Twenty years of tallgrass prairie restoration in northern Illinois, USA

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Abstract

1. Ecosystem restoration projects need to measure progress toward project goals and deliver desired outcomes.
2. This study examines longitudinal plant community data collected from permanent transects at the Nachusa Grasslands preserve in northern Illinois, USA. Managers established permanent transects for repeated plant community monitoring beginning in the mid-1990s.
3. Native plant communities, including rare species, have persisted, or improved with management over two decades.
4. Planted prairies have lower proportions of native species than native prairies but have generally maintained native-dominated communities and in some cases, increased presence of native species.
5. Savannas have shown a distinct transition from shrub-dense communities to herbaceous understories dominated with native species.
6. Restoration efforts at Nachusa Grasslands have been successful at sustaining unique native plant communities through management practices like prescribed fire, brush removal and aggressive invasive species control. As a disturbance-dependent ecosystem that has developed with human management over millennia, tallgrass prairie and savanna can thrive through restoration and active management.

Keywords

coefficient of conservatism, conservation, grassland, invasive species, plant community, prescribed fire, savanna, species richness

INTRODUCTION

Central North America was once covered in a mosaic of open grasslands and savannas, which include partial tree canopy cover, (Paciorek et al., 2021; Samson et al., 2004). For millennia, Indigenous people managed this ecoregion in central North America to support an astounding diversity and abundance of plants, insects, birds, mammals and herptiles (Sleeper-Smith, 2018). Crop fields were integrated into expanses of hunting grounds and Indigenous people set regular fires to support biologically diverse grasslands and savannas to attract numerous game species (Kimmerer & Lake, 2001). Large networks of wetlands and rivers wove through the prairie landscape, supporting abundant fish,
fur bearing mammal and bird communities. Numerous indigenous cultures and their activities were essential to sustaining these ecosystems. Over the past 200 years, European colonists largely extirpated native people and transformed land use so that today this region is dominated by highly productive intensive row-crop agriculture. With less than 5% of tallgrass prairie and less than 1% of Midwestern savannas persisting in their historic range, both are among the most endangered ecosystems on Earth (iPbES, 2018). With that transformation has come significant decreases in both diversity and abundance of native plant and animal communities. And yet, both biological communities and indigenous cultures persist, remaining important parts of our landscape and society today.

In the past century, many people have recognized the ecological loss experienced across central North America, launching some of the earliest ecological restoration efforts (Mlot, 1990; Sperry, 1994). This regional mosaic of tallgrass prairie and savanna has been foundational to the development of restoration ecology as a discipline. Restoration ecology has often focused on creating plant communities to stabilize habitats (SERI, 2004), support animal diversity (McAlpine et al., 2016) and test ecological theory (Falk et al., 2006). Plant communities can provide indicators of habitat that has not experienced extensive soil disturbances and are often used to prioritize habitats for conservation (White, 1978). Many restorations focus on restoring plant communities because seeds can be planted more easily than animal reintroductions, outcomes can be measured relatively easily and changes can often be observed across a few years, especially in grasslands (Mlot, 1990). Just as these characteristics make plant communities popular for ecological research, they also serve a strong foundation in establishing goals and monitoring outcomes of ecological restoration projects. It is relatively easy to measure and track plant communities. Other taxa of concern, including insects and birds, are known to be highly reliant on plant communities, so many restoration projects adopted goals around plant community diversity and composition (Ruiz-Jaen & Aide, 2005). Plants form the foundation of tallgrass prairie and savanna restoration because efforts often focus on recreating native plant communities observed in unploughed sites.

There are a variety of ways to measure progress toward plant community restoration goals. Managers have used the floristic quality index and associated mean coefficient of conservatism to evaluate and monitor plant communities on the preserve (Swink & Wilhelm, 1994). These metrics were developed in the region around Chicago, IL (USA) and have been adopted in many regions across North America. Robust evaluation of the regional plant communities and development of coefficients of conservatism for essentially all plants (Swink & Wilhelm, 1994; Wilhelm & Rericha, 2017), makes these metrics a valuable approach to quantify plant community rareness in the current landscape. The coefficient of conservatism ranks the fidelity of a plant species to habitats experiencing minimal modern human disturbance on a scale from 0 to 10 (Freyman et al., 2016; Swink & Wilhelm, 1994; Taft et al., 1997). A score of 0 means the plant species is non-native, a score of 1 means the species is found commonly even in the most altered habitats (e.g., edge of a parking lot) and a score of 10 means the plant species is essentially only observed in high-quality native habitats that have experienced minimal human disturbance in modern times. The goal of the floristic quality index and mean coefficient of conservation is to provide a repeatable and relatively straightforward assessment tool for botanists and land managers to use in prioritizing natural areas for protections and conservation management, and in practice, they achieve these goals (Spyreas, 2019), especially in regions with florae having coefficients of conservatism robustly developed for all plant species.

Understanding long-term trajectories in ecosystems is a major challenge for restoration projects, especially when restoration goals include diverse native biological communities. One approach to capture long-term trends in restorations has been the chronosequence approach. A chronosequence of sites include multiple sites of various ages/stages of restoration and trends across time are interpolated from multiple replicated sites (Baer et al., 2002; Hansen & Gibson, 2014). Chronosequence research has provided valuable insights into tallgrass prairie restoration trajectories. Plant communities have generally shown a decline in species diversity and increase in warm season grass cover (Baer et al., 2002; Munson & Lauenroth, 2012), leading to a decrease in the mean coefficient of conservatism and floristic quality index (Hansen & Gibson, 2014). However, plant phylogenetic diversity can be maintained even with a decline in total plant species (Barber et al., 2017). Reduced plant diversity in older plantings is also consistent with observed reductions in seedling presence of sown species and increased role of below-ground buds and ramets (Willand et al., 2013).

An alternative strategy, longitudinal studies, provide valuable insights into ecological trends and changes (Reemts & Eidson, 2019; Stouffer et al., 2021), but are rare because they require sustained and consistent data collection across timeframes beyond research grant cycles and even careers. The Long-term Ecological Research Network (LTER) supports this type of long-term research at a network of sites representing habitats across North America (and the International LTER extends this model globally). Konza Prairie in Kansas is the tallgrass prairie LTER and has provided a wealth of longitudinal research deepening our understanding of native tallgrass prairie. Across 19 years of surveys at Konza Prairie, where regular prescribed fire was applied, plant species richness remained relatively constant yet in upland communities, diversity generally declined, driven by increases in the dominant grass Andropogon gerardii (Collins et al., 2012). It took 10–12 years of differing fire return intervals before differences in shrub cover became evident, and over 15 years before it was recognized the changes were leading to a change in state for the ecosystem (Ratajczak et al., 2014). Synthesis of long-term studies from Konza shows that fire and grazing are important drivers of plant (and animal) community richness and composition in tallgrass prairie (Bruckerhoff et al., 2020). Similarly, legacy studies from Wisconsin prairie and savannas have shown declines in native plant species and increased presence of ruderal species, both native and non-native, in the past 60 years (Alstad et al., 2016; Ladwig et al., 2018). The extent and rate of those changes varied by habitat and increased with the absence of regular fire and reduction in site size. In northwest Illinois, prairies resampled after 25 years showed that sites with more frequent fire supported more late-successional forbs (Bowles & Jones, 2013).
Less research has applied the long-term approach to examining change in restored grasslands. In a 20-year study of restored prairie in Kansas, differences in plant community diversity did not become apparent between restoration approaches altering soil heterogeneity until 16 years after planting (Baer et al., 2020). A longitudinal study of a single site in northeastern Illinois showed consistent plant diversity across 34 years, driven by decreases in non-native species and increases in native species (Glennemeier et al., 2020). Many restoration projects set up regular plant monitoring, but sampling is not always repeated consistently. Where longitudinal data are collected, they are more likely to be used internally for management decisions and not published in the scientific literature.

In this longitudinal study, we investigate plant community changes across 20 years of tallgrass prairie restoration efforts at the Nachusa Grasslands preserve in north-central Illinois. Managers at Nachusa Grasslands set up permanent transects in the mid-1990s for repeated plant community monitoring at native prairies, savannas (unploughed, but degraded) and planted prairies (former crop fields) across the site. In this study, we address two central questions: (1) Are management practices sustaining plant diversity, including rare plants, in native prairies and savannas? and (2) Do restored prairies support comparable levels of plant diversity and conservatism to native prairies? We evaluated data collected from 12 permanent transects across 20 years of restoration management to determine how overall plant community structure has changed. We further investigated changes in total plant species richness, proportion of native plant species and mean coefficient of conservatism.

2 | METHODS

2.1 | Study site

Nachusa Grasslands is a ~1600 ha preserve, owned and managed by The Nature Conservancy, in north-central Illinois, USA (41°53′27″ N, 89°20′34″ W). Please see Supporting Information 1 for a detailed description of Nachusa Grasslands management history. Conservation and restoration management began at the site in 1986. The mean annual high and low temperatures are 14 and 3 °C, respectively, and mean annual precipitation is 949 mm (1981–2010). Soils are a mixture of loams, sandy loams and silt loams formed from sandstone erosion, glacial outwash and loess deposits. The site contains native and restored tallgrass prairie, savanna and wetland. Restoration plantings began in 1987 and new plantings have been done every year since. Management practices include frequent prescribed fire, aggressive invasive species control and brush removal. In 2014, a herd of bison (Bison bison) was reintroduced to the preserve; however, all data presented in this study pre-dates bison grazing.

Between 1994 and 1996, managers set-up transects in 12 independent sites within the preserve to evaluate and monitor plant community changes in both native and restored prairie units across the preserve (Figure 1; Table 1). Sites are replicated within three habitat types: native prairie (n = 4), restored planted prairie (n = 4) and savanna (n = 4). Native prairie sites in this study are unploughed hilltops with very sandy soils and shallow bedrock. These sites were grazed by cattle for much of the 20th century, prior to the early 1980s (Table 1). Each of the four sites support unique, highly diverse native plant assemblages. Each of these native prairie plant communities is unique, including some native plant species not found at other native prairie sites within the preserve. Savanna sites differ from native prairie due to the presence of large trees that pre-date European contact. Savannas do not have a history of ploughing and include long-lived trees (Quercus velutina, Carya ovata, Quercus macrocarpa) with an understorey of mixed native grasses and forbs. Some sites do have a history of grazing. Land managers have removed dense understory brush, largely non-native Lonicera mackii, young Prunus serotina and Ulmus sp. Large native trees remain, and native herbaceous plants have been over-seeded into the understory (Table 1). Herbicide is used to prevent shrub resprouting (e.g., Kleiman et al., 2018). Restored prairies in this study have planting histories ranging from 1986 to 1994 (Table 1). Restored prairies have been planted into former row-crop agricultural fields in the fall after final crop harvest. Native plant seeds are collected by hand from native prairie (never ploughed) on the preserve and from within an 80 km radius. Planting practices in the earliest restorations primarily include hand-broadcasting seed. Later restorations include mechanical broadcast seeders pulled behind a tractor or truck. Species are intentionally collected from habitats that matched the planting (e.g., dry upland, mesic lowland). Exact species mixes and seeding rates vary from year to year as restoration practices developed; additional details can be found at https://www.nachusagrasslands.org/planting-histories-in-chronological-order.html.

Transects in native prairie each include 15 quadrats (1 m²) and transects in restored and savanna habitat each include 10 quadrats. All quadrats are spaced approximately 1 m apart on alternating sides of the transect tape. In 1994, we believe 0.5 m² quadrats were used instead of 1 m², although no documentation could verify one way or the other. Given that adjusting the number of species to a per meter basis does not reflect the true species richness at 1 m², we opt to keep the 0.5 m² data in the seven instances that it occurs. Transect orientation varies by site. In all quadrats, plants are identified to species level. The transects are permanently marked and resampled over time, although not at a consistent interval. In this study, we synthesize the plant community data collected between 1994 and 2016, analyzing total plant species richness, proportion of native plants and mean coefficient of conservatism. Due to differences in cover metrics used over the years, we consider species presence/absence only.

The mean coefficient of conservatism reflects the mean value of the coefficient of conservatism assigned to all species observed (Taft et al., 1997). The mean coefficient of conservatism is calculated as follows:

\[
\bar{C} = \frac{\sum C}{S},
\]

where \(\bar{C}\) is the mean coefficient of conservatism, \(C\) is the coefficient of conservatism and \(S\) is the total number of plant species. For these transects, we use the total number of species found in the transect across all quadrats, counting each species only once if it appeared
in multiple quadrats. Non-native species are included in the calculation with a $C$ value of 0. Mean coefficient of conservatism is calculated at the transect level with one transect per site. To be consistent and facilitate future comparisons, we use coefficient of conservatism values from (Wilhelm & Rericha, 2017), which differ only minimally from original assignments from Swink and Wilhelm (1994). The flora fits the observed flora at Nachusa well (e.g., most species observed at Nachusa are included, except ferns, mosses and liverworts which are not included) and is the primary botanical reference used by Nachusa staff and volunteers.

We used mean coefficient of conservatism to compare changes within the same transect over time because it is less sensitive to sample area than FQI (Spyreas, 2016). We standardized the length of the transects, so all communities would be equalized by number of quadrats. However, the length of the transects varied somewhat between the sites, largely in relation to size of the habitat it was meant to represent. We used total plant species richness, proportion of native species and mean coefficient of conservatism to holistically evaluate change over time in native habitats and restored. There were numerous native species that are valuable members of the plant community that do not have high coefficient of conservatism values (e.g., do not have a strong affinity for undisturbed prairie sites). Observing changes in mean coefficient of conservatism allowed us to evaluate if management sustained conservative members of the community, and if conservative species
TABLE 1 Summary of transects surveyed for plant community composition at Nachusa Grasslands

<table>
<thead>
<tr>
<th>Transect</th>
<th>Habitat type</th>
<th>Years surveyed</th>
<th>Restoration activities</th>
</tr>
</thead>
<tbody>
<tr>
<td>P08</td>
<td>Savanna</td>
<td>1996, 2003, 2013</td>
<td>Brush removal, prescribed fire</td>
</tr>
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established in adjacent restorations. It should be noted the surveys in different years were conducted by different botanists, although these botanists worked together extensively and sometimes there was overlap in data collectors between sampling events. It is possible that some observer bias resulted, and all efforts were made to minimize this impact. In addition, mean coefficient of conservatism has been shown to not strongly respond to observer bias or occasional misidentification (Spyreas, 2019). In addition, we reviewed all original data used in this analysis to ensure reported species are observed in multiple years and/or are known to occur in the immediate area.

We conducted all statistical analyses using R Studio (version 1.3.959). Overall plant communities were visualized using non-metric multidimensional scaling (NMDS) using the vegan package (Oksanen et al., 2019). We used permutational multivariate analysis of variance (adonis function) to statistically test for effects of site, sampling year and their interaction. Tukey’s honestly significant difference determined differences between factor levels. When there was a statistically significant interaction between site and sampling year, we leveraged envfit to conduct centroid and vector-fitting analysis. This allowed us to parse out effects of the categorical factor site and treat sample year as a continuous variable to perform vector correlation analysis. To better understand what changes in the plant community led to observed differences over time, we correlated total species richness, proportion of native plants and mean coefficient of conservatism with sampling year using regression analysis. We leveraged indicator species analysis (Dufrêne & Legendre, 1997) to identify plants most likely to be uniquely found in the transects in various sampling years. Because we used presence/absence values, the frequency with which a species was present in a transect was used to calculate the indicator species value. Plant species with higher indicator species values were more likely to be found in a specific transect in a given year and species with low values had a low probability of occurring. Indicator species analysis was conducted using the multipatt function in the indicspecies pack-

3 RESULTS

Across all data, habitat type (native prairie, savanna and restored prairie) interacted with sampling year (ADONIS $R^2 = 0.07, p = 0.001$), driven by differences in how the habitat types changed over time. Differences in habitat type contributed the most explanation of the variance ($R^2 = 0.21$). Comparison of only native and planted prairies also produced a habitat by sampling year interaction, driven by changes in different directions over time within each habitat type (ADONIS: $R^2 = 0.14$). Across all data, habitat type (native prairie, savanna and restored prairie) interacted with sampling year (ADONIS $R^2 = 0.07, p = 0.001$), driven by differences in how the habitat types changed over time. Differences in habitat type contributed the most explanation of the variance ($R^2 = 0.21$). Comparison of only native and planted prairies also produced a habitat by sampling year interaction, driven by changes in different directions over time within each habitat type (ADONIS: $R^2 = 0.14$). To better understand the changes across time within each of the habitats, we subset the data by each habitat type (native prairie, savanna, planted prairie) and performed independent multivariate analyses. Within each habitat type there was a statistical interaction between site and sampling year within each (Figure 2).

3.1 Native prairie

In native prairie, this interaction (ADONIS: $R^2 = 0.04; p = 0.001$) was driven by each site community shifting in different directions over time. Vector-fitting analysis of each site showed that site P14 did not change through time, P15 ($R^2 = 0.67, p = 0.001$) and P17 ($R^2 = 0.82, p = 0.001$) became more similar to each other over time and P19 ($R^2 = 0.26, p = 0.006$) became less variable over time (Supporting Information 3). Within native prairie transects, the total number species increased in P19 between 1994 and 2015 ($R^2 = 0.99, p = 0.03$; Figure 3a), but proportion of native species remained similar. Trends in all sites...
FIGURE 2 Non-metric multi-dimensional scaling (NMDS) ordinations exhibiting plant communities from repeated vegetation surveys at twelve permanent transects at Nachusa Grasslands preserve (Illinois, USA). Native prairie communities shown in (a), savanna in (b) and planted prairie in (c). Each point represents the mean community from multiple quadrats along each transect. Lines represent ±1 standard error. Bolder colours represent early surveys, more translucent colours represent more recent surveys.

exhibited general increases in total plant richness, maintaining proportion of native species and mean coefficient of conservatism across twenty years. In P17, mean coefficient of conservatism increased more than 80% ($R_{adj}^2 = 0.75, p = 0.035$) between 1994 and 2013 (Figure 3a).

We performed indicator species analysis to better understand which plant species drove the differences in trajectories in community change over time. Most of the native prairie sites had more indicator taxa associated with recent surveys (Supporting Information 4). Site P15 was distinguished by Carex brevior ($p = 0.005$) and Antennaria neglecta ($p = 0.005$) in the 1996 survey and in 2015 there were 11 indicator species, primarily native species characteristic of prairies. Site P17 has several indicator species for each of the sampling years. In 1994 and 1996 it was distinguished by several weedy species and more recent surveys are distinguished by native species like Euthamia graminifolia ($p = 0.005$), Tradescantia ohiensis ($p = 0.005$), Polygala sanguinea ($p = 0.045$) and Sorghastrum nutans ($p = 0.05$). In early surveys, site P19 was distinguished by uncommon native grasses like Koleria macrantha ($P = 0.015$), Bouteloua curtipendula ($p = 0.01$), Dichanthelium leibergii ($p = 0.005$) and in 2015 several rare native forbs such as Amorpha canescens ($p = 0.005$), Symphoricarpos sericeus ($p = 0.005$) and Geum triflorum ($p = 0.01$) appear as indicator species (Supporting Information 4). These shifts demonstrate the unique nature of each native prairie plant community and increasing diversity of indicator species, including highly conservative forb species.

3.2 Savanna

In savanna sites, differences in how plant communities changed over time resulted in a strong interaction between site and sample year, (ADONIS: $R^2 = 0.10, p = 0.001$, Figure 2b). Within the savannas, P08 ($R = 0.60, p = 0.001$) and P39 ($R = 0.209, p = 0.01$) shifted in a similar direction over time, while P24 ($R = 0.774, p = 0.001$) and P41 ($R = 0.26, p = 0.02$) shifted in a different direction (Supporting Information 3). There were no statistical changes in total plant species, proportion native species or mean coefficient of conservatism in any of the savanna sites (Figure 3b). Distinguished in 1996 by Phytolacca americana and Parthenocissus quinquefolia, by 2013 transect P08 was
distinguished by some native herbaceous plants like \textit{Sanicula odorata} ($p=0.01$), \textit{Circaea canadensis} ($p=0.035$), \textit{Ageratina altissima} ($p=0.005$) and \textit{Solidago ulmifolia} ($p=0.005$). In 1996, P24 was distinguished by weedy \textit{Arctium minus} ($p=0.005$), \textit{Ambrosia trifida} ($p=0.005$) and \textit{Urtica gracilis} ($p=0.005$). In 2013, a mix of native and non-native/weedy species were indicative of this site. Site P39 shows a strong transition from woody indicator species like \textit{Lonicera maackii} ($p=0.005$) and \textit{Ulmus americana} ($p=0.01$) in 1997 to herbaceous understory plants like \textit{Eutrochium purpureum} ($p=0.005$), \textit{Phryma leptostachya} ($p=0.005$), \textit{Solidago canadensis} ($p=0.005$) and \textit{Ratibida pinnata} ($p=0.005$) in 2013. In 1997 and 2003, site P41 was distinguished by common savanna sedges \textit{Carex pensylvanica} ($p=0.005$) and \textit{Carex vulpinoidea} ($p=0.005$). In 2013, this site was distinguished by numerous native forbs and grasses (Supporting Information 4). 

3.3 | Planted prairie

In planted prairie, a three-dimensional ordination was required to accurately depict the spread of plant communities (Figure 2c). All plant communities changed with time ($p \leq 0.001$ for all), but the direction of these shifts differed, leading to a site by sampling year interaction (ADONIS: $R^2 = 0.11, p = 0.001$). Sites P26 and P32 shifting in a slightly different ecological direction than sites P23 and P31 (Supporting Information 3). Site P31 (1986 planting) showed a 25% increase in the proportion of native species ($R^2_{adj} = 0.95, p = 0.002$) and quadrupling of mean coefficient of conservatism ($R^2_{adj} = 0.94, p = 0.004$) observed between 1995 and 2015 (Figure 3c). The mean coefficient of conservatism also increased in site P32 ($R^2_{adj} = 0.90, p = 0.03$).

Like native prairies, planted prairies generally had more indicator species in recent surveys (Supporting Information 3). Indicator species for P23 (1991 planting) shifted from three non-native species in 1994 to 10 species, of which more than half were native, in 2016. The P26 planting was distinguished by non-native species like \textit{Lactuca serriola} ($p=0.005$), \textit{Daucus carota} ($p=0.005$) in 1996 and surveys in 2003 and 2016 revealed different non-native and early successional native species were indicator species. This planting is one of the ‘weeder’ plantings, although overseeding and invasive species removal have reduced some of the most noxious non-native plants. In P31, indicator species in 1994 are non-native and weedy species, and by 2013,
indicator species include several native species of high conservation values, like *Polygala polygama* \( (p = 0.005) \), *Dianthus deltoides* \( (p = 0.005) \) and *Echinacea pallida* \( (p = 0.02) \). Continuous management has allowed some native species to integrate into the plant community, although some new non-native weeds, like *Medicago lupulina* appear in the more recent surveys. Site P32 had few indicator species in early surveys. While weedy and non-native species remain part of the community in 2013 (e.g., *Melilotus* and *Poa* species), the presence of species within the genera *Silphium*, *Ratibida* and *Oligonueron* as indicators in 2013 indicate that native species, including some late-successional species, are becoming a greater part of the community (Supporting Information 4).

4 | DISCUSSION

Twenty years of plant community monitoring at Nachusa Grasslands in north-central Illinois (USA) shows that management practices like prescribed fire, brush removal and aggressive invasive species control have sustained, and in some cases enriched, native plant communities in native prairies, savannas and planted prairies. It should be noted all these data precede reintroduction of bison grazing at the preserve in 2014. Indigenous people actively managed this region for generations, so it is hardly surprising that active and consistent management has a strong influence on tallgrass prairie and savanna plant communities. Planted prairies are generally dominated by native plant species, although their community structure is distinct from native prairie. They have lower proportions of native plants than native prairies and savanna, consistent with previous comparisons (Sluis et al., 2017). Within these restorations, proportion of native species and mean coefficient of conservatism either increased or remained unchanged over 20 years of management. These data show that restoration and conservation can effectively protect and increase native plant species presence on the landscape.

4.1 | Native prairies

A 1978 survey of natural areas in Illinois identified less than 930 ha (2,300 acres) total of native tallgrass prairie habitat across the entire state (White, 1978). Despite overwhelming loss of habitat area, it is estimated that only 4%–5% of the historic native plant community has actually been extirpated from the Chicago region (Wilhelm & Rericha, 2017). Each native prairie is an important contribution to the persistence of native plant and animal communities as well as ecological understanding of the eastern tallgrass prairie region. The unique character of the native prairies at Nachusa Grasslands mirror the variation observed regionally across native prairies (Barak et al., 2017; Bowles & Jones, 2013). These data show that conservation efforts including frequent prescribed fire, aggressive invasive species control and large-scale restoration efforts on surrounding land have largely preserved the unique plant community members of the native prairie hilltops.

Active management is central to protecting native tallgrass prairie habitat. A key management approach at Nachusa Grasslands is to plant prairie restorations around native prairie areas, reconnecting the native prairies and expanding habitat through contiguous landscape-scale restoration. Planting restored prairies around native prairies reduces non-native species encroachment in native prairies, and this effect has been consistent with both high and low plant diversity plantings (Rowe et al., 2013). Restoration efforts at Nachusa have now reconnected all these once isolated native prairies. Research has shown this landscape context is central to supporting diverse animal communities as well (Griffin et al., 2020). Another critical management approach at Nachusa has been regular prescribed fire, and the average fire return interval is less than 2 years. Regular fire is critical to maintaining levels of plant species richness and coefficient of conservatism (Carlson et al., 2020), and has consistently been identified as necessary to maintain intact tallgrass prairie habitat (Alstad et al., 2016; Bowles & Jones, 2013; Ratajczak, Nippert, Briggs, & Blair, 2014). Regular prescribed fire was likely the primary driver in sustaining the rare native plant communities in Nachusa native prairies. Although aggressive invasive species control is common across the preserve, the management approach on native prairie sites is more cautious in deference to sensitive plant communities. As a result, native prairies do support some non-native plants; however, we observed the highest proportion of native plants in the native prairies (> 85% native; Figure 3). Given the great abundance of non-native plants in planted prairies, efforts to control invasive plants are concentrated in planted prairies.

All these management actions have been applied to all the native prairies in this study, and yet we observed differences in how the plant communities shifted over time. Sites P15 and P17 became more similar to each other. Both of these native prairies were more highly degraded than the others, and this change reflects a stronger decline in invasive species and replacement with native species. Site P19, which showed a strong increase in total plant species, but no change in proportion of native species, is considered the highest quality native prairie at Nachusa Grasslands. The initial surveys in 1995 and 1997 were likely only 0.5 m² quadrats, so some of this increase may result from including additional species in larger quadrats. We are aware of native species that have been observed at that site only after several years of management.

4.2 | Savannas

Oak savannas are an important habitat type at Nachusa Grasslands. These sites include long-lived large hardwood trees, which are not reflected in the understory vegetation surveys conducted in this study (young trees were included). Prior to restoration efforts, savannas at Nachusa look like they do throughout the Midwest: overgrown with non-native shrubs (Nowacki & Abrams, 2008). Repeated surveys in southern Wisconsin savannas showed number of trees per acre nearly doubled and 61% of species present in 1950 were no longer present in 2014 (Ladwig et al., 2018). In Iowa, removal of non-oak woody species from over-grown savannas led to increased understory
plant species richness and diversity, driven primarily by graminoid species (Brudvig, 2010). Similarly, our data show a decrease in woody 'brush' like non-native Lonicera mackii and 'weedy' Cornus racemosa and Ulmus americana and increase in herbaceous understory plants, including both native and non-native. These changes generally cancelled out any changes in total plant species or proportion of native species. Active management of these savanna systems, particularly frequent prescribed fire, have prevented invasive woody species from re-establishing.

Within our study, savannas P08 and P39 responded similarly across time, although they remained distinct communities. These sites are located on opposite sides of a series of savanna hills. They have very similar histories, and both received extensive brush removal. In both cases, these communities showed a distinct loss of non-native woody brush replaced with native herbaceous plants. Sites P24 and P41 also responded similarly, but in different ways from the other two sites. These savannas are located on different parts of the preserve and both had higher cover of native herbaceous understory initially, so the plant communities exhibited stronger expressions of what was already present rather than the more dramatic shifts in species composition observed at the other sites.

4.3 | Planted prairies

The goal of prairie plantings is to transform row crop agricultural fields into diverse native plant communities. These data reflect the earliest plantings at Nachusa Grasslands. It is interesting to note that sites P31 and P32 exhibited different directions of community shift over time. These are the oldest plantings, done in 1988 and 1987, and immediately adjacent to one another. Both showed increases in mean coefficient of conservatism, but P31 showed stronger recovery of native species including multiple indicator species that were not likely to be found in P32. It is possible weather and planting conditions in 1987 and 1988 have impacted the long-term trajectory of these plant communities (Groves et al., 2020).

Across all the planted prairies, plant communities contained 25–40 species in 2015, 75%–80% of which were native, which is lower than native prairie and savanna habitats, but a significant improvement over the agricultural fields they replaced. Previous research on chronosequences have documented declines in plant diversity and conservatism as restorations mature both at Nachusa Grasslands (Blackburn et al., 2020; Hansen & Gibson, 2014; Taft et al., 2006) and in tallgrass prairie generally (Baer et al., 2002; McLachlan & Knispe, 2005). These declines in chronosequences could reflect two ecological forces: (1) loss of species from the community through competition and other selecting forces and (2) more recent restorations include greater numbers of species in seed mixes than older restorations. In many cases, and certainly at Nachusa Grasslands, both forces are likely at play.

Longitudinal studies allow us to isolate the loss of species from the community from the confounding factor of seed mixtures and restoration practices. Our longitudinal study showed some increases in native plant community metrics in restored prairies (Figure 3), indicating species loss may not be a prevalent community assembly force in these restored prairies. Reasons for this may include the landscape nature of Nachusa Grasslands where these restorations are surrounded by high quality grasslands, including seed source. In addition, active management, including some native species overseeding, has been essential to sustaining restoration outcomes.

Restoration practices have evolved at Nachusa Grasslands, and newer plantings are planted with much higher diversity of plants (~150 species), greater seeding rates (55–80 kg/ha, milled seed (not cleaned) (Goldblum et al., 2013), and greater proportion of forbs (around 65% forbs by weight). Prairies planted with more species-rich seed mixes have less non-native species establishment and overall greater plant species richness (Grman et al., 2013; Kaul & Wilsey, 2020). We are monitoring several restored prairies planted since the late 1990s, and we hope to have enough future data to contrast the longitudinal development of these younger prairies with the older plantings to further understand the interaction of community assembly processes and restoration practices.

5 | CONCLUSION

Increasingly, political agendas, such as the UN Decade on Restoration, are upholding ecosystem restoration as a transformative approach to addressing environmental challenges. There is tremendous potential from ecosystem restoration, and it is imperative that restoration practitioners and scientists understand how well restoration efforts deliver the outcomes promised. As communities and land managers prioritize and set goals for restorations, it is equally important to consider how to measure progress towards those goals. At Nachusa Grasslands, initial restoration goals largely centred around protecting and restoring diverse, native prairie plant communities. Establishing permanent transects and resampling those transects three to five times across 20 years has allowed us to evaluate the success of restoration at Nachusa Grasslands and overall, we are satisfied with the outcomes. There are areas for improvement, particularly in increasing and sustaining native plant diversity in plantings. Work continues to meet these goals, particularly with the addition of bison grazing, which was not captured in this data set. Indigenous people actively set fires and encouraged grazing over thousands of years of tallgrass prairie development. We have learned these active and sustained management practices are critical to the long-term success of tallgrass prairie restoration. Future re-evaluations of new data after the incorporation of grazing disturbance will provide additional insights. As a disturbance dependent ecosystem that has developed with human management over millennia, tallgrass prairie restoration will never thrive with a ‘one and done’ approach. We recognize all restoration projects are limited by funds, time and staff and all too often, regular monitoring of restoration outcomes is the first task to fail to the wayside. However, without measuring outcomes, it is difficult, if not impossible to make the case for restoration success or future restorations. In this situation, a thoughtful long-term...
experimental design allowed time, effort and funds to be used judiciously to yield a dataset directly measuring the initial goals of the restoration project.

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CONFLICT OF INTEREST
The authors declare no conflict of interest.

AUTHORS’ CONTRIBUTIONS
BPK designed the experiment, oversaw field data collection and edited and approved the manuscript. EMB coalesced and analyzed the data and wrote the manuscript.

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REFERENCES


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