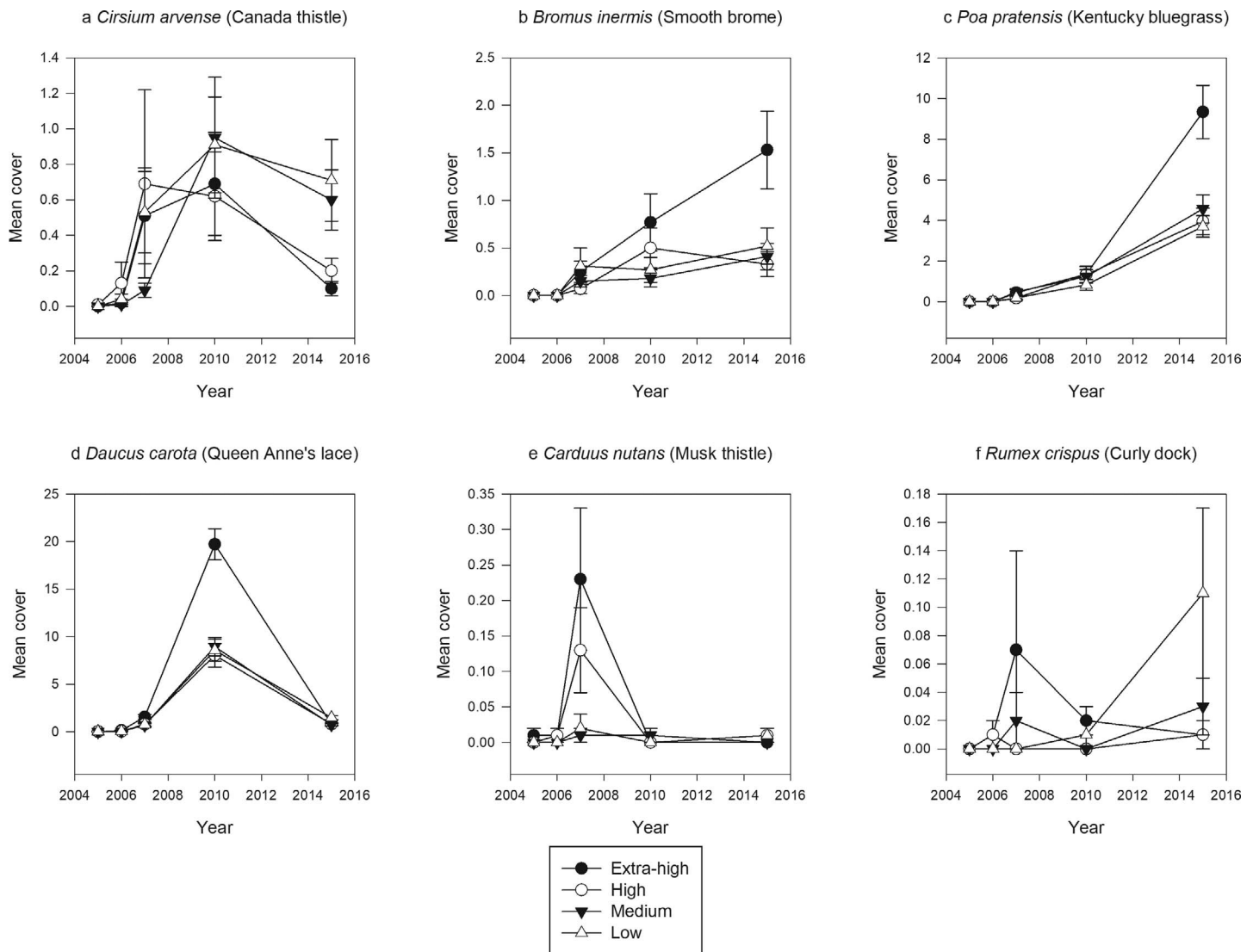


Figure 6.—Mean cover of noxious and troublesome invasive species (a) *Cirsium arvense*, (b) *Bromus inermis*, (c) *Poa pratensis*, (d) *Daucus carota*, (e) *Carduus nutans*, and (f) *Rumex crispus* by year and diversity level. Shown are least square means \pm 1 standard error of the mean.

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