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RESEARCH ARTICLE

Are we close enough? Comparing prairie reconstruction chronosequences to remnants following two site preparation methods in Missouri, U.S.A.

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Prairie reconstruction has become a common method for reestablishing tallgrass prairie communities in the central United States. With the objective of creating plant communities that approximate remnant (reference) prairies, managers are interested in identifying: (1) best methods for reconstructing reference community conditions; (2) the rate of change in plant communities through time following reconstruction; and (3) species present in remnant communities but missing from reconstructed communities. This information is important in the development of adaptive management strategies during active reconstruction. We used a chronosequence approach to assess the success of two reconstruction methods in emulating local, reference remnant prairie plant communities. We compared broadcast dormant seeding following two types of site preparation, agricultural cropping (Crop) or herbicide control in existing grass assemblages (Grass), and remnant communities. The Crop site preparation method resulted in a rapid increase in richness shortly following seeding. Although more similar to remnant assemblages initially, the Grass method took longer for mean coefficient of conservatism and floristic quality index to approach conditions of the reference communities. However, neither method resulted in plant community compositions that converged with the reference through time. Further, indicator species analysis identified a diverse assemblage of species lacking from the reconstructed prairies. These results suggest the need to develop management strategies for establishing the "missing" species during reconstruction and provide further support for protection and conservation of existing remnant prairies.

Key words: nonmetric multidimensional scaling, prairie reconstruction, remnant plant community, restoration success, site preparation

Implications for Practice

- Site preparation can have lasting effects on prairie reconstruction. Long-term site preparation (i.e. multi-year cropping) encouraged more rapid establishment and more diverse prairies than short-term site preparation (i.e. herbicide prior to seeding).
- Although diverse prairies were established through reconstruction, they did not reach the diversity and comparable species composition of nearby reference, remnant prairies. Species missing from the reconstructions may be due to: (1) difficulty collecting seed or (2) poor establishment or persistence following seeding.
- To better emulate remnant prairie communities, improved seed collection and establishment techniques are needed, particularly for native spring blooming, understory, and woody species.
- Vegetation sampling across planted reconstructions and remnant communities provide adaptive management feedback for prairie reconstruction and similar approaches could be adopted elsewhere.

Introduction

The tallgrass prairie is one of the most endangered ecosystems in North America, with over 85% decline across its historic range (Samson et al. 2004; Hoekstra et al. 2005). In Missouri, this decline is even more acute, with less than 1% of the original 6 million ha of tallgrass prairie remaining (Schroeder 1981; Samson & Knopf 1994). As economic forces continue to encourage conversion of prairie to agricultural uses (Lark et al. 2015), the loss of the biodiversity and ecosystem functions that prairies provide will continue. To combat this loss, prairie reconstructions have recently become more common as a management practice in the Midwest (Packard & Mutel 2005; Anderson & Benda 2016; Rothrock et al. 2016).

Prairie restorations (i.e. management to rehabilitate degraded prairie communities that still hold some relict species) and reconstructions (i.e. reestablishment of prairie communities on

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previously converted agricultural lands where prairie species no longer exist) are two land management practices that can be used to mitigate the loss of prairie biodiversity and ecosystem function (Smith et al. 2010). Prairie reconstruction practitioners attempt to emulate reference prairie communities by seeding diverse plant assemblages often collected locally from remnant prairies (Dickson & Busby 2009; Goldblum et al. 2013). Studies evaluating the success of restorations and reconstructions have not always used reference sites as comparative benchmarks (Wortley et al. 2013), despite the International Standards for the Practice of Ecological Restoration recommending to do so (McDonald et al. 2016).

Prior to seeding, site preparation methods are commonly implemented to reduce undesirable plant species (such as non-native [NN] species) or improve the likelihood of establishment success of the seed mixture. Site preparation methods may have a lasting effect on reconstructed plant communities (Millikin et al. 2016). Most prairie reconstruction managers prefer planting on sites that have had existing vegetation removed (Rowe 2010). Removal of existing vegetation can be easily accomplished by using commercial agricultural practices to prepare a site. However, due to a variety of reasons (lack of equipment or nearby producers, nonarable lands, etc.) commercial agricultural practices as a site preparation method may not be feasible in all prairie reconstruction efforts. In these cases, other forms of vegetation control to reduce competition with native remnant plants are used, although practitioners have indicated that these methods may be less effective than cropping (Rowe 2010).

Although prairie reconstructions may never fully support the biodiversity and ecosystem function provided by remnant prairie communities (Polley et al. 2005; Bullock et al. 2011; Barak et al. 2017), they can provide conservation benefits, especially when compared to degraded and NN grassland communities (Rey Benayas et al. 2009; Tonietto et al. 2016; Trowbridge et al. 2016). Studies have shown that increased floristic diversity through prairie reconstruction can result in increased diversity of other taxa (Rowe & Holland 2012; Tonietto et al. 2016; Port & Schottler 2017). With time, reconstructed prairies can approximate the soil characteristics of undisturbed prairies (Rosenzweig et al. 2016). Further, reconstructed prairies can provide resistance against invasion from NN plants (Blumenthal et al. 2005; Foster et al. 2015).

The documented benefits of prairie reconstruction offer promise for conserving tallgrass prairie ecosystems, yet evaluating restoration success has remained a challenge for practitioners, due in part to different perspectives regarding success criteria (Higgs 1997; Zedler 2007; Wortley et al. 2013). Studies commonly use measures of plant diversity or vegetation structure to evaluate success, but few prairie reconstruction projects have quantified the outcomes of different reconstruction methods relative to reference conditions to provide feedback to an adaptive management process (Ruiz-Jaen & Aide 2005; Larson et al. 2018). Explicitly, an adaptive management framework is a two-stage iterative process whereby learning through time influences subsequent management through adaptation (Williams 2011). Based on this approach, it is important to identify (learn) how close the reconstruction approaches approximate remnant community composition and what species are missing to target for future management efforts (adapt). Using a chronosequence approach, we present plant community dynamics through 14 years after reconstruction in comparison to remnant tallgrass prairies in central Missouri. Our objectives are to: (1) describe how plant communities of prairie reconstructions change through time relative to nearby remnant reference communities; (2) compare response patterns for two prairie reconstruction site preparation methods (cropping vs. herbicide control with no cropping); and (3) compare plant community composition between reconstructions and remnant reference communities to identify species or species groups missing from reconstructions.

Methods

Study Sites

Prairie Fork Conservation Area (PFCA) is a 367 ha property located in the southern portion of Missouri's Claypan Till Plains Subsection (Nigh & Schroeder 2002) (Fig. 1) and managed cooperatively between the Missouri Department of Conservation (MDC), Prairie Fork Trust (PFT), and the Missouri Prairie Foundation (MPF). For most of the twentieth century, PFCA had a history of agricultural use that included conversion of most of the area's original natural communities to cropland and NN grasslands. In 2004, MDC, PFT, and MPF started a project with the goal of reconstructing PFCA's pre-European tallgrass prairie. Remnant tallgrass prairies identified as reference communities for the project included Tucker Prairie Natural Area (TPNA) and Marshall Diggs Conservation Area (MDCA), each within 23 km of PFCA (Fig. 1). TPNA is a 59 ha original claypan prairie, with Mexico and Armstrong soil series (Soil Survey Staff 2019), that has never been plowed and represents the largest remaining known tract of intact claypan prairie in this ecological subsection of Missouri. MDCA is a 410 ha area that contains a mix of woodland, savanna, and prairie communities with several small (≤4 ha) scattered claypan prairie remnants comprised of Calwood and Keswick soil series. The remnant prairie at TPNA is generally described as mesic, whereas remnants at MDCA are considered more xeric. PFCA is comprised of both mesic and xeric site types and soil series found at MDCA and TPNA.

Prairie Reconstruction Management

The steps taken for prairie reconstruction at PFCA include: (1) site preparation; (2) seeding native plants collected from reference communities; and (3) mowing and prescribed burning for establishment and maintenance of the reconstructed prairies. Prior to reconstruction activities, Grabner and Grabner (1999) reported that vegetation at PFCA was dominated by undesirable NN and native ruderal species (RD) (top 10 recorded species in order of coverage abundance: *Festuca arundinacea* [Tall fescue] Schreb. [NN], *Solidago altissima* [Tall goldenrod] L. [RD], *Lespedeza cuneata* [Silky bush clover] [Dum. Cours.] G. Don [NN], *Kummerowia stipulacea* [Korean bushclover] [Maxim.] Makino [NN], *Setaria faberi* [Giant foxtail] Herrm., *Desmodium perplexum* [Confusing trefoil] B.G. Schub. [RD],

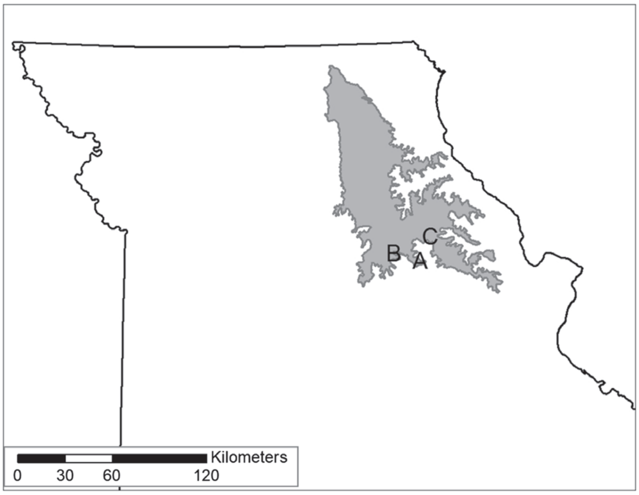

Figure 1. Location of Claypan Till Plains Subsection of Missouri and (A) Prairie Fork Conservation Area, (B) Tucker Prairie Natural Area, and (C) Marshall Diggs Conservation Area.

Trifolium pratense [Red clover] L. [NN], *Ambrosia artemisiifolia* [Common ragweed] L. [RD], *Vernonia baldwinii* [Western ironweed] Torr. [RD], and *Eupatorium altissimum* [Tall boneset] L. [RD]).

For this study, two methods of site preparation for prairie reconstruction were compared (see Table S1 for schedule of all management actions). The first method (referred to as "Crop") consisted of planting and harvesting glyphosate-resistant crops (e.g. soybeans and corn) by privately contracted agricultural producers for ≥3 years prior to seeding prairie species. This method removed most of the established undesirable species from the site, prepared a seed bed for good soil–seed contact, and was generally cost effective because the commercially harvested crops covered the cost of herbicide treatments. The second method (referred to as "Grass") consisted of broadcast broadleaf herbicide (triclopyr) application (June–August) for at least 1–2 years, followed by 2–3 applications of glyphosate (May–June, August–September, and if needed, October–November) in the growing season prior to planting. All herbicide rates followed label directions and applications were determined based on manager assessment of current conditions. The Grass site preparation method also removed residual vegetation and prepared the seed bed for good soil–seed contact but was generally conducted over a shorter time period when compared to the Crop method.

Following both methods of site preparation, all reconstructions were seeded with local ecotype native collections from TPNA, MDCA, other local (within 75 km distance from PFCA) remnant natural communities, and mature reconstruction plantings from PFCA. Seed was harvested throughout the year using a combination of hand and machine (Woodward Flail-Vac Seed Stripper, Ag-Renewal, Inc., Weatherford, OK, U.S.A.) collection methods. From 2004 to 2016, 268 species of native grasses, sedges, and forbs were collected for reconstruction plantings, with an average of 179 species collected per year (Table S2). Although seed collections contained over 75% of the same species each year, specific species and quantities varied based upon annual seed production of the plants in the population. Both common and uncommon native prairie species were targeted for seed collection each year. After collecting seed throughout the growing season, reconstruction plantings occurred the following dormant season (January–February) by broadcast seeding on prepared ground (Crop or Grass). Seed viability tests were not conducted on collected seed and therefore Pure Live Seed seeding rates are not available. Seeding rates of bulk material varied across years (ranged from 13.4 and 18.2 kg/ha) but did not vary across Crop and Grass prepared sites within planting years.

After seeding, reconstruction management included two mowing treatments (to residual heights of 15–20 cm) in the first growing season and one mowing treatment in the second growing season. Mowing treatments were designed to reduce dominance of fast-growing annual species that competed with new germinants for light and soil resources. Prescribed fire was introduced to the reconstructions during the dormant season prior to the second or third growing season (Table S1). Additionally, annual growing season spot foliar herbicide applications were conducted to control NN invasive species, particularly *L. cuneata*. Following the first prescribed burn, the reconstruction plantings entered a 2–4 year adaptive management prescribed fire return interval using both growing and dormant season burns. For example, once the seeded vegetation was well established, growing season burns were applied to diminish the dominance of competitive C_4 grasses. Similarly, the remnant sites were managed using spot herbicide applications to control invasive species and a combination of both growing and dormant season burns with an average fire return interval of 2.5 years (i.e. a late winter/early spring burn followed 2.5 years later with a late summer/early fall burn; Table S1).

These prairie reconstruction methods have occurred at PFCA since 2004, with 16–25 ha typically planted each year. Both Crop and Grass site preparation treatments were used during this period, with treatment designation dictated by management considerations rather than from an experimental design. When the monitoring plots were installed, the treatments were assigned opportunistically in that some areas were already in cropping (Crop) and others in pasture (Grass). As the reconstructions continued through time, decisions on Crop or Grass areas were often made based on compatibility with other research and educational activities, with some consideration of accessibility for permit farmers to implement the cropping treatment. As a result, PFCA included a patchwork of reconstructions that varied in age across the two site preparation methods. Although these treatments were not randomly assigned at the beginning of the project, the site factors and land use legacies are similar across the range of treatments.

Vegetation Sampling

In 2000, prior to reconstruction at PFCA, permanent vegetation sampling sites were established to provide feedback to area management activities. These sites were stratified across soil types. Each site was marked with a point location that then had four sampling plots established in cardinal directions at random distances (between 15 and 90 m). This sampling design resulted in 23 sampling sites, totaling 92 sampling plots, located in the areas designated for prairie reconstruction. Each sampling plot had four 1-m^2 quadrats located 3 m from center at bearings 45°, 135°, 225°, and 315°. In 2017, similar sampling plots were randomly located within remnant prairies at TPNA (24 sampling plots) and MDCA (20 sampling plots).

Vegetation sampling occurred from 20 June to 25 July of 2017 at PFCA, TPNA, and MDCA. Within each 1-m^2 quadrat, all rooted vascular plants were identified to species or genera and assigned a cover class based on their aerial coverage: (1) 0–5%; (2) 5–15%; (3) 15–25%; (4) 25–50%; (5) 50–75%; (6) 75–95%; and (7) 95–100%. When possible, plants were identified to species following Yatskievych (1999, 2006, 2013), with >95% of species encounters recorded at the species level. However, when specimen maturity or condition did not allow positive identification to species, plants were recorded to genera. Of the 19 genera for which this occurred, 14 occurred in less than 3% of the sampling plots (≤4 of 135; *Aristida* (Threeawn) L., *Carya* (Hickory) Nutt., *Convolvulus* (Bindweed) L., *Cuscuta* (Dodder) L., *Cyperus* (Flat sedge) L., *Galium* (Bedstraw) L., *Helianthus* (Sunflower) L., *Lactuca* (Lettuce) L., *Plantago* (Plantain) L., *Prunus* (Plum or Cherry) L., *Rubus* (Blackberry) L., *Symphyotrichum* (Aster) Nees, *Trifolium* (Clover) L., and *Vitis* (Grape) L.). The other unidentified genera lumped were *Carex* (Sedge) L., *Crataegus* (Hawthorn) L., *Ulmus* (Elm) L., *Juncus* (Rush) L., and *Melilotus* (Sweet clover) (L.) Mill., which occurred in 51, 8, 6, 4, and 4% of the sampling plots, respectively. Unidentified *Carex* species made up the bulk of plants identified only to genera and summed to 1.6% of the total vegetation coverage observed across the sample plots. Nomenclature was based on Ladd and Thomas (2015).

Data Analysis

For each species, cover was converted to the cover class mid-point and averaged at the sample plot level (total of four 1-m^2 sampling quadrats) for analyses. For each sample plot, we calculated total species richness, total native species richness, mean species density (species richness per m^2), and mean native species density. Following the Floristic Quality Assessment (FQA) system (Swink & Wilhelm 1994; Matthews et al. 2015), we calculated mean coefficient of conservatism (mean C) and floristic quality index (FQI) for each sample plot. Coefficients of conservatism (C values) for each species were assigned by Ladd and Thomas (2015), and we assigned a C value of zero to each NN species. Occurrences recorded at the genera level were excluded from these analyses to provide a conservative estimate of species richness and to avoid introducing uncertainty into the FQA calculations.

We analyzed changes in the reconstructed plant communities using a chronosequence approach. For some analyses, we grouped age since reconstruction into classes, including pre-reconstruction seeding (PS; Crop, $n = 10$; Grass, $n = 21$), 1–3 years since reconstruction (A1–3; Crop, $n = 20$; Grass, $n = 4$), 4–7 years since reconstruction (A4–7; Crop, $n = 9$; Grass, $n = 7$), >8 years since reconstruction (A8+; Crop, $n = 13$; Grass, $n = 7$), and remnant communities (RM; $n = 44$). Best-fit bivariate models, using linear or nonlinear regression, determined relationships between age since reconstruction and plant community metrics for each of the site preparation methods (Crop and Grass). Model fit was assessed by comparing statistical significance, mean square error, and r^2 values. For each model, we calculated the 95% confidence interval. Similarly, we calculated the mean values and 95% confidence intervals from the remnant community plots (both TPNA and MDCA combined). We considered overlap in the confidence intervals to indicate no statistical difference in the plant community metric between site preparation methods or compared to the reference communities. Regression analyses were conducted using SAS 9.4 Software (SAS Institute Inc., Cary, NC, U.S.A.).

We used nonmetric multidimensional scaling (NMDS) to assess similarity among plant communities through time for Crop, Grass, and the remnant communities. For the ordination, we used the Bray-Curtis distance measure with six initial dimensions, random starting coordinates, and a maximum of 500 iterations. The dataset used mean coverage per m^2 for each species and for those grouped by genera for all sample plots. The secondary matrix included age since reconstruction for each sample plot and the method of site preparation. For visual display, we indicated the age since reconstruction group and both reference sites (MDCA and TPNA). To determine the distance of the reconstruction plots to the remnant plots, we first determined the centroid of the plots within the remnant communities. Then to determine community dynamics through time, we calculated the Euclidean distance of each reconstruction sampling plot from the remnant centroid in ordination space (Rydgren et al. 2019). We used bivariate regression to model the rate of community recovery through time and plotted regression lines with 95% confidence intervals for the Crop and Grass site preparation treatments, as well as the mean and 95% confidence intervals for the remnant sample plots.

To determine species missing in the reconstruction treatments, indicator species analysis was used to identify species associated with each age since reconstruction group (i.e. PS, A1–3, A4–7, A8+, and RM) using the same data matrix as used for the NMDS ordination. The indicator species analysis calculates an indicator value (IV) based on the proportional abundance of a species in a group relative to the abundance of that species in all groups and the proportional frequency of the species in each group (McCune et al. 2002). For each species, the age since reconstruction group with the greatest IV was determined, and 4,999 Monte Carlo permutations were calculated to determine if the probability that the observed IV was greater than randomly generated mean IV. For the indicator species analysis, we combined the Crop and Grass site preparation datasets because we were primarily interested in identifying species in remnant communities that were not present in reconstructed communities, and we presented only significance for plants identified to species. We calculated mean C for indicator species of each age since reconstruction group and summarized the distribution of C values to the relative Importance Value for all species by age since reconstruction group. Importance Values were calculated for each species by summing their relative coverage and relative frequency across each sample plot. The NMDS ordination and indicator species analysis were conducted using PC-ORD 6.08 Software (MjM Software Design, Gleneden Beach, OR, U.S.A.). For all statistical analyses, we considered significance for $p < 0.05$.

Results

In total, 241 taxa were identified across all plots, including 222 unique species and 19 additional genera groups (Table S3). A total of 183 taxa were recorded at PFCA, including 134 across all age classes of reconstruction plantings (A1–3, A4–7, and A8+). Prior to the completion of site preparation and broadcast seeding (PS), there were 16 species identified in the Crop plots and 124 species identified in the Grass plots. Across the remnant plots (MDCA and TPNA), there was a total of 139 taxa identified.

For the Crop site preparation, the reconstructed prairies showed patterns of rapid increase of each plant community metric in the first few years following reconstruction, reaching maximum by around year 4 (Fig. 2). Based on the bivariate models, age since reconstruction had a significant, positive relationship with each plant community metric for Crop site preparation. For Grass site preparation, however, age since reconstruction had a significant positive relationship for only native density, mean C, and FQI (Fig. 2, Table S4). While native density for Grass site preparation was best fit with an exponential rise to maximum model form, mean C and FQI were best fit with linear models (Table S4). For the Crop site preparation, the 95% confidence intervals overlapped with the reference community, indicating no statistical difference, for total species density, total species richness, mean C, and FQI (Fig. 2). Although the Grass site preparation initially had greater values than Crop for all metrics, by around 2 years after treatment each metric was higher for the Crop site preparation. However, for mean C and FQI, the Grass site preparation reached levels similar to the Crop site preparation and the remnant communities at around 10 years after treatment.

The NMDS was fit with a two-dimensional ordination, with a final stress of 17.52 and 77 iterations for the final solution. Axis 1 accounted for 51.6% of the variation in the ordination and Axis 2 accounted for an additional 12.4% of the variation (cumulative r^2 of 0.64). The ordination indicated separation of Crop and Grass site preparation prior to the prairie reconstruction (PS), with communities moving closer to the remnant communities through time (Fig. 3). The two remnant sites used as reference communities (MDCA and TPNA) separated along Axis 2 of the ordination. The plant communities in the Crop site preparation differed more from the remnant communities than those in the Grass site preparation at the start of the reconstruction. By 6 years after reconstruction the Crop and Grass communities were not different (Fig. 3B). Age since reconstruction explained 93.1% of the variation in the distance to the remnant centroid for the Crop site preparation and 78.1% of the variation for the Grass site preparation (Table S4). Neither the Crop nor Grass communities overlapped with the 95% confidence interval of the remnant communities at any point in time.

The indicator species analysis identified 20 species associated with the PS condition, of which 8 were NN species (Table S5). There were 12, 7, and 17 species identified as indicator species for A1–3, A4–7, and A8+ age groups, respectively. The remnant sampling plots had 33 species identified as indicator species, none of which was NN. The mean C of indicator species increased with age since reconstruction, with the greatest mean C for the remnant communities (Fig. 4A). Similarly, the relative Importance Value for the PS group was dominated by NN or low C value species; as age since reconstruction increased, the contribution of more conservative species (C values 4–8) generally increased (Fig. 4B).

Discussion

Our results show clear differences in plant community dynamics between the Crop and Grass site preparations used in reconstruction. The Crop sites were initially limited in species but quickly developed after seeding, with most community metrics approaching the remnant prairie sites through time. In contrast, sites that did not receive agricultural site preparation (Grass) took longer to develop remnant levels of floristic quality (mean C and FQI) and maintained lower levels of species richness. These patterns might be explained by reduced competition, available growing space, and favorable conditions for germination and establishment in Crop versus Grass treatments. Initially, Crop site preparation was much more effective at reducing or eliminating competing residual vegetation than noncropped sites (16 vs. 124 species observed prior to planting in the Crop and Grass sites, respectively). With less competition, germination and initial establishment of new seedlings from broadcast seed may have been more successful in the cropped sites.

Furthermore, longer periods of reduced competition in Crop versus Grass sites, particularly from C_4 grasses, may allow other perennial species to mature more quickly. To reduce competition during the establishment phase, seed mixes used for reconstruction at PFCA purposefully contain low proportions of *Andropogon gerardii* (Big bluestem) Vitman and *Sorghastrum nutans* (Indiangrass) Nash, two dominant C_4 prairie grasses. These two species are not specifically targeted in seed collections and are only gathered incidentally as other species are collected and cleaned. Both grass species occur within the plantings, presumably from secondary seed collections, colonization from nearby sites, persistence in the seed bank, and as surviving plants particularly in noncropped sites. The abundance of these species immediately after seeding was greater in the Grass sites than in the Crop sites (28.8% and 13.3% cover within 2 years, respectively), with these grasses becoming dominant (i.e. > 50% cover) in plantings by around age 3 in Grass sites and age 6 in Crop sites. Previous studies have suggested that dominance of C_4 grasses may cause reductions in species richness of forbs (Camill et al. 2004; McCain et al. 2010; Pfeifer-Meister

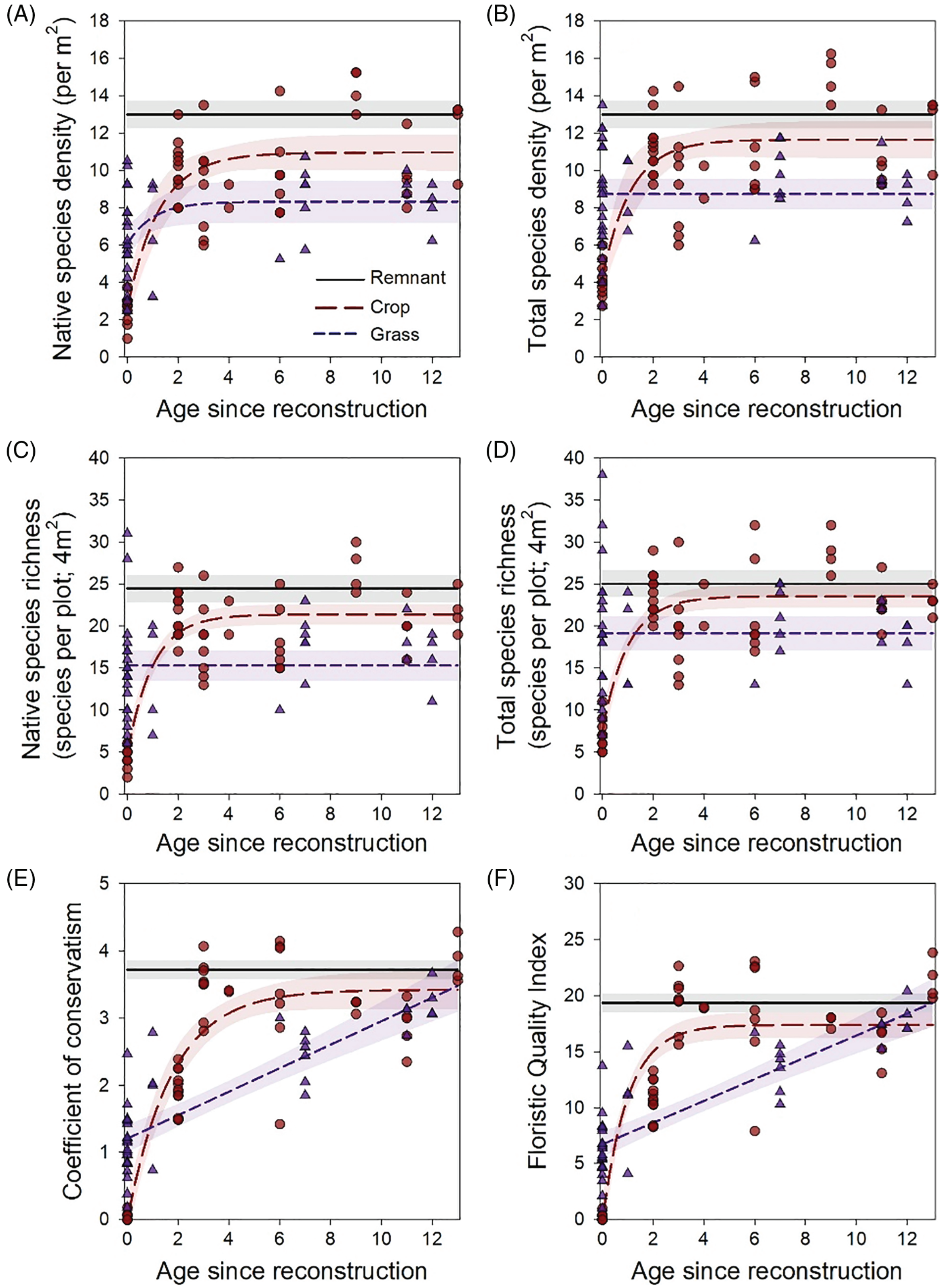

Figure 2. Relationships between age since reconstruction and plant community metrics: species density (number of species per m^2) for native species (A) and total species (B); species richness (number of species per sampling plot, 4 m^2) for native species (C) and total species (D); coefficient of conservatism (E); and floristic quality index (F). Vegetation data were collected in 2017 across all plots, with Crop (red circles) and Grass (blue triangles) site preparation methods fit with equations provided in Table S4. Shading indicates 95% confidence intervals, and data from remnant plots are shown for comparison to treatments.

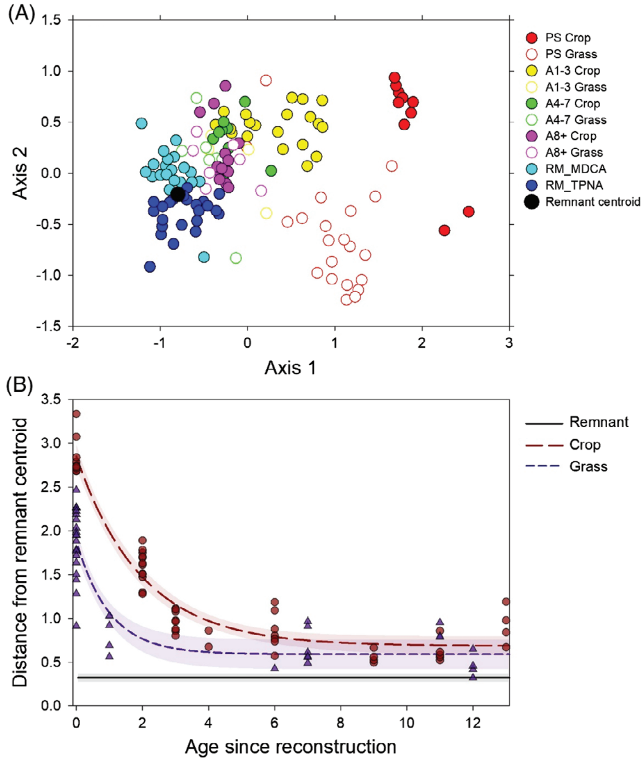

Figure 3. NMDS ordination of each sampling plot (A), showing age since reconstruction group, site preparation treatment, and remnant prairie communities and centroid. Regression of distance to remnant centroid by age since reconstruction (B) for Crop (red circles) and Grass (blue triangles). Shading indicates 95% confidence intervals, and data from remnant plots are shown for comparison to treatments.

et al. 2012; Baer et al. 2016). Thus, the additional period of lower competition in the Crop sites may benefit many prairie forb species in establishment and early persistence. From an operational standpoint, the suggestion that cropping for site preparation encourages greater native prairie planting establishment is fortunate given that commercial agricultural operators can conduct site preparation and costs can be recovered through harvested crops.

Our reconstruction plantings have not shown declines in floristic quality or species richness across older reconstructions, as reported by others (Sluis 2002; Camill et al. 2004; Hansen & Gibson 2013). The oldest reconstruction planting at PFCA was 14 years old in 2017, and it is possible that declines in richness and floristic quality may occur as the plantings continue to age. However, PFCA management in mature (>7-year-old) plantings is often directed at limiting the dominance of C_4 grasses, specifically by periodically conducting late growing season (August–October) prescribed fires. Late summer-early fall prescribed fires have been shown to reduce the relative cover of C_4 grasses (Weir & Scasta 2017) and increase prairie forb biomass and diversity when compared to late winter-early spring burns (Towne & Craine 2014). Although not tested in this study, targeting C_4 grasses with maintenance burns through time may contribute to the sustained diversity in PFCA reconstructions.

Based on results from the ordination, the reconstruction plant communities moved toward but did not converge with the remnant reference communities over time. In fact, reconstruction communities seem to mature by 6 years of age, with little additional movement toward remnant prairie communities. The distributions of Importance Values by C value provide insight into general compositional differences. Remnant prairies had a unimodal distribution centered on species with C values of 4 and 5, which are typical of matrix prairie species (Ladd & Thomas 2015). In contrast, all reconstruction plantings exhibited bimodal distributions, with the primary mode centered on species with C values of 4 and 5 and a secondary mode centered on RD with C values of 0 and 1 (Ladd & Thomas 2015). Although the contribution of higher C value species increased with age since reconstruction, the reconstructions maintained a higher proportion of disturbance-adapted species than the remnants. Future monitoring will be needed to see if disturbance-adapted species continue to persist through time in the reconstruction plantings and to provide feedback to the adaptive management cycle.

The indicator species analysis identified several species that are generally missing from the prairie reconstructions. Species significantly associated with remnant prairies occurred in three general categories: (1) native ruderal and woody species that are not typically collected for PFCA reconstructions; (2) spring ephemerals and other prairie "understory" species that produce seed that is difficult to collect in the late growing season; and (3) species that are typically collected and seeded but inexplicably do not seem to successfully establish across the PFCA reconstructions. Species in the first category include *Potentilla simplex* (Common cinquefoil) Michx., *Vernonia baldwinii*, *Cornus* (Dogwood) L. spp., and *Rhus* (Sumac) L. spp., with the latter two documented to encroach upon prairies and degrade plant biodiversity (Ratajzac et al. 2011, 2012). Inclusion of these often-overlooked species in seed collections might be warranted to better emulate remnant prairie communities. Native shrub species play an important role in providing structural diversity on remnant prairies and their establishment in reconstructions may provide benefits to some prairie fauna (i.e. shrub nesting birds, small mammals, etc.). For example, the lack of availability of grassland-shrub breeding habitat for Bell's Vireo (*Vireo bellii*) throughout the central United States is a contributing factor in its decline (Budnik et al. 2000). Similarly, other passerine Midwestern shrub obligates are experiencing population declines due to a lack of available food or nest substrates, or both (Mabry 2013). Managers would need to weigh the structural and compositional diversity benefits native woody shrubs would provide in prairie reconstructions against their long-term prairie encroachment threat.

A majority of the remnant prairie indicator species fit into the category of having difficult seed to collect (e.g. *Antennaria* [Pussy toes] Gaertn. spp., *Crotalaria sagittalis* [Rattlebox] L., *Fragaria virginiana* [Wild strawberry] Duchesne, *Lysimachia lanceolata* [Lance-leaved loosestrife Michx.], *Hieracium*

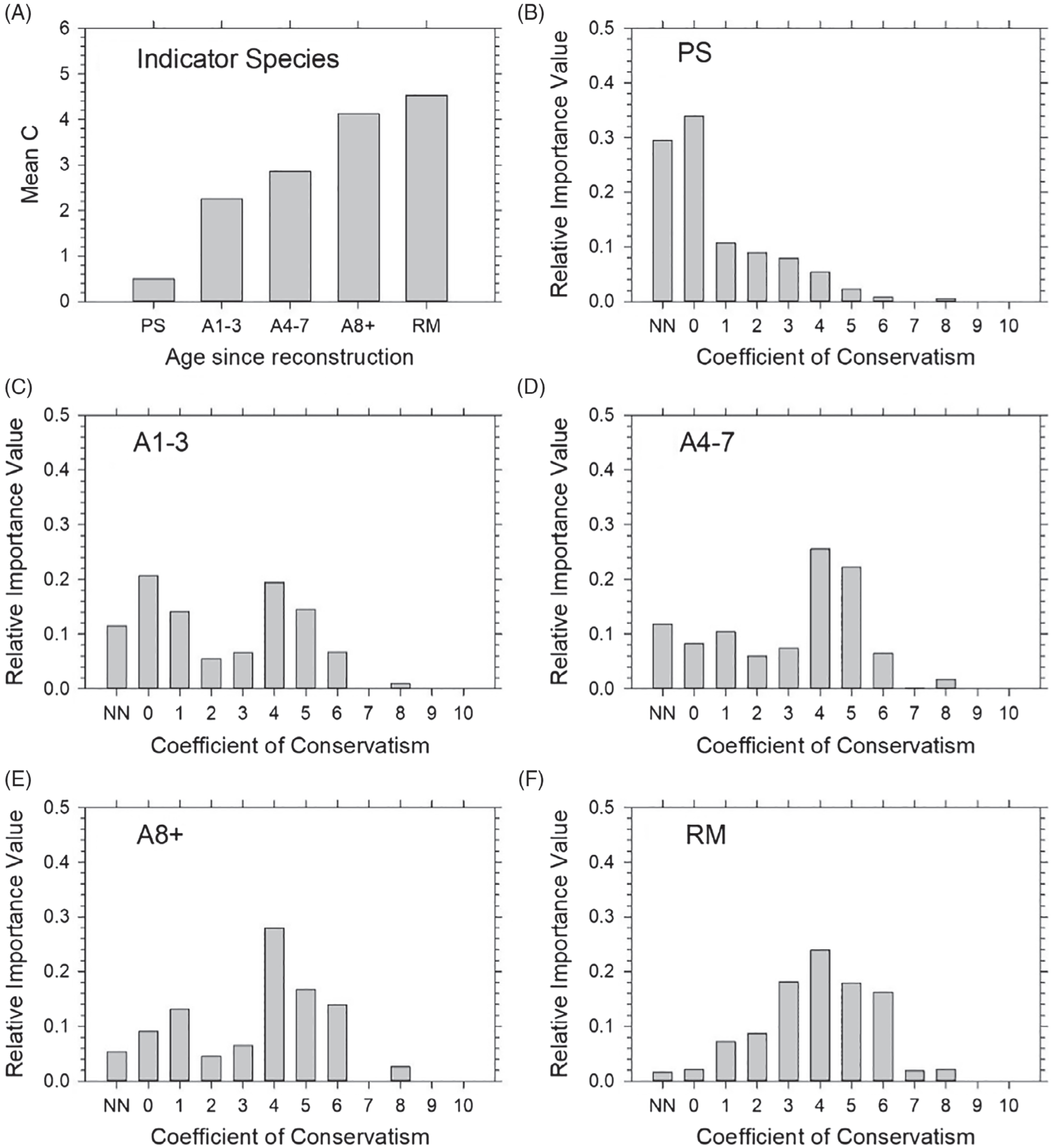

Figure 4. Mean coefficient of conservatism (C) of indicator species for each age since reconstruction group (A), with nonnative species assigned "0" for the summary, and the relative Importance Value by C value for each age since reconstruction group (B–F), calculated from all sampling plots within a group. Relative Importance Value sums to 1 for each age group.

longipilum [Long-bearded hawkweed] Torr., and *Viola sagittata* [Arrow-leaved violet] Aiton) and include many spring flora species. Many of these species are important components of prairie communities. For example, *V. sagittata* is an important larval food for the Regal fritillary (*Speyeria idalia* Drury) and thus provides known conservation value. Sluis et al. (2017) reported that spring flowering species (flowering before 1 July) are often poorly represented in prairie reconstructions, likely due to difficulty collecting the seed of spring flowering species that are often small and hidden by later growing species. Furthermore, due to the difficulty of collecting these species they are also not widely available for purchase from commercial vendors. Improved collection strategies such as increasing collection efforts or establishing production plots for these species would be needed to increase seed availability for reconstruction plantings. Planting small populations of propagated seedlings may be an alternative establishment practice for hard to collect and rare species. Propagation methods using plugs have been documented as increasing germination probability by 3–12 times that of direct seeding of C_4 grasses (Gallagher & Wagenius 2016), with establishment twice as successful for perennial herbs (Wallin et al. 2009). However, limited long-term survival without maintenance, proper species by site selection, and additional costs associated with plug production may limit the feasibility of this viable method for establishment (Morgan 1999; Wallin et al. 2009).

Finally, some species that were associated with remnant prairies (e.g. *Amorpha canescens* [Leadplant] Pursh, *Baptisia bracteata* [Cream wild indigo] Muhl. ex Elliott, *Liatris aspera* [Rough blazing star] Michx., and *Rosa carolina* [Pasture rose] L.] often have fair amounts of seed collected and seeded within the PFCA reconstructions yet are not commonly observed. For early maturing species, establishment may be improved by seeding during the growing season (Frischie & Rowe 2011). However, establishment limitation for many species is not clear and may be complex. Generally, seedling recruitment under field conditions is low (Clark et al. 2007) and variable by species and site condition (Grman et al. 2015). Possible contributing factors include viability of collected seed, modified soil microbial communities (Tipton et al. 2019), soil structure and porosity, water stress following sowing, litter buildup, sowing grass density, or a host of other unknown factors (Clark et al. 2007; Grman et al. 2015). Repeated overseeding of these, and other missing species associated with remnants, may eventually help establish them in reconstruction plantings (Sluis et al. 2017). Spatially patterned seeding or propagule planting techniques (Grygiel et al. 2009; Rayburn & Laca 2013) might assist with establishment of missing species into older, established plantings. Our results suggest that improved understanding of species-level responses would help identify and overcome limitations to establishment success of key species associated with remnant communities.

Our results provide evidence that operational prairie reconstructions can move plant communities toward remnant conditions, despite some limitations associated with the sampling design of this study. For example, total species richness differences between remnants and reconstructions should be interpreted with caution. Remnant sites had the greatest number of sampling sites, and therefore could have the highest total species richness due to expected species-area relationships (Gotelli & Colwell 2001). Additionally, the preseeded Grass sites had the greatest number of plots ($n = 21$) across all reconstruction age classes and this relatively high sampling effort could have contributed to the relatively high total species richness (124 total taxa) observed in this treatment. Our density (species/m^2) and floristic quality measures, however, should not be impacted by this uneven sampling effort across sites. In addition, our sampling design would not have detected all species present at any site, may not have detected rare species, and was not designed to track small changes in the plant community. For example, scattered populations of *Delphinium carolinianum* (Carolina larkspur) Walter (C value = 6), *Asclepias sullivantii* (Prairie milkweed) Engelm. ex A. Gray (C value = 8), and *Melanthium virginicum* (Bunchflower) L. (C value = 9) have been observed in both remnant and the older reconstructions at PFCA but were too localized to be detected by our sampling design. A more detailed sampling design, like the use of modified Whittaker plots (Barnett & Stohlgren 2003), would likely be able to better detect smaller changes over time and differences among prairie reconstruction ages and remnants.

Although the reconstruction plantings at PFCA have established diverse prairie communities, they have not yet matched the remnant reference sites after which they are modeled. This fact provides further evidence as to the value of protecting and conserving the last remaining tallgrass prairie remnants in Missouri. Our results suggest that additional research is warranted to understand (1) limitations to establishment or persistence for those species commonly included in the seed mix but not present in reconstruction plantings and (2) methods for improving seed collection of other species. Moreover, identification of native ruderal/woody species as indicators of remnant prairie suggests the need to consider these species in prairie reconstructions when evaluating success criteria. Our work demonstrates that site preparation prior to seeding can quickly promote the development of a diverse prairie planting during reconstruction. Site preparation methodology affects the rate of development and may have lasting impacts on species richness and density. Maintaining and increasing an established reconstruction planting's diversity will require ongoing monitoring and adaptive management and may include management practices such as control of aggressive C4 grasses and NN invasive species, repeated overseeding of missing species, and establishment of species colonies through propagule plantings.

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Supporting Information

The following information may be found in the online version of this article:

Table S1. Summary information for each sampling plot.
Table S2. List of species in the seed collections across study years.
Table S3. Mean cover by species for each site preparation treatment.
Table S4. Model form, parameters, and statistical summary for bivariate relationships.
Table S5. Indicator species identified for each age since reconstruction group using the combined dataset.

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