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Rapid and transient changes during 20 years of restoration management in savanna-woodland-prairie habitats threatened by woody plant encroachment

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Abstract Open-structured habitats, such as heathlands, grasslands, and savannas, support unique plant diversity but are threatened by woody plant encroachment in diverse locations globally. During 20 years of vegetation management aimed at restoring and sustaining oak savannas, woodlands, and wet prairies in a Midwestern USA oak savanna region, we examined change in 17 plant community metrics ranging from cover of rare species to pollinator floral resources. Metrics indicative of open-habitat quality increased rapidly but also declined rapidly with time since disturbance spanning a first decade of intensive management (tree cutting and 4–5 fires/decade) and a second decade of less-intensive management ($>$ 4 years between fires). After initial restoration treatments reduced overstory tree density, changes in cover of open-habitat specialist species correlated with fluctuations of a brushy layer of small trees 1–10 cm in stem diameter. Between 2002 and 2018, 92% of sites where small trees increased by over 100/ha had declines in open-habitat species, whereas 72% of sites not experiencing that level of woody encroachment had sustained or increasing open-habitat species. Conserving open habitats in contemporary environments likely requires perpetually frequent low-severity disturbance (at least every 3–4 years), periodic severe disturbance (e.g., growing-season fires), or multiple treatment types (e.g., managed herbivory and fire) to synergistically limit woody encroachment. Fluctuations between positive and negative trends in the 20-year dataset also highlight that perhaps restoration success should not be evaluated on the basis of a net change from beginning to end, but rather on a time-weighted accrual of restoration benefits.

Keywords Community dynamics · Ecological restoration · Floristic quality · Open habitat · *Quercus* · Specialist species · Rare species

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Introduction

Open-structured habitats, such as heathlands, grasslands, and savannas, support unique floras within climatic regions capable of supporting forest in diverse locations globally (Ascoli et al. 2013; Kirkman et al. 2013; Poniatowski et al. 2020). Perpetuation of open habitats commonly requires recurrent disturbances (e.g., fire, herbivory, and clearing), often interacting with edaphic factors or droughts (Haney et al. 2008). If disturbances were habitually anthropogenic in origin, as they were in many regions, open habitats are considered cultural ecosystems developing under dual human and non-human influences on evolutionary timescales. For example, humans maintained species-rich grasslands on marl soil in Europe for millennia via tree clearing and pasturing of livestock (Görzen et al. 2019). In recent decades, cultural-origin open habitats have continued disappearing globally with changing land use and ongoing woody plant encroachment associated with interruption of traditional anthropogenic disturbances (Middleton 2013). When disturbances cease, encroachment by tall woody plants proceeds at varying rates within and among open habitats, as does the accompanying loss of open-habitat flora (Ridding et al. 2020). Many countries have prioritized working toward reversing these trends in protected areas, believing that the cultural origins of open habitats do not undermine (and instead may enhance) their habitat values, biodiversity, and unique species composition (Carboni et al. 2015).

While interest in sustaining open habitats is keen, restoring and maintaining them on contemporary landscapes has been uncertain and challenging. Uncertainties include effects and persistence of benefits to open-habitat species of initial restoration interventions (typically involving reducing woody encroachment or reintroducing disturbances), responses of non-native plants as reinstating open conditions and disturbances are precisely settings in which non-natives often thrive (Rossman et al. 2018), long-term changes in open communities under different disturbance scenarios, and long-term relationships of tree and brushy layers of encroaching woody plants with herbs and small shrubs in managed open habitats. Illustrating some of these challenges and uncertainties, studies in European heathlands and American savannas reported that reinstating disturbance was not necessarily able to reverse woody encroachment into open habitats or to sustain populations of open-habitat species (Borghesio 2009; Miller et al. 2017). Many interacting factors could influence treatment effectiveness, which could further hinge on dynamic contingencies, such as coincidence of treatments with droughts (O'Connor et al. 2014). As another example of uncertainties, non-native plants have increased after restoration activities in some open habitats, and the possibility of invaders persisting and competing with rare and specialist native species is a concern (Huebner 2006).

In North America, one of the largest expanses of open habitats historically was the Midwestern oak savanna region, extending across 11 million ha from western Missouri, USA, in the south, to southern Ontario, Canada, in the north (Nuzzo 1986). The region supported a mosaic of oak savanna, prairie including herbaceous wetlands, open oak woodland with tree canopy cover intermediate between savanna and forest, and forest (such as along floodplains) along gradients of edaphic factors and fire (Grimm 1983). By the 1980s, Nuzzo (1986) estimated that 99.8% of the region's open habitats were lost via conversion to other land uses (e.g., agriculture), hydrological disruption (e.g., draining wetlands), and cessation of frequent fire. Presently, much of the opportunity for recovering biodiverse open habitats is in small (often < 2000 ha), fragmented preserves now dominated by forest on sites of former open habitat. Here, we report plant community change across a 20-year period in oak savannas, woodlands, and prairies undergoing restoration management within part of the Midwestern USA oak savanna region. We divide our study period into phases representing initial restoration activities to reduce woody encroachment and subsequent intensive and less-intensive management periods intended to maintain open habitats. Our specific objectives were to (1) assess change in vegetation metrics in three categories describing tree and woody understory layers, plant community quality (e.g., specialist and rare native species, non-native species), and plants providing floral resources for priority pollinators including endangered butterflies; and (2) develop a model estimating change in cover of prairie-savanna species with variation in overstory tree layers and degree of understory woody encroachment.

Methods

Study area

We performed the study in the 1692-ha Oak Openings Preserve (41° 33′ 12″ N, 83° 50′ 8″ W) within the 47,000-ha Oak Openings region in northwestern Ohio, USA (Schetter and Root 2011). The preserve, managed by Metroparks Toledo, is 40 km southwest of the city of Toledo. From 1950 through 2018, the temperate climate, measured at the Toledo Airport 4 km from the preserve, averaged 85 cm/year of precipitation and daily temperatures of − 9/0 °C (minimum/maximum) in January and 16/29 °C in July (Midwestern Regional Climate Center, Champaign, IL, USA). Soils are sandy, deposited by Pleistocene glacial lakes, with soil drainage constraining community distribution. Low-lying, poorly drained soils are mapped as Haplaquolls of the Granby series (Stone et al. 1980). From lowlands, a few meters of topographic rise to sand ridges and uplands support drier soil classified as Udipsamments of the Oakville and Ottokee series. US Government land surveys in 1817–1832, before Euro-American settlement, revealed that the region and preserve supported three main fire-dependent vegetation types: mostly treeless wet prairies with abundant herbaceous plants on poorly drained soils; upland oak savannas with 4–40 trees/ha (≥ 13 cm in stem diameter at 1.4 m) and herbaceous-woody understories; and oak woodland with over 40 trees/ha and herbaceous-woody understories (Brewer and Vankat 2004). The dominant oaks include *Quercus velutina* (black oak) and *Q. alba* (white oak) on uplands and *Q. palustris* (pin oak) on lowlands.

Restoration design and management activities

Restoration was implemented to reestablish the open-structured oak savanna, woodland, and wet prairie habitats that, through transition to forest, were rare when the study began in the 1990s. The vegetation types targeted to restore at particular sites were based on the distribution and structure of habitats present during the 1817–1832 land surveys (Brewer and Vankat 2004), contemporary tree structure, and soil maps and physical evidence of hydrological manipulation (Online Resource 1). Locations for oak savanna or woodland restoration were uplands with drier soil (Oakville and Ottokee series) and that were forest with oak-dominated overstories and sub-canopy trees of *Acer rubrum* (red maple), *Prunus serotina* (black cherry), and *Sassafras albidum* (sassafras). Historically, either oak savanna or woodland apparently could have inhabited uplands through time, such as during fluctuations in fire and drought frequencies (Brewer and Vankat 2004). Consequently, contemporary stand structure guided if a savanna or woodland was targeted for restoration. Contemporary sites with fewer overstory oaks were targeted for savanna restoration while sites with more oaks were designated for woodland restoration. Wet prairies were targeted for restoration on poorly drained soils (Granby series) containing young (< 100 years old) *A. rubrum* forests near drainage ditches, indicative of past hydrological manipulation.

Restoration was performed at 20 sites ranging in size from 1 to 5 ha. Proportional to their availability, there were 12 sites targeted for savanna, 5 for woodland, and 3 for wet prairie restoration. Initial restoration treatments of cutting and prescribed fire were applied beginning in 1998 to each of the three managed vegetation types to reestablish open conditions (Table 1). Cutting removed non-oak trees that exceeded about 15 cm in diameter at 1.4 m (smaller trees were to be top killed by fire) on sites targeted for oak savanna or woodland restoration. To reestablish wet prairies, cutting removed all trees. Cutting was performed by hand using chain saws, and logs and slash were removed. In the first decade of the study from autumn 1998 to spring 2008, oak savanna and woodland sites were burned an average of five times (mean fire interval = 2 years) and wet prairie sites four times (mean fire interval = 2.5 years). During this intensive management period, fire-free intervals did not exceed 4 years. Burn seasonality was approximately evenly split between spring (March–May, 55% of fires) and autumn (November, 45%). Burns included backing and head fires and were low severity with typical flame heights < 2 m. During the less-intensive management decade (2009–2018), intended as a maintenance period sustaining open habitats, each managed site was burned once.

Vegetation surrounding restoration sites was mainly closed-canopy forest with *Quercus* (uplands) or *A. rubrum* (lowlands) overstories. In addition to the 20 sites where restoration occurred (termed "managed"), 10 randomly located sites (seven in upland oak forest and three in lowland wet forest dominated by

Table 1 Summary of restoration management activities in open-structured vegetation types and data collection during a 20-year period in the Oak Openings region, northwestern Ohio, USA

	Managed			Unmanaged	
	Oak savanna	Oak woodland	Wet prairie	Oak forest	Wet forest
Plots (n)	12	5	3	7	3
Tree cutting	1998–1999	1998–1999	1998–1999	None	None
1998-2008 max. FFI (yrs)[a]	3–4	3–4	4	No fire	No fire
1998-2008 no. burns/10 yrs	5	5	4	0	0
2009-2018 no. burns/10 yrs	1	1	1	0	0
Data collection: early[b]	1998–2000	1998–2000	1998–2000		
Data collection: mid	2002, 2004/2006	2002, 2004/2006	2002, 2004/2006	2002	2002
Data collection: late	2015, 2018	2015, 2018	2015, 2018	2015, 2018	2015, 2018

[a]Maximum fire-free interval as the maximum number of years between fires

[b]Data collection categorized as the early period of the study before (1998), during (1999), and one year after completion (2000) of initial restoration; the mid-part of the study as the latter part of the first decade of intensive management; and the late part of the study representing the second decade when management was less intensive. All managed plots were not able to be sampled each year in 2004–2006 but all plots were sampled in one of the years, so these years were combined and described as 2004/2006

A. rubrum) served as unmanipulated controls ("unmanaged").

Data collection

We collected data in seven of the years (including in 1998 before treatment) within the 20-year study period to characterize phases of dynamics during restoration management on the 20 managed sites according to the schedule in Table 1 and illustrated in Fig. 1. We established a permanent 0.05-ha (20 m × 25 m) plot in the center of each of the 20 managed and 10 unmanaged sites for collecting tree and understory plant community data. Each study year, sampling occurred near peak vegetation biomass during mid-late summer (July–August). On each plot, we recorded the species and diameter at 1.4 m for each tree ≥ 1 cm in diameter. Understory plant communities (synonymously termed groundlayers in savanna and woodland literature) were defined as all vascular plants inclusive of herbaceous and woody species, including individuals < 1 cm in diameter at 1.4 m for tree species. We visually categorized aerial cover of each understory species on each plot as 0.1%, 0.25%, 0.5%, 1% intervals from 1 to 10%, and 5% intervals above 10%. Cover could not exceed 100% on a plot for a species but could exceed 100% in sum for all species through layering of different species' foliage. Classification of species by growth form (e.g., forb), native/non-native status to the US, and nomenclature followed the 2019 US Natural Resources Conservation Service PLANTS Database.

Response metrics

We derived and analyzed 17 response metrics in three categories. Four metrics of (i) tree and woody understory layers included tree basal area (all stems ≥ 1 cm in diameter at 1.4 m of tree species), tree density (divided into small stems 1–10 cm in diameter and large stems > 10 cm in diameter), and cover of understory woody plants (shrubs and trees < 1 cm in diameter at 1.4 m). As a multivariate metric of (ii) understory plant community quality, we derived species × plot-year matrices of relative cover, calculated for each plot-year combination as cover of $\text{species}_i/\sum$ cover of all species in a plot-year combination. Eight univariate metrics included understory non-native and native cover and richness (species/0.05 ha); a floristic quality index; and the number (per

Fig. 1 Changes in two example plots in managed oak savannas in the Oak Openings region, northwestern Ohio, USA. The first plot is in the left column and the second plot is in the right column, with views progressing through time down columns. From top to bottom, years progress from 1998 (before restoration management), 1999 (during), 2002 (4 years into management), 2005 (7 years), 2015 (17 years), and 2018 (20 years). After initial tree cutting and prescribed fires, herbaceous plants dominated (e.g., the purplish-blue forb, *L. perennis*, in the left column 2005 photo) in 2002 and 2005, with comparatively low cover of woody plants. By 2015 and 2018, woody plants had increased and while herbaceous species persisted, their cover was low. Photos by Jaeger (1998, 1999, 2005) and Abella (2002, 2015, 2018)

0.05 ha) of state-listed rare species, wetland species, and species on lists of taxa diagnostic for historical reference ecosystems. To calculate floristic quality, we obtained coefficients of conservatism for each species from lists for Ohio (Andreas et al. 2004). The coefficients rank the fidelity of native species to high-quality natural habitats and range from 0 (widespread species inhabiting a variety of sites) to 10 (species restricted to natural habitats). Floristic quality was calculated for each plot and year as the sum of native species coefficients divided by the square root of native species richness (Andreas et al. 2004). State-listed rare species were obtained from 2018 to 2019 lists provided by the Ohio Department of Natural Resources (Columbus, Ohio, USA). Rankings for species' affinities for wetlands were obtained from Andreas et al. (2004) and included three categories: dry (upland and facultative upland species), intermediate (facultative), and wetland (facultative wetland and obligate wetland species). Species considered diagnostic of historical reference ecosystems recorded in 1817–1832 land surveys were totaled from Brewer and Vankat (2004).

Four metrics of (iii) pollinator habitat indicators included cover of *Rubus* spp., *Lupinus perennis* (wild lupine), nectar plants favored by *Lycaeides melissa samuelis* (Karner blue butterflies), and prairie-savanna forbs and small shrubs. We chose *Rubus* as an indicator because it was the most visited genus by bees in a study 8 km from ours (Arduser 2010). We selected *L. perennis* because it is the larval host plant of *L. samuelis*, listed by the US Endangered Species Act (Plenzler and Michaels 2015). To represent nectar plants favored by these butterflies in Midwestern savannas and occurring in our study area, we totaled cover of *Arabis lyrata* (lyrate rockcress), *Asclepias tuberosa* (butterfly weed), *Euphorbia corollata* (flowering spurge), and *Monarda punctata* (spotted beebalm; Grundel et al. 2000). We used published literature to compile a list of 70 native, open-habitat specialist species (65 forb and 5 small shrub species such as *Tephrosia virginiana* [goat's-rue]) recorded in our study that provide floral resources and are largely restricted to prairie-savanna habitats (Bray 1958; Leach and Givnish 1999; Arduser 2010; Grundel et al. 2011; Pavlovic et al. 2011). These 70 species indicate open-habitat quality for both plants and pollinators, given coupling of plant and insect composition in Midwestern savannas (Shuey et al. 2012; Lettow et al. 2018).

Data analysis

In a first set of analyses, we assessed temporal change across the seven measurement years, spanning 1998 (before treatment) through 2018 (20 years after initial restoration), within each managed vegetation type (oak savanna, woodland, and wet prairie). We analyzed univariate response metrics using generalized linear models including plot as the subject, year, and autoregressive correlation structure for repeated measures (PROC GENMOD in SAS 9.4). Continuous variables were modeled using a normal distribution and identity link function. Count data (e.g., species richness) were modeled using a negative binomial and log link function. We used Tukey tests for multiple comparisons of least-squares means among years. Variation in understory species composition (species × plot-year matrices of relative cover) was explored using non-metric multidimensional scaling in PC-ORD 7.07. Ordinations were computed with "thorough" default settings, Sørensen distance, and a secondary matrix of the 16 univariate metrics and species cover input to display correlations with understory compositional gradients.

In a second set of analyses, we used generalized linear models and non-metric multidimensional scaling to compare all five vegetation types (managed types and dry and wet unmanaged forests) within years (2002, 2015, and 2018) for which data were also available for unmanaged forests. As in the first set of analyses, we used data distributions appropriate to univariate variables, Tukey tests for multiple comparisons, and default settings for ordinations.

To model cover of the 70 open habitat-specialist species as a function of woody plant abundance, we used regression and classification trees. These models estimate continuous (regression tree) or categorical responses (classification tree) by partitioning data into increasingly homogenous subsets using explanatory variables (Breiman et al. 1984). For the regression tree, the response metric was cover of open-habitat species in 2002 during intensive management. For the classification tree, the response metric was whether a plot experienced a decline in cover of open-habitat species between 2002 and 2018 (the end of the study's second decade during less-intensive management).

Explanatory variables included the density of small (1–10 cm in diameter) and large (> 10 cm) trees, basal area, and cover of woody plants in the understory. We used the RandomTree algorithm for the regression tree and the J48 algorithm for the classification tree in Weka 3.8.

Results

Tree and woody understory layers

Density of large trees and basal area were stable or changed consistently following initial restoration treatments within vegetation types, contrasting with the sharply fluctuating density of small trees (1–10 cm in diameter) and cover of understory woody plants in managed habitats (Fig. 2). Density of large trees significantly declined during restoration management in all managed habitats and remained lower than in unmanaged forests in all measurement years within the last 16 years of the study. Following completion of initial restoration treatments, density of large trees stabilized in savannas while it consistently slowly declined in woodlands. Via growth of residual trees, basal area changed little through time in oak savannas and woodlands. For small tree density and understory woody cover in managed habitats, the highly variable fluctuations and transitions between size classes (i.e. stems of tree species attaining diameters of 1 cm and therefore no longer contributing to measured understory woody cover) limited statistical significance of some comparisons. However, changes that were statistically significant, combined with descriptive trends in means, indicated a general trend of declining or low abundance from before management to the middle part of the study's first decade during intensive management. By 2018 following less-intensive management during the study's second decade, cover of understory woody plants or density of small trees, or both, were generally greater than before management or in 2002 and 2004–2006 during the middle part of the intensive management decade. The numerical changes accompanied physiognomic shifts between herbaceous- and woody-dominated understories (Fig. 1).

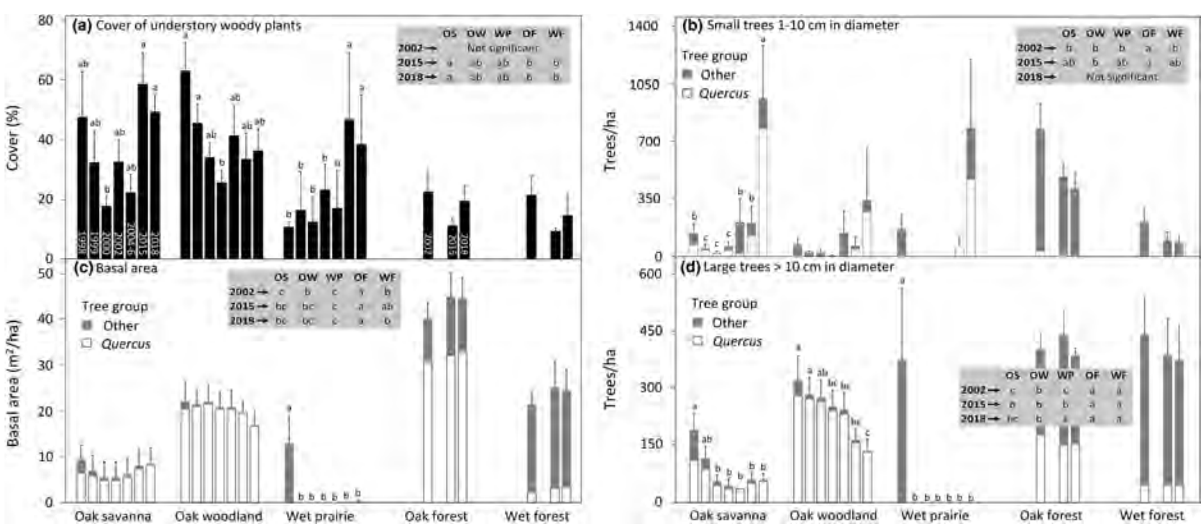

Fig. 2 Changes in abundance of woody plants during a 20-year period of restoration management aimed at conserving open-structured habitats and compared with unmanaged forests in the Oak Openings region, northwestern Ohio, USA. Values are means and error bars are one standard error of means. In cases where means are subdivided into categories for descriptive purposes, standard errors and statistics are for non-subdivided total means. Within each panel and separately within each managed vegetation type (savannas, woodlands, and prairies), letters compare means through time. If letters are absent for a managed vegetation type, no difference significant at $P < 0.05$ occurred among years. Data were collected for unmanaged forests in three of the years (compared among vegetation types within a year but not across years). Inset gray boxes summarize comparisons of means across all five vegetation types (abbreviated by the first letters of vegetation type names) within each available year (2002, 2015, and 2018) separately

Understory plant community quality

We detected a total of 401 plant species on plots during the study. Of these, 85% (341 species) were native and 15% (60 species) were non-native. Most of the species were perennial (90%, 360 species), with the remainder including 21 annual (5% of total species), 13 annual-biennial (3%), and 7 biennial species (2%). Forbs comprised 53% (211 species) of the total species, followed by graminoids (18%, 73 species), shrubs (15%, 62 species), trees (9%, 35 species), ferns (3%, 12 species), and vines (2%, 8 species).

Each of the managed vegetation types exhibited unique understory species composition in 1998 before restoration management and this diversity was generally maintained during the next 20 years (Fig. 3a). For example, the highest average Sørensen similarity between vegetation types was only 22% (between savannas and woodlands) in 2002 and 15% in 2018 (Fig. 3b). Species composition of oak woodlands and wet prairies was only 4–6% similar. Illustrated for 2002 mid-way into the first decade of intensive management and for 2018 after less-intensive management in the second decade, several species and vegetation structural variables were correlated with species compositional variation across vegetation types (Fig. 3c). For example, conservative, rare, and open-habitat specialist species were associated with managed habitats in 2002. Some of these species included the annual forb *Krigia virginica* (dwarf dandelion), perennial forb *L. perennis*, and the perennial grass *Schizachyrium scoparium* (little bluestem) associated with oak savannas (Online Resource 3). The shrub *Vaccinium pallidum* (Blue Ridge blueberry), fern *Pteridium aquilinum* (brackenfern), and sedge *Carex pensylvanica* (Pennsylvania sedge) were among those associated with oak woodlands. Species associated with wet prairies included the perennial forbs *Coreopsis tripteris* (tall tickseed) and *Euthamia graminifolia* (grass-leaved goldenrod) and the perennial grass *Dichanthelium clandestinum* (deertongue). By 2018, however, associations of conservative, rare, and open-habitat species with community compositional variation weakened after many species declined (Fig. 3d, Online Resource 3).

Univariate metrics characterizing specialist species (floristic quality index, rare species, wetland species, and species typifying reference ecosystems) were higher in oak savannas and wet prairies in one or more middle years of the study than either before (1998) or during (1999) early restoration (Fig. 4). Metrics of specialist species changed less in woodlands, except that post-restoration increases in species typifying reference ecosystems occurred some years. Plots in unmanaged forests did not contain any state-listed rare species throughout the study, while plots in managed habitats had numbers of rare species when management began that were at least maintained through the next 20 years.

Although species composition fluctuated, native species dominated all vegetation types throughout the study (Fig. 5). There was no statistically significant change in non-native species cover through time in managed vegetation types. Non-native species richness either did not significantly change (oak savannas and woodlands) or significantly decreased from early to some later years (wet prairies). Native richness generally peaked in the study's middle or later years in managed habitats. Conservative (coefficients 7–10) and moderately conservative (coefficients 4–6) native species contributed to increased richness in managed habitats, particularly mid-way through the study although several of these species remained present in 2018. Oak forests were the least species-rich, harboring significantly fewer species than at least one other vegetation type in all years. Native cover, in general, was lowest during an early or middle year of the study in oak savannas and woodlands, before increasing to not differ in the later years from the 1998 pre-treatment levels. Woody plants, along with *Pteridium aquilinum* in woodlands, supplied much of the cover in savannas and woodlands. Forbs and graminoids, in contrast, supplied most of the cover in wet prairies, although woody plants proportionally increased later in the study.

Pollinator habitat quality

Indicator plants for pollinator habitat quality fluctuated widely through time in managed habitats but persisted with at least some cover in all years, compared to being nearly absent from unmanaged forests (Fig. 6). In oak savannas, cover of *L. perennis*, the larval host plant for endangered *Lycaeides melissa samuelis*, peaked in 2004–2006 during intensive management. Cover of *Rubus* spp., providing floral resources to a variety of insects, was generally higher

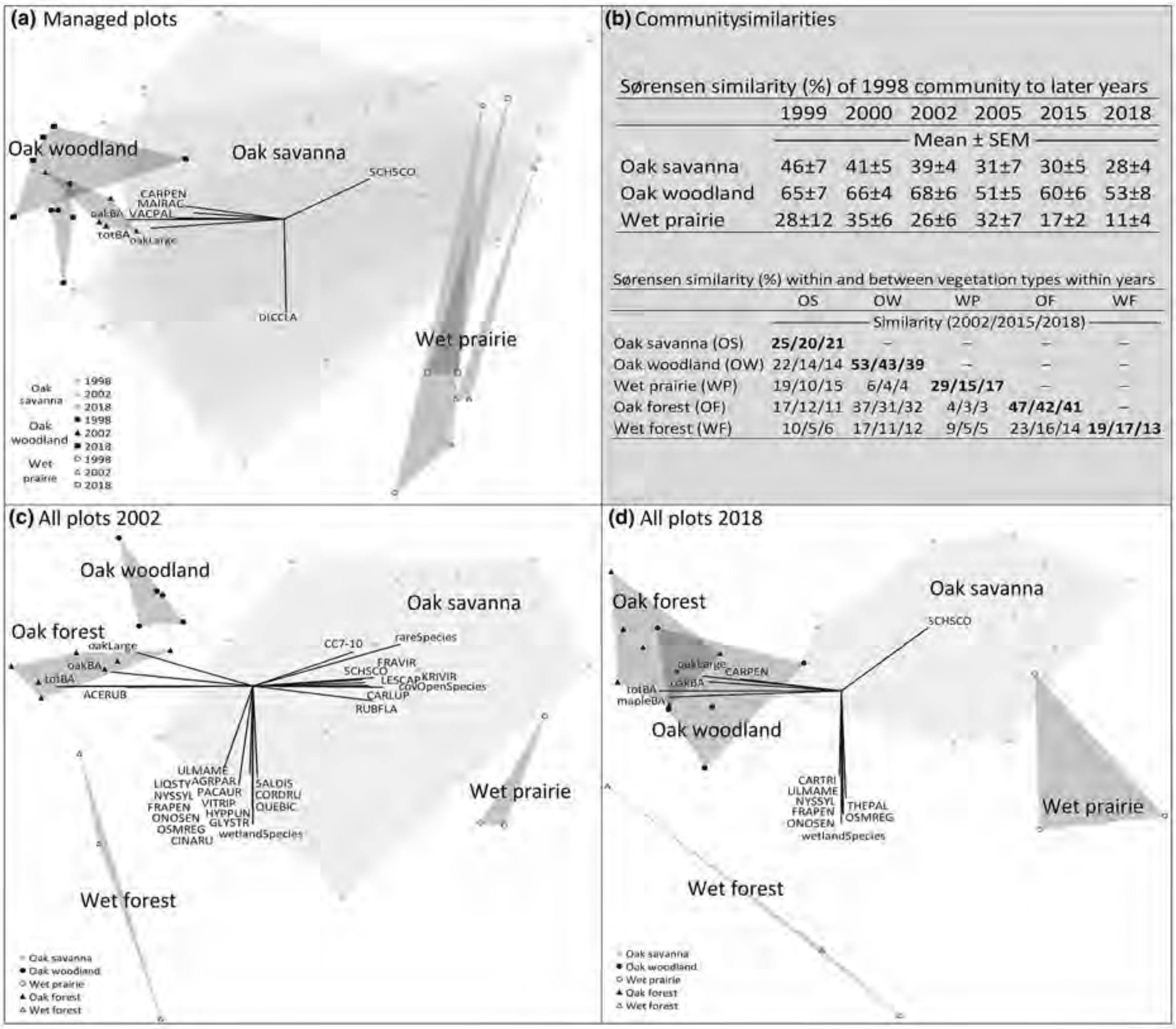

Fig. 3 Variation in plant community composition during a 20-year period of restoration management aimed at conserving open-structured habitats and compared with unmanaged forests in the Oak Openings region, northwestern Ohio, USA. Vectors in the ordinations (**a**, **c**, **d**) depict variables and species correlated ($r > 0.33$) with community composition. Full names for the abbreviations are in Online Resource 2

in oak savannas later in the study during less-intensive management. Oak woodlands and forests had minimal cover of *Rubus*.

Relationships of prairie-savanna species with tree layers

Cover of 70 species of prairie-savanna forbs and small shrubs did not exhibit significant temporal change within vegetation types (Fig. 6d), as instead, their cover was correlated with among-site variation in tree layers. Cover of prairie-savanna species in 2002, mid-way through the first decade during intensive management, and their change between 2002 and 2018, was modeled by dual variation in tree basal area and number of small trees (Fig. 7). In 2002, cover of prairie-savanna species was maximized at low tree basal areas, but within this low basal area range, cover was halved if the density of small trees exceeded 100/ha. For plots that subsequently experienced an increase of over 100 small trees/ha between 2002 and 2018, 92% had a concomitant decline in cover of prairie-savanna species. This decline occurred even when total tree basal area (driven by large overstory

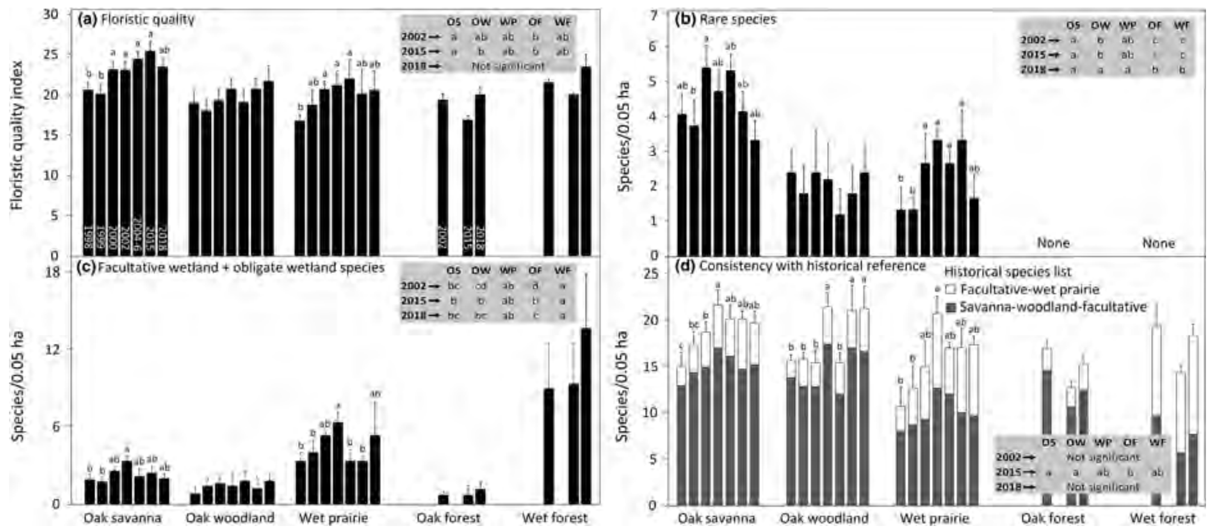

Fig. 4 Changes in floristic quality, number of rare species, species associated with wetlands, and the number of species found that were on lists characterizing historical reference ecosystems. Measurements were made during a 20-year period of restoration management aimed at conserving open-structured habitats and compared with unmanaged forests in the Oak Openings region, northwestern Ohio, USA. Values are means and error bars are one standard error of means. In cases where means are subdivided into categories for descriptive purposes, standard errors and statistics are for non-subdivided total means. Within each panel and separately within each managed vegetation type (savannas, woodlands, and prairies), letters compare means through time. If letters are absent for a managed vegetation type, no difference significant at $P < 0.05$ occurred among years. Data were collected for unmanaged forests in three of the years (compared among vegetation types within a year but not across years). Inset gray boxes summarize comparisons of means across all five vegetation types (abbreviated by the first letters of vegetation type names) within each available year (2002, 2015, and 2018) separately

trees) changed little. In contrast, 72% of plots without increases exceeding 100 small trees/ha exhibited sustained or increased cover of prairie-savanna species between 2002 and 2018.

Discussion

Temporally fluctuating benefits and evaluations of restoration success

Benefits of ecological restoration appeared quickly but were lost nearly as quickly when restoration management became less frequent. Similar findings were reported when restoring some other open habitats affected by woody plant encroachment, such as heathlands in Italy (Borghesio 2009), grasslands in Romania (Görzen et al. 2019), and elsewhere in Midwestern USA oak savannas (Anderson et al. 2000; Reinhardt et al. 2017). The initial increases in desirable metrics that we observed during intensive restoration management in the first decade is noteworthy, however, in illustrating that these ecosystems can quickly respond to restoration, as opposed to being recalcitrant. In fact, it may be that the initial restoration of these open habitats is easier to accomplish than is the subsequent management or maintenance phase. This feature may be inherent to open habitats threatened by woody encroachment, differing from ecosystems where initial restoration may be long and arduous, but once achieved, relatively self-sustaining.

Results may also represent a case where evaluating restoration success based on time-weighted accrual of benefits, prevention of undesirable conditions, and the concept of an ecological bridge is more representative than evaluating success based on the net change from beginning to end. Exemplifying time-weighted accrual of benefits, increased floristic quality after restoration of savannas and prairies characterized more of the 20-year study than did no increase indicated in the last measurement by the lack of net change from beginning to end. By not incorporating fluctuating intervening habitat values, perception of restoration success using net change would be contingent on the final measurement's time since most recent management activity. In another example of time-

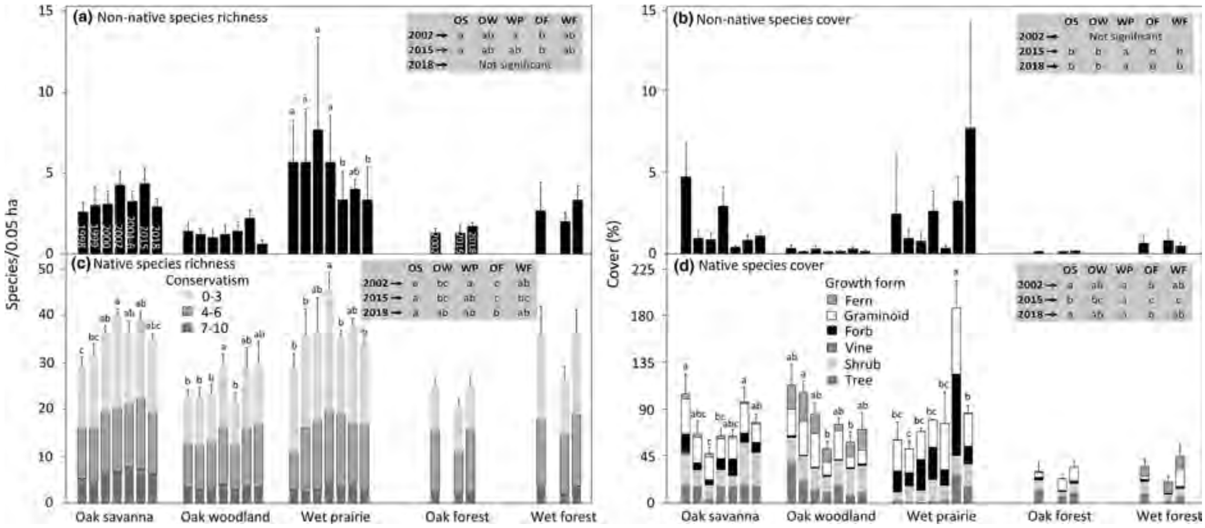

Fig. 5 Changes in species richness and cover of non-native and native understory plants during a 20-year period of restoration management aimed at conserving open-structured habitats and compared with unmanaged forests in the Oak Openings region, northwestern Ohio, USA. Values are means and error bars are one standard error of means. In cases where means are subdivided into categories for descriptive purposes, standard errors and statistics are for non-subdivided total means. Within each panel and separately within each managed vegetation type (savannas, woodlands, and prairies), letters compare means through time. If letters are absent for a managed vegetation type, no difference significant at $P < 0.05$ occurred among years. Data were collected for unmanaged forests in three of the years (compared among vegetation types within a year but not across years). Inset gray boxes summarize comparisons of means across all five vegetation types (abbreviated by the first letters of vegetation type names) within each available year (2002, 2015, and 2018) separately

weighted accrual of benefits, meta-population theory suggests that transient habitat in space and time can be crucial to certain species. In Midwestern savannas, the endangered butterflies *Lycaeides melissa samuelis* quickly colonize burned areas and utilize them for 3 years before moving to other recently burned areas, avoiding habitat unburned for 4 or more years (Pickens and Root 2009). Relative to prevention of undesirable conditions, our site selection criteria established a stringent benchmark of initial settings against which to assess post-restoration changes, because sites targeted for oak savanna restoration were among the more open sites on the landscape and contained some populations of open-habitat species before restoration activities. While restoration management did not produce a net increase in all desirable metrics, conservation-priority open-habitat species (e.g., *L. perennis*) were at least maintained, potentially preventing the loss of such species that has been widespread with forest maturation (Milbauer and Leach 2007). It is also possible that even only brief, intermittent periods of open conditions enable open-habitat species to replenish their regeneration potential as an ecological bridge to withstand periods of woody encroachment (Middleton 2002). In a previous investigation in the study area in 2018, we found that persistent soil seed banks were unusually rich in restoration-target species including rare prairie-savanna species not necessarily found in vegetation (Abella et al. 2020). This is significant because seeds of some prairie-savanna species can persist in soil for at least 8 years (Kaeser and Kirkman 2012). In calcareous grasslands in Switzerland, Stöcklin and Fischer (1999) found that risk of local extinction was halved for species that formed seed banks persisting at least 5 years.

Our results and those of interval-burning experiments (e.g., Peterson and Reich 2008; Knapp et al. 2015) suggest that benefits for open-habitat species decline with increasing time since most recent management activity, but perhaps restoration value of brief periods of woody encroachment between management intervals should not be overlooked within long-term restoration assessments. Brushy habitats consisting of resprouting *Quercus* stems and possibly those of other deciduous tree species after frequent fires, extensively noted in early 1800s descriptions of Midwestern savanna landscapes, are considered part of reference

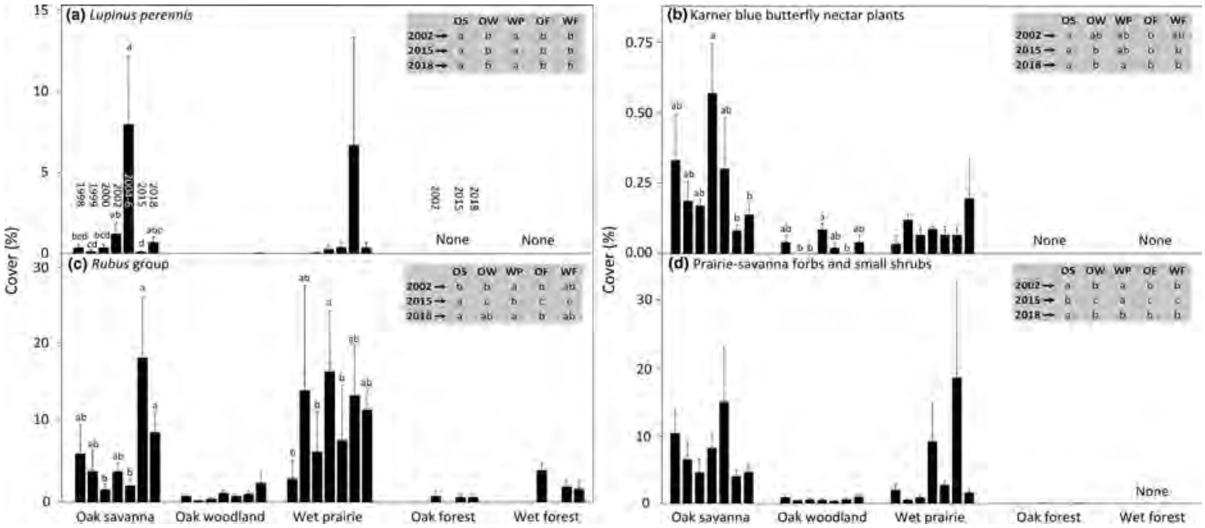

Fig. 6 Changes in indicator plants of pollinator habitat quality during a 20-year period of restoration management aimed at conserving open-structured habitats and compared with unmanaged forests in the Oak Openings region, northwestern Ohio, USA. Response variables include: **a** *L. perennis*, the larval host and **b** favored nectar plants of endangered *Lycaeides melissa samuelis* (Karner blue butterflies); **c** *Rubus* spp., important nectar plants for *L. samuelis* and other pollinators; and **d** 70 species of forbs and small shrubs supplying floral resources to a variety of pollinators. Values are means and error bars are one standard error of means. In cases where means are subdivided into categories for descriptive purposes, standard errors and statistics are for non-subdivided total means. Within each panel and separately within each managed vegetation type (savannas, woodlands, and prairies), letters compare means through time. If letters are absent for a managed vegetation type, no difference significant at $P < 0.05$ occurred among years. Data were collected for unmanaged forests in three of the years (compared among vegetation types within a year but not across years). Inset gray boxes summarize comparisons of means across all five vegetation types (abbreviated by the first letters of vegetation type names) within each available year (2002, 2015, and 2018) separately

ecosystem models (Nuzzo 1986). However, spatial and temporal variability and ecological features of the brushy layers are poorly understood in reference models, and post-settlement changes essentially eliminated brushy savanna remnants available to study (Grimm 1983). Contemporary restored savannas and woodlands with moderately dense brushy understories comprise optimal habitat for some birds (Reidy et al. 2014), and plant diversity can peak at the transition point in time between herbaceous- and woody-dominated understories (Anderson et al. 2000; Peterson and Reich 2008). The challenge for restoration management is that densification and increasing stem size of woody understory layers can quickly degrade habitat even for species benefitting from some brush cover and complicate using fire or cutting to reduce the layers (Taft 2009).

Factors in the development of woody understory layers

While increasing influence of the woody understory layer was correlated with less-intensive management, three other factors could have contributed: accumulation of stems, lack of large herbivores, and climatic changes. Nearly all sapling-sized individuals (i.e. the 1–10 cm diameter class in our study) of the deciduous tree species (mainly *Quercus* spp., *A. rubrum*, *P. serotina*, and *S. albidum*) forming much of the woody understory layer resprout after cutting, fires, and other low-severity disturbances top kill stems (Abella et al. 2019). With each successive top-killing event, resprout shoots can continue accumulating to levels even greater than found initially (Peterson and Reich 2001; Haney et al. 2008; Knapp et al. 2015). As a result, when overstory canopies are relatively open—precisely the conditions created by restoring open habitats—repeated management activities such as prescribed fire (Hutchinson et al. 2012) ironically

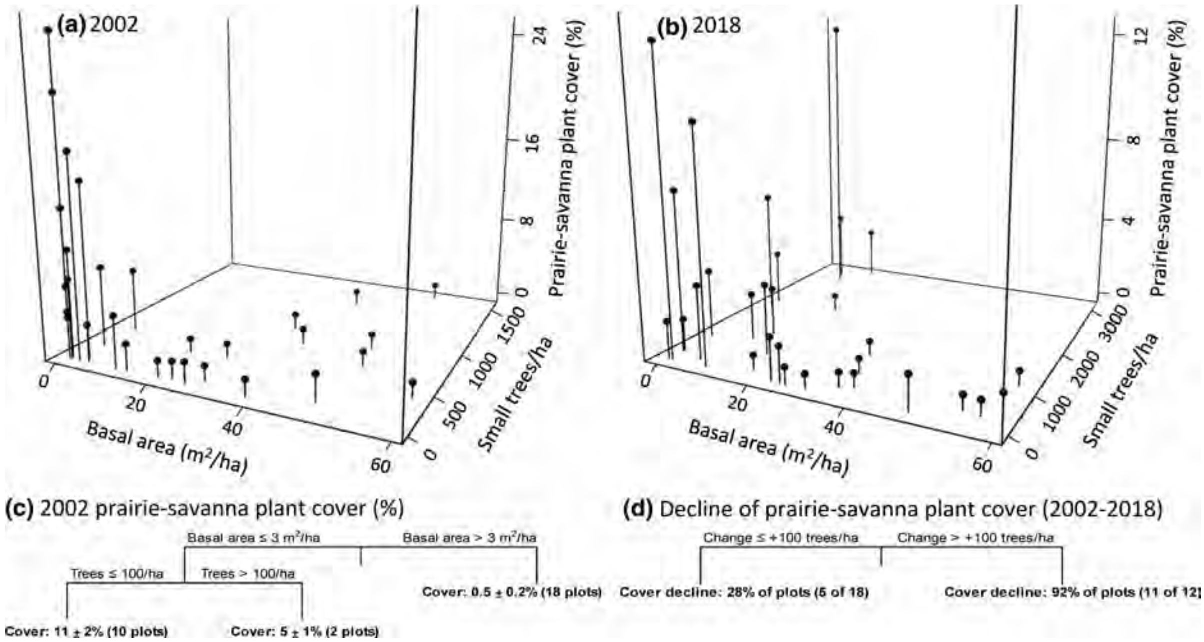

Fig. 7 Variation in the total mean cover of 70 prairie-savanna species along gradients of tree basal area and density of small trees (1–10 cm in diameter) on 30 plots across open and forest habitats in the Oak Openings region, northwestern Ohio, USA. Scatterplots show associations in 2002 and 2018 (note the difference in scales of y axes). The (**c**) regression tree provides estimates of cover (mean ± SEM) of prairie-savanna species for 2002 as a function of stand basal area and density of small trees (model r = 0.60). The (**d**) classification tree estimates the percentage of plots showing a decline or increase in cover of prairie-savanna species between 2002 and 2018, with the best-fitting model requiring only density of small trees (model classification accuracy = 80%, fivefold cross-validation accuracy = 77%, kappa statistic = 0.53)

could increase susceptibility of restoration sites over time to woody encroachment in the event management activities cease or become less frequent.

Presence of the large ungulates *Bison bison* (bison) and *Cervus canadensis* (elk) are part of historical reference conditions of Midwestern ecosystems, including in Ohio which both species inhabited (Allen 1876). In northwestern Ohio around our study area, "vast herds" of *B. bison* were described along southern and western Lake Erie during the 1600s and 1700s before the species was largely extirpated from the state by the late 1700s (Allen 1876). Historical functions of these ungulates are poorly understood but potentially substantial, as losing them could have curtailed a factor limiting woody plant layers (Hess et al. 2014; O'Connor et al. 2014). On modern landscapes in the Great Plains, *B. bison* primarily consume grasses, but sometimes browse woody plants and reduce woody cover through trampling and abrasion (Coppedge and Shaw 1997). As a surrogate for wild ungulates in a Wisconsin savanna, managed herbivory by domestic ungulates (*Bos taurus* [Scottish Highland cattle]) halved woody plant density and acted synergistically with fires to reduce woody cover (Harrington and Kathol 2009).

While tree thickets have long rapidly developed during fire-free intervals in prevailing climates of Midwestern savannas and woodlands based on numerous accounts in the 1700–1800s (e.g., Bourne 1820), the potential role of contemporary climatic change in exacerbating woody encroachment could be significant (Kulmatiski and Beard 2013). The Midwest has been shifting toward moister early summers, illustrated by the Palmer Drought Severity Index for northwestern Ohio encompassing our study area (Online Resource 4). For example, in the 58 years from 1931 to 1988, May–June droughts occurred on average every 4 years but only once (2012) in the 31 years since. Consecutive droughts two or more years in a row happened four times between 1931 and 1966 but were absent the last 54 years. Extending the climatic history using tree rings in eastern Ohio, Matheus and Maxwell (2018) found that summer droughts from 1680 to 1895 were more frequent, lengthy, and severe than those of the past 125 years. The severest drought of the last 55 years, in 1988, ranked as merely the 40th driest since 1680 (Matheus and Maxwell 2018). Early summer moisture correlates with annual growth in *Q. velutina* and the study area's other major tree species (LeBlanc and Stahle 2015). Furthermore, given water availability, trees have increased growth the most among plant groups with increasing atmospheric CO_2, while forbs and C_4 grasses minimally responded (Long et al. 2004). Although management factors such as burn frequency rather than climate may still primarily govern change in managed open habitats, it is possible that climatic conditions of recent decades are among the most conducive to woody encroachment of at least the past three centuries.

Restoration management options for sustainability

Woody encroachment and rapid declines of open-habitat species on restoration sites pose formidable challenges to restoration management, especially in small, fragmented preserves. Three main options, not necessarily mutually exclusive, seem potentially feasible for sustaining restoration gains, at least intermittently. Sites could be designated to undergo frequent, low-severity management essentially indefinitely. Potentially varying with climate, site productivity, herbivory, and traits of the constituent species, the frequency of typical low-severity, dormant-season burns (or partial surrogates such as cutting) needed to forestall woody encroachment in open habitats ranges globally from a few years to decades (e.g., Dunwiddie 1998; Borghesio 2009; Petersen and Drewa 2014). Many sites in the Midwestern oak savanna region, including apparently in our study, require the frequent end of the spectrum (Taft 2003; Bowles et al 2011; Abella et al. 2018). A threshold of a maximum of 3–4 years between low-severity fires may generally exist for limiting development of dense tree thickets in these ecosystems (Peterson and Reich 2001; Haney et al. 2008; Knapp et al. 2015). Within this frequency range, variation in fire frequency of just 1–2 years can apparently influence the short- and long-term proportional cover of different plant functional groups, such as graminoids and forbs (Peterson and Reich 2008), as well as some pollinator species associated with them (Pickens and Root 2009). Frequent burning is challenging in contemporary preserves owing to variable weather narrowing suitable windows for fire, smoke management and other human and ecological considerations, and a need for perpetually available resources for management (Schwartz and Hermann 1997). Alternatively, areas could be managed as shifting mosaics where sites are temporarily intensively restored to open habitats, abandoned for a decade or more during which woody encroachment would likely proceed, then intensively restored again. The shifting mosaic concept may be consistent with spatio-temporal dynamics on historical reference landscapes but would likely be constrained by the small size of contemporary preserves and resources required for intensive restoration (Brudvig 2010). Another option could include further exploring using higher-severity disturbances, management activities timed when woody plants may be most vulnerable (e.g., growing-season fires), and combinations of multiple treatments potentially synergistically producing more persistent effects (Dunwiddie 1998; Harrington and Kathol 2009; Ascoli et al. 2013). In a rare published example of testing high-severity fire in Midwestern savannas, Haney et al. (2008) surmised that periodic high-severity fires could enhance effectiveness of repeated low-severity fires for curtailing woody encroachment.

Lack of increase in non-native plants

Non-native species did not increase significantly during the study, despite reinstating open tree canopies and disturbances, conditions often conducive to non-native plant invasions including in some previous savanna-woodland restoration studies (Lezberg et al. 2006; Brudvig 2010). Non-natives might not have increased in our study because non-native abundance was low when treatments began and in adjacent forest habitats, soil seed banks were generally dominated by native species (Abella et al. 2020), non-native species most benefiting from fire were not prevalent (Huebner 2006), and treatments are routinely performed for non-natives around the study area. Non-natives could also have been suppressed during the study's second decade precisely because woody encroachment (via native species) occurred, though it is noteworthy that many of the most invasive non-native species in eastern oak ecosystems are woody plants themselves capable of creating woody encroachment (Becker et al. 2013). We also found no increase in non-natives in unmanaged forests. This is significant for conserving forests as native-dominated habitats and for providing initial conditions of few non-natives if future open-habitat restoration is undertaken in forests.

When is ecological restoration complete and ecosystems self-sustaining?

Changes in response metrics during the 20-year period provide perspective for achieving restoration goals based on the degree of attaining (or trajectory toward attaining) some attributes of restored ecosystems (Society for Ecological Restoration International Science and Policy Working Group 2004). Focusing on the first three attributes, which relate to species composition, restoration sites did attain a trajectory toward overall increases in species characteristic of reference ecosystems (Attribute 1; Fig. 4d), were dominated by native species (Attribute 2; Fig. 5d), and contained essential plant functional groups at least transiently (Attribute 3). For example, the functional groups of wetland plants (Fig. 4c) and some plants for pollinators (Fig. 6a, c) transiently increased after restoration in one or more vegetation types. Additionally, while too much *Quercus* recruitment would undermine goals of reestablishing open habitats, *Quercus* trees are a key functional group to sustain oak savanna and woodland habitats. *Quercus* recruitment failure has been widespread in eastern North American forests (e.g., Hutchinson et al. 2012), but post-restoration conditions in open habitats of our study supported profuse *Quercus* recruitment (Fig. 2b). Considering the ninth attribute (centering on sustainability), restored ecosystems following the initial restoration treatments may have been self-sustaining to a degree similar to reference ecosystems. While many restoration gains for open-habitat features were lost in the second decade during reduced disturbance frequency, historical reference ecosystems would also lose open-habitat features when disturbances became infrequent (Bourne 1820). However, the details of to what extent (or in what timeframes) open habitats were cyclic with woody encroachment in reference ecosystems are poorly understood, complicating comparing sustainability of contemporary restored and reference ecosystems under periodic disturbance. Two of the major unknowns in reference ecosystems include the roles of severer disturbances (e.g., fires) and synergy among multiple disturbance types (e.g., fires and herbivory) in sustaining open habitats. Further experimentation with incorporating severe or synergistic disturbances into open-habitat restoration may offer insight into past and present self-sustaining processes within open habitats susceptible to woody plant encroachment.

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Author contributions JFJ conceived the research idea; all authors designed and performed the data collection; SRA performed analyses and primarily wrote the paper with help and ideas from all authors; all authors edited the manuscript.

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Compliance with ethical standards

Conflict of interest The authors declare they have no conflict of interest.

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Online Resource 1 Illustration on example study sites of criteria for identifying target vegetation types for restoration in the Oak Openings region, northwestern Ohio, USA. Upper photos: on dry upland sites historically supporting either oak savanna or woodland, existing stand structure guided whether oak savanna or woodland was targeted for restoration. Sites containing few overstory oaks were targeted for savanna restoration while sites with many overstory oaks were targeted for woodland restoration. The site in the left photo contained only 20 *Quercus velutina* trees/ha that were > 30 cm in diameter (compared with a total of 140 *Prunus serotina* trees/ha) and thus was targeted for savanna restoration. The site in the right photo had 140 trees/ha of *Quercus alba* and *Q. velutina* that were > 30 cm in diameter and was targeted for woodland restoration. Bottom photos: sites on hydric soils with young *Acer rubrum* (shown in the left photo with 800 trees/ha) and that typically contained evidence of hydrological manipulation (e.g., the drainage ditch in the right photo just north of the location of the left photo) were targeted for wet prairie restoration. Top and bottom left photos taken in 1998 (pre-treatment) by JFJ. Bottom right photo taken in 2015 by SRA

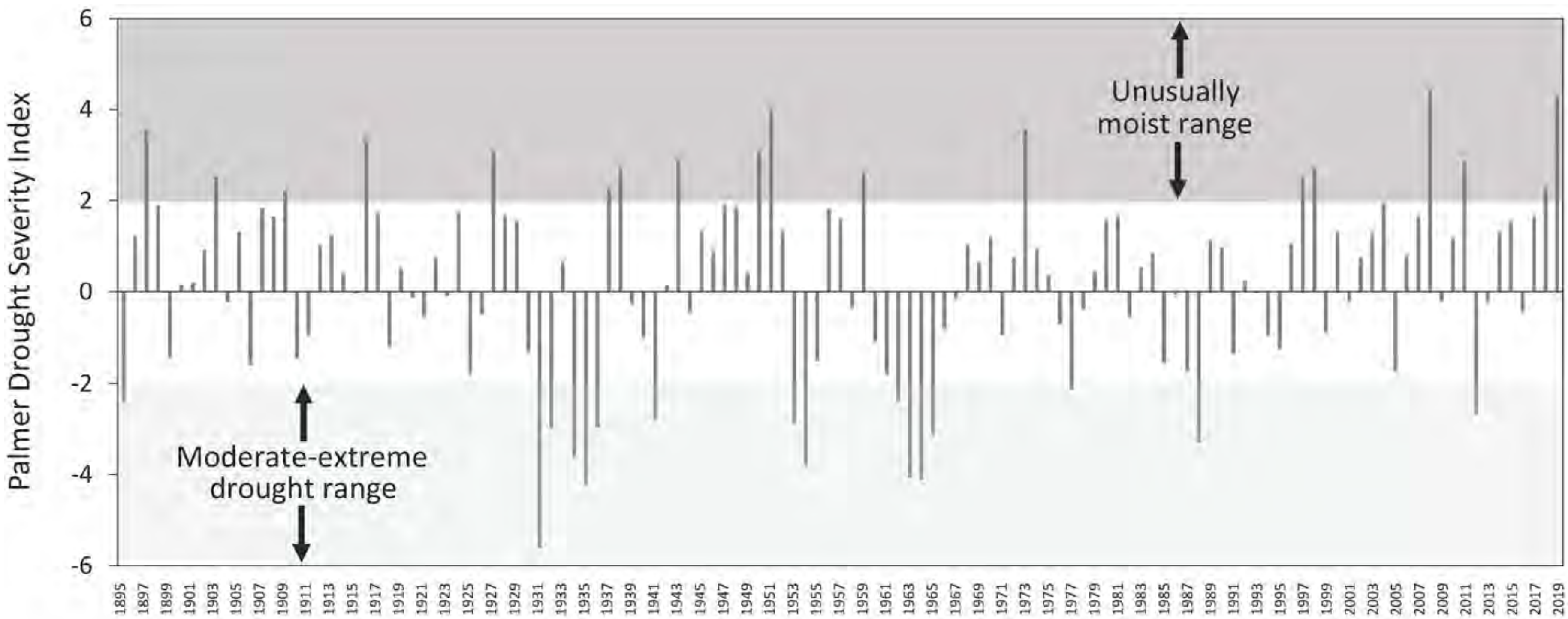
Online Resource 2 Abbreviations for vectors in Fig. 3. The six-letter codes represent understory species (cover), including individuals of tree species < 1 cm in diameter at 1.4 m

Abbreviation	Full name or description
ACERUB	*Acer rubrum*
AGRPAR	*Agrimonia parviflora*
CARLUP	*Carex lupulina*
CARPEN	*Carex pensylvanica*
CARTRI	*Carex tribuloides*
CC7-10	Number of species (0.05 ha) with coefficients of conservatism from 7-10
CINARU	*Cinna arundinacea*
CORDRU	*Cornus drummondii*
covOpenSpecies	Cover of 65 forb and 5 small shrub species typifying open habitats
DICCLA	*Dichanthelium clandestinum*
FRAPEN	*Fraxinus pennsylvanica*
FRAVIR	*Fragaria virginiana*
GLYSTR	*Glyceria striata*
HYPPUN	*Hypericum punctatum*
KRIVIR	*Krigia virginica*
LESCAP	*Lespedeza capitata*
LIQSTY	*Liquidambar styraciflua*
MAIRAC	*Maianthemum racemosum*
mapleBA	Basal area (m^2/ha) of *Acer rubrum* trees
NYSSYL	*Nyssa sylvatica*
oakBA	Basal area (m^2/ha) of trees of *Quercus* spp.
OakLarge	Trees/ha of *Quercus* spp. individuals > 10 cm in diameter
ONOSEN	*Onoclea sensibilis*
OSMREG	*Osmunda regalis*
PACAUR	*Packera aurea*
QUEBIC	*Quercus bicolor*
rareSpecies	Number of state-listed rare species (0.05 ha)
RUBFLA	*Rubus flagellaris*
SALDIS	*Salix discolor*
SCHSCO	*Schizachyrium scoparium*
THEPAL	*Thelypteris palustris*
totBA	Total basal area (m^2/ha) of trees
ULMAME	*Ulmus americana*
VACPAL	*Vaccinium pallidum*
VITRIP	*Vitis riparia*
wetlandSpecies	Number of facultative wetland and obligate wetland species (0.05 ha)

Online Resource 3 The top 20 indicator species for vegetation types during a 20-year period of restoration management of open-structured habitats in the Oak Openings region, northwestern Ohio, USA. These species have indicator values ≥ 50 and significant at $P < 0.05$ in at least one vegetation type. Data shown are indicator values (which can range from 0-100, with 100 representing maximum fidelity to a vegetation type) with those in bold significant at $P < 0.05$. The study years shown correspond with the middle part (2002) of the first decade of intensive restoration management and the end of the study (2018) following a decade of less intensive management. Indicator values were computed based on relative cover and their significance was assessed using 4,999 permutations in PC-ORD 7.07 following Dufrêne and Legendre (1997)[1]. Abbreviations for vegetation types: OS, oak savanna; OW, oak woodland; WP, wet prairie; OF, oak forest; and WF, wet forest. Oak savannas, woodlands, and wet prairies received restoration management while forests were unmanaged. Abbreviations for species longevity: A, annual; B, biennial; and P, perennial. All species are native except *Alliaria petiolata*

	2002					2018				
Species	OS	OW	WP	OF	WF	OS	OW	WP	OF	WF
Krigia virginica (A forb)	**61**	0	23	0	0	0	0	0	0	0
Lupinus perennis (P forb)	**58**	0	8	0	0	**45**	0	10	0	0
Schizachyrium scoparium (P grass)	**46**	0	15	0	0	**54**	2	10	0	0
Vaccinium pallidum (shrub)	5	**68**	0	12	0	1	**70**	0	18	0
Pteridium aquilinum (fern)	8	**79**	0	4	1	4	**90**	0	1	0
Carex pensylvanica (P sedge)	6	**49**	0	34	2	3	28	0	**59**	3
Coreopsis tripteris (P forb)	2	0	**59**	0	0	3	0	27	0	0
Dichanthelium clandestinum (P grass)	1	0	**62**	0	3	2	0	**61**	0	2
Euthamia graminifolia (P forb)	2	0	**95**	0	0	2	1	**78**	1	0
Maianthemum racemosum (P forb)	1	13	0	**68**	1	1	34	0	**45**	0
Acer rubrum (tree)	1	5	1	**67**	25	1	8	1	**65**	15
Hamamelis virginiana (tree)	0	7	0	**75**	0	1	13	0	**70**	0
Alliaria petiolata (A-B forb)	0	0	2	**62**	6	0	0	0	14	0
Desmodium nudiflorum (P forb)	0	0	0	**70**	0	0	1	0	**66**	0
Aralia nudicaulis (P forb)	0	0	0	**56**	1	0	0	0	**40**	3
Spiraea alba (shrub)	0	1	4	0	**85**	0	0	9	0	**72**
Nyssa sylvatica (tree)	0	1	0	1	**84**	0	0	0	0	**67**
Cinna arundinacea (P grass)	0	0	0	0	**33**	0	0	0	0	**66**
Osmunda cinnamomea (fern)	0	1	0	0	**96**	0	0	1	0	**97**
Osmunda regalis (fern)	0	0	0	0	**100**	0	0	0	0	**99**

[1]Dufrêne M, Legendre P (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecol Monogr 67:345-366



Online Resource 4 Long-term climatic drought index averaged for May-June for northwestern Ohio, USA. Data from the National Climatic Data Center, National Oceanic and Atmospheric Administration, Asheville, North Carolina, USA