Biological Conservation 212 (2017) 265–273

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Restoring and conserving rare native ecosystems: A 14-year plantation removal experiment

Scott R. Abella[a,*], Timothy A. Schetter[b], Timothy L. Walters[c]

[a] University of Nevada Las Vegas, School of Life Sciences, Las Vegas, NV 89154-4004, USA
[b] Metropolitan Park District of the Toledo Area, 5100 Central Avenue, Toledo, OH 43615, USA
[c] EnviroScience, Northwest Ohio Field Office, 6027 County Road 1, Swanton, OH 43558, USA

ARTICLE INFO

Keywords:
Conifer plantation
Floristic quality
Oak savanna
Prairie
Rare species
Wetland

ABSTRACT

Forest plantations occupy 2% of Earth's land surface and are increasingly important in biological conservation both through their establishment and removal. To restore conservation-priority oak savannas and prairies in the Midwestern United States, we began a conifer plantation removal experiment in northwestern Ohio in 2002 and measured plant community response, including nectar plants for conservation-priority invertebrates, during a 14-year period. Oak (*Quercus*) trees, crucial to restoring savanna structure, only became established on plots where conifers were cut. In the understory, native species richness/0.05 ha was 34–50% higher on plots where conifers were cut than on control plots in uncut plantations. By year 14, cut plots accrued 13 species with high coefficients of conservatism (specialist species typifying high-quality natural habitats) and 10 state-listed rare species; uncut plantations did not contain any such species. With 71 wetland species detected during the experiment (out of 370 total plant species), only cut plots developed a wetland-upland biophysical gradient diagnostic of diverse Midwestern savanna-prairie landscapes. Between year 1 and 14 after plantation cutting, cover of nectar plants utilized by federally endangered Karner blue butterflies (*Lycaeides melissa samuelis*) doubled, while cover of these plants remained negligible in uncut plantations. Similarly, cover of plants utilized by bees increased by 24 × after plantation cutting. Cutting plantations rapidly and persistently benefited native species for at least 14 years, with minimal increase in non-native plants.

1. Introduction

Tree plantations, defined as planted forests of native or non-native trees primarily evenly aged and spaced, are increasingly important in biological conservation both through their establishment and removal. Between 1990 and 2015, the global area of natural forest declined by 6%, but an increase in forest plantations partly offset total forest loss by half, to 3% (Keenan et al., 2015). Forest plantations nearly doubled, increasing from 168 million to 278 million ha, to occupy 2% of Earth's land area (Payn et al., 2015). From a perspective of conserving native ecosystems, the increase in plantations has advantages and disadvantages. Intensively managed plantations produce half of the wood output of some countries, reducing pressure on natural forests for wood production (Aubin et al., 2008). Plantations have also stabilized eroding soils, facilitating recovery of natural ecosystems over time (Newmaster et al., 2006). However, plantations can negatively impact native biodiversity by having low diversity compared to natural ecosystems and by occupying space otherwise inhabitable by native biota (Bremer and Farley, 2010). Land-use, timber markets, and management priorities are often dynamic, and while plantations are increasing in some areas, in other areas priorities have shifted toward resource values not supplied by plantations. Where plantations occupy habitat within regions supporting conservation-priority rare or declining native ecosystems, there is growing interest in converting plantations to native ecosystems. For example, potential for converting plantations to native ecosystems has been evaluated for plantations within tropical wet forests of Sri Lanka including in a World Heritage Site (Ashton et al., 2014), European rare old-growth deciduous forests (Spracklen et al., 2013; Atkinson et al., 2015; Brown et al., 2015), coastal heathlands of the United Kingdom (Sturgess and Atkinson, 1993), oak-beech forests of the Netherlands (Jonášová et al., 2006), imperiled oak savannas in eastern Canada (Catling and Kostiuk, 2010), and pine savannas of the southeastern United States (Hu et al., 2016).

When a plantation is no longer desired, three general options exist: allow the plantation to gradually senesce, remove some or all of the plantation trees to encourage natural colonization by native species, or directly introduce new species to intact or cut plantations (Artigas and Boerner, 1989; Hirata et al., 2011; Onaindia et al., 2013). A question is

* Corresponding author.
E-mail addresses: scott.abella@unlv.edu (S.R. Abella), tim.schetter@metroparkstoledo.com (T.A. Schetter), twalters@enviroscienceinc.com (T.L. Walters).

http://dx.doi.org/10.1016/j.biocon.2017.06.034
Received 12 February 2017; Received in revised form 12 June 2017; Accepted 21 June 2017

what is gained for the restoration and conservation of native biodiversity by removing plantations, compared to passively allowing senescence of plantations? While many studies have compared biological characteristics of plantations with natural forests, relatively few have assessed actively removing plantations (Stephens and Wagner, 2007; Brockerhoff et al., 2008). Furthermore, the few studies that did reported mixed results. For example, heavily thinning or removing plantations can increase understory plant diversity, but trajectories toward recovery of conservation-priority species typifying natural habitats are not always evident (Harrington, 2011). Dominance by non-native plants has also occurred after cutting plantations (Parker et al., 2001). Because of this uncertainty, some studies have concluded that allowing plantations to gradually senesce most effectively encourages the establishment of native, specialist species restricted to natural habitats (Artigas and Boerner, 1989; Atkinson et al., 2015; Brown et al., 2015). In other situations, this passive approach might require decades or centuries if the plantation trees are long-lived, and may never work if non-native plantation trees continue recruiting (Catling and King, 2007). Effectiveness of the passive approach could also be ecosystem-specific. Outcomes can vary if plantations have replaced natural forests of shade-tolerant species able to recruit within plantations, compared to where plantations replaced prairies, savannas, or shrublands containing light-demanding species unable to recruit in plantation understories (Bremer and Farley, 2010). With the global increase in plantations, geographic and temporal shifting of plantation and conservation priorities, and uncertainty in strategies for converting plantations to native ecosystems, further research could help choose among options for managing plantations.

To assess if removing plantations of non-native conifer trees could meet a goal of restoring rare oak savanna-prairie ecosystems in the Midwestern USA, we experimentally cut plantations and measured vegetation changes over 14 years. Our objective was to determine how removing plantations affected the establishment of deciduous trees, understory communities, wetland plants forming wetland-upland biophysical gradients important to the diversity of Midwestern savanna landscapes, rare plant species, and nectar plants utilized by pollinators and a federally endangered butterfly species. Our specific questions included: 1) Do sapling layers of native deciduous species, including oaks, develop after plantation cutting? 2) How does plantation cutting affect understory species composition including native and non-native species? and 3) How do measures of diversity, including at species, community, and landscape scales (such as development of wetland-upland gradients), change after plantation cutting?

2. Methods

2.1. Study area

The Midwestern oak savanna region stretches from northern Texas, USA, north to the Great Lakes area and has a northwestern terminus in the Canadian province of Alberta (Fig. 1). Before extensive Euro-American settlement in the mid-1800s, landscapes with mixtures of oak savanna, woodland, and prairie (both wet and dry) covered over 12 million ha within this region (Nuzzo, 1986). By 1985, these habitats occupied only 0.02% of their former range, due to clearing for agriculture and infrastructure, conversion to closed-canopy forest via excluding frequent surface fires and draining wet prairies, and conversion to conifer plantations (Anderson, 1998). The few remnants with some semi-natural Midwestern oak savanna and prairie are recognized as among the most biodiverse areas of the United States and Canada, including supporting Karner blue butterflies (*Lycaeides melissa samuelis*), endangered under the U.S. Endangered Species Act and of conservation-priority in Canada (Leach and Givnish, 1999; Chan and Packer, 2006; Grundel et al., 2010).

We conducted our experiment within the 47,000-ha Oak Openings Region, centered in northwestern Ohio, USA, an eastern part of the Midwestern oak savanna region (Fig. 1). As of the 2000s, most (73%) of the Oak Openings region was in agriculture/urban/suburban land use, with the remaining 27% being natural/semi-natural (Schetter and Root, 2011). Ten percent was in parks and preserves, but 14% (627 ha) of their area was in conifer plantation (Schetter and Root, 2011). There is no record of conifer trees being native to the region (Moseley, 1928). The conifer plantations were established in the 1940s and 1950s, primarily by local and state agencies to afforest agricultural lands abandoned during the economic depression and acquired for parks and preserves. The main planted trees were eastern white pine (*Pinus strobus*) and red pine (*Pinus resinosa*), species native to the United States but not to the Oak Openings region, plus some conifer species not native to North America (Paton et al., 1944).

Within the Oak Openings region, our study site was the 1497-ha Oak Openings Preserve (41°33′12″N, 83°50′8″W), the largest protected area in the region, and managed by the Metropolitan Park District of the Toledo Area, 40 km southwest of the City of Toledo, Ohio. Similar to elsewhere in the region, plantations were established on land that was oak savanna-prairie based on early 1800s land surveys (Brewer and Vankat, 2004) and that was cleared for agriculture by the 1930s before plantation establishment in the 1940s–1950s (Abella, 2010). Based on aerial photos, all plantations of the present study were agricultural fields before plantations were established. The conifer trees were planted evenly spaced every 3.2 m. It was originally intended that plantations would be periodically thinned, but due to shifting timber markets and management priorities, thinning did not occur. The plantations went unmanaged until they were 47–63 years old in 2002 at the beginning of our experiment.

2.2. Experimental design and treatments

Twenty-four plantations, ranging from 1 to 5 ha and averaging 2 km apart, were identified to be equally distributed between pine species (12 white pine and 12 red pine plantations) and in areas accessible to logging machinery. Fifteen of the plantations received a cutting treatment, while 9 served as uncut controls (Fig. 2). In early 2002, 50–100% of pines were mechanically cut in plantations assigned cutting by systematically removing at least every other tree. It was originally intended to compare different levels of pine cutting, but cutting was consolidated to one treatment because many residual pines died. This could have resulted from several factors, such as disturbance during cutting, increased susceptibility to windthrow after more open stands were created, and mortality of unhealthy trees with poorly developed crowns that had grown in dense stands. Pre-cutting pine density did not differ significantly between cut and control plots, but after cutting, pine density decreased 93% on cut plots and was 14 times lower than on control plots by 14 years after cutting (Fig. 3). During cutting, logs were removed and slash was scattered on site. Based on an initial study (Abella, 2010), the 24 plantations similarly had sparse understories (8% average plant cover) and thick O horizons (4–6 cm) before treatment. There also was no consistent difference in response to cutting between plantations of white or red pine, so plantation types were combined.

2.3. Data collection

We measured plant communities in a 0.05-ha (20 m × 25 m) permanent plot in the center of each plantation. We recorded the diameter (at a height of 1.4 m) for every live tree ≥ 1 cm in diameter. Including herbaceous plants, shrubs, and tree seedlings < 1 cm in diameter, we categorized the areal percent cover of each understory vascular plant species on each plot as 0.1%, 0.25%, 0.5%, 1% increments from 1 to 10% cover, and 5% increments above 10% cover. Cover categorizations were aided by dividing plots into grid cells, where, for example, a 5-m^2 area covered by a species corresponded to 1% cover. The same investigator (S.R. Abella) made cover categorizations during all inventories, excluding the possibility of among-observer variation in

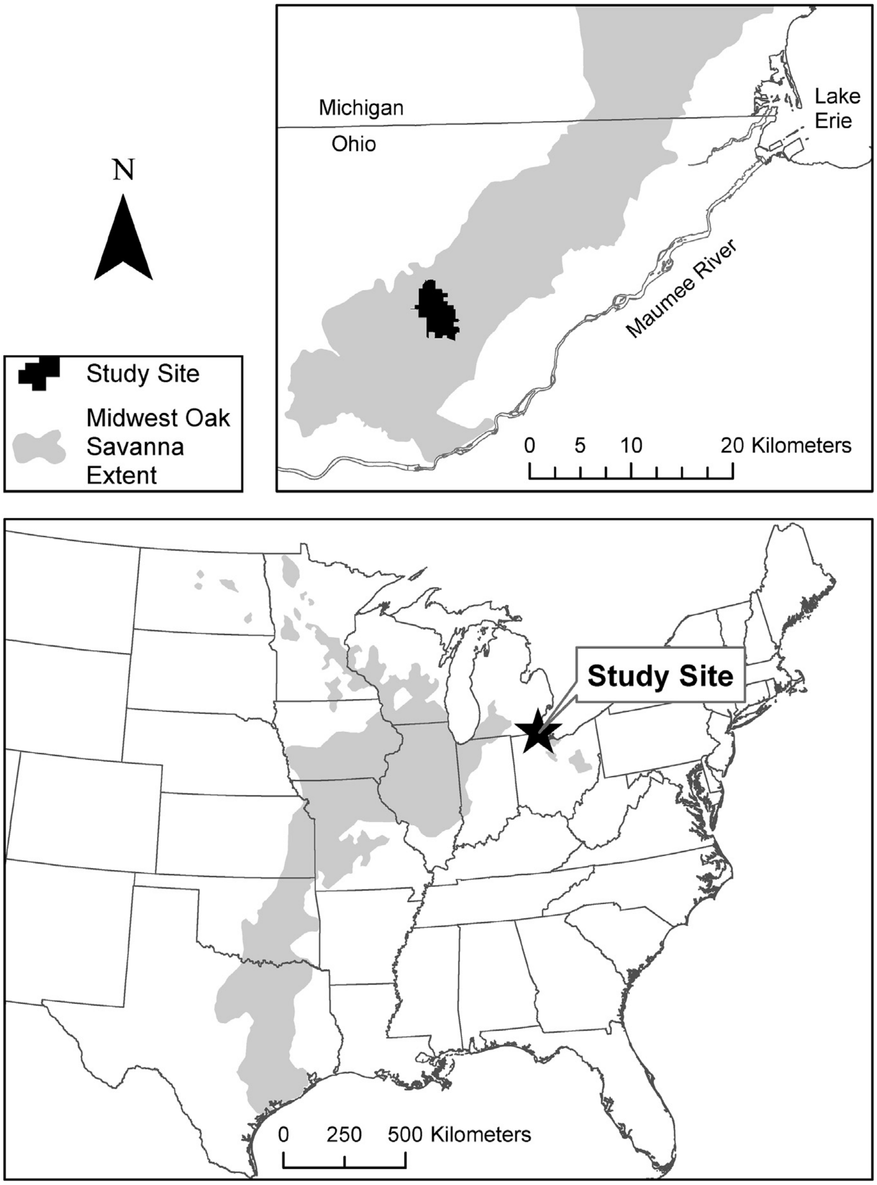

Fig. 1. Location of the Oak Openings Preserve study site within the Oak Openings region (top map) and in relation to the Midwest oak savanna region, USA (bottom map). Top map adapted from Brewer and Vankat (2004); bottom from Nuzzo (1986).

cover estimation. Nomenclature, classification of growth form (e.g., perennial forb), and native/non-native status follow Natural Resources Conservation Service (2016). Data were collected in June–September 2002 (the growing season after pine cutting), 2004 (3 years after cutting), and 2015 (14 years after cutting). During this period, precipitation averaged 92 cm/yr (109% of the 1955–2015 average, measured at Toledo Express Airport, adjacent to the study area), with six years below average and eight years above average.

2.4. Data analysis

We augmented field data by calculating additional plant community metrics and using published data. Using published values for Ohio (Andreas et al., 2004), we assigned to each species a coefficient of conservatism, representing how restricted species are to particular habitats within landscapes. The coefficients range from 0 to 10. Generalist species occurring in a broad range of habitats usually associated with human disturbance are assigned low values, and specialist species typifying high-quality natural habitats are assigned higher values (McIndoe et al., 2008). Non-native species are omitted. Using the coefficients, we calculated a floristic quality index for each plot as the sum of the coefficients divided by the square root of native species richness/0.05 ha (McIndoe et al., 2008). We also compiled the number of rare species per plot listed as state endangered, threatened, or potentially threatened (Ohio Department of Natural Resources, Columbus, OH). To qualify the relative distribution of species among moisture gradients, we used wetland status rankings for Ohio and tabulated the number of species classified as obligate wetland, facultative wetland, facultative, facultative upland, and upland (Andreas et al., 2004). Soil data of the upper 15 cm of mineral soil, collected in 2004 and including texture, pH (1:1 soil:water), and loss-on-ignition (300 °C at 2 h) as a surrogate for organic matter (Konen et al., 2002), were obtained for each plot from earlier work (Abella, 2010).

We analyzed response variables with descriptive or inferential statistics. The number of state-listed rare species was evaluated only descriptively (total numbers of species detected and frequency based on 0.05-ha plots), because no rare species were detected in control plots and hence there was no variation. Response variables analyzed inferentially included: pine tree density and basal area, oak tree density (stems ≥ 1 cm in diameter at 1.4 m), species richness/0.05-ha and cover of native and non-native plants, species richness of conservative species with coefficients ≥ 5, and the floristic quality index. We analyzed these variables using a repeated measures analysis of variance (ANOVA), including treatment (cutting, control) and time (years of

Fig. 2. Repeat photos of three plots in 2002 (top row) and 2015 (bottom row) representing control (left photo pair) and pine plantation cutting treatments (middle and right photo pairs) designed to restore rare oak savanna and prairie ecosystems in northwestern Ohio, USA. Between the first (2002) and fourteenth year (2015) of the experiment, minimal change occurred in the control. Shown in the middle photo pair, a major change occurred with a transition from dominance by American pokeweed (*Phytolacca americana*; 13% cover) and pilewort (*Erechtites hieraciifolius*; 6%) in 2002 to a community typifying dry-soil oak savanna containing 6% cover of four species of *Quercus* seedlings, 8% of big bluestem (*Andropogon gerardii*), and 40% total of Allegheny blackberry-northern dewberry (*Rubus allegheniensis-Rubus flagellaris*). In the right-side photo pair, a *Juncus-Cyperus-Phytolacca* community in 2002 transitioned in 2015 to one with 50% cover of *Rubus* spp. (Allegheny blackberry, northern dewberry, and swamp dewberry [*Rubus hispidus*]), 20% deertongue (*Dichanthelium clandestinum*), 10% Canada goldenrod (*Solidago canadensis*), and 5% steeplebush (*Spiraea tomentosa*) typifying wet prairies.

measurements) followed by Tukey's tests for multiple comparisons at the appropriate level of main effects or interactions as determined by the overall ANOVA (SAS Institute, 1999). Plots spanned a gradient of dry to moist soils, so wetland species became established on some plots while other plots were upland and unsuitable habitat for wetland species (Brewer and Vankat, 2006). Consequently, we used linear regression to assess development of a wetland-upland biophysical gradient by relating soil variables to the number of obligate wetland + facultative wetland species/0.05 ha.

As indicators of habitat quality for conservation-priority invertebrates, we tabulated cover of nectar plant species known to be utilized by federally endangered Karner blue butterflies (Grundel et al., 2000) and by bees (Arduser, 2010). Data for Karner blue plant utilization was from Indiana Dunes National Lakeshore, 250 km west of the study area and a similar landscape of mixed oak savanna-prairie (Grundel et al., 2000). Bee utilization data included 124 species of bees found visiting 51 plant species in Kitty Todd Preserve, within the Oak Openings region and 8 km northeast of our study site (Arduser, 2010). We calculated means and standard errors by treatment and year for cover of Karner blue and bee nectar plants and for cover of *Rubus* spp. utilized by both (Grundel et al., 2000; Arduser, 2010).

3. Results

3.1. Tree and sapling layer

Cutting treatments shifted dominance from pine to either saplings (≥ 1 cm in diameter) of native deciduous trees or to prairies without trees. On cut plots, the density of pines decreased by 93% between pre-cutting in 2001 and 14 years post-cutting in 2015 (Fig. 3, Table S1). Pine basal area decreased by 82%. In contrast, on control plots, pine density and basal area did not change significantly through time. In 2015, uncut controls exceeded 800 pine trees/ha and 65 m^2/ha of basal area. Cut plots were the only ones to contain oak stems over 1 cm in diameter during the study. Between 3 and 14 years after treatment, 47% of cut plots contained new oak stems at least 1 cm and up to 15 cm in diameter. Their density averaged 87 stems/ha among the 15 cut plots and 186 stems/ha on the seven cut plots oaks inhabited. At years 1 and 3, 33% of control plots contained saplings (≥ 1 cm in diameter) of deciduous species, increasing to 44% with one additional plot at year 14 in 2015 (Table S2). However, deciduous species remained sparse (< 50 trees/ha) on control plots and were nearly all black cherry (*Prunus serotina*) and red maple (*Acer rubrum*), rather than oak typifying natural oak savanna.

3.2. Understory composition and response of native and non-native species

In the understory, including herbs, shrubs, and tree seedlings (< 1 cm in diameter at 1.4 m), 370 vascular plant species were detected among all plots and years. Of these species, 82% were native and 18% were non-native. The most common growth forms were perennial forbs (31% of all species), perennial graminoids (21%), shrubs (15%), trees (9%), and annual forbs (5%). The remaining 19% included forbs that were biennials or ranged from annual-perennial life spans (11%), vines (3%), ferns (3%), and annual graminoids (2%).

Both native and non-native species richness and cover increased between the first and third year after cutting on cut plots, and as the community matured, native species richness at year 14 decreased to a level intermediate between the first and third year (Fig. 4). Native species richness was 34–50% higher on cut compared to control plots all years (Table S1). Conversely, non-native species richness was twice as high on cut compared to control plots among years, but both treatments were always dominated by natives (at least 80% of species). Species richness did not change significantly through time for native or non-native species on control plots.

Cover of native species tripled between years 3 and 14 on cut plots, while cover of non-native plants significantly decreased (Fig. 4, Table S1). At year 14, native species comprised 98% of total cover on cut plots. Cover of native species also increased on control plots between years 3 and 14, but it was only half the amount found on cut plots. Unlike on cut plots, non-native plant cover increased on control plots between years 3 and 14. Non-native plants comprised twice as much of

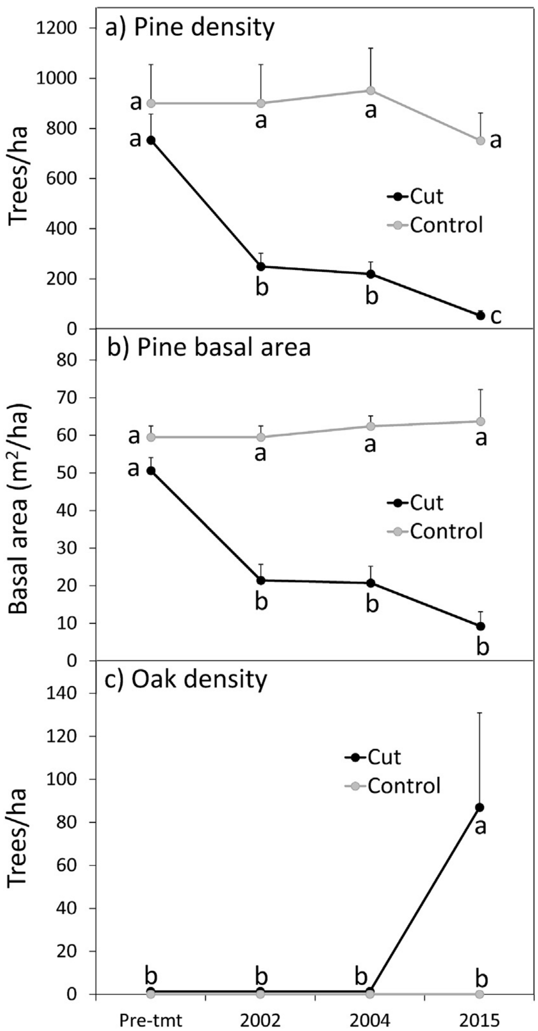

Fig. 3. Change in abundance of pine and oak trees (≥ 1 cm in diameter at 1.4 m) during a pine plantation removal experiment to restore native oak savanna-prairie ecosystems in northwestern Ohio, USA. Data are from pre-treatment to one (2002), three (2004), and 14 years (2015) after pine cutting, as compared to uncut controls. Means without shared letters within a graph differ at $P < 0.05$. Error bars are one standard error of means.

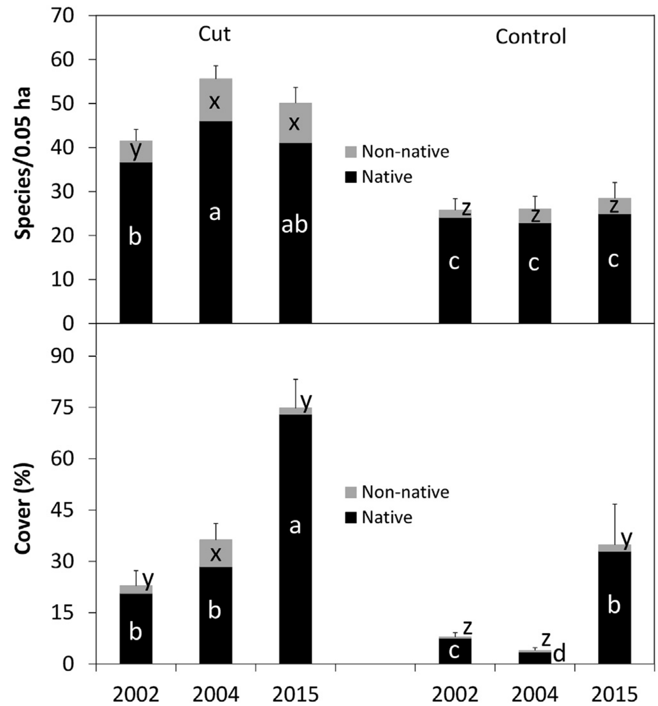

Fig. 4. Mean plant species richness and cover during a pine plantation removal experiment to restore native oak savanna-prairie ecosystems in northwestern Ohio, USA. Data are from one (2002), three (2004), and 14 years (2015) after pine cutting, as compared to uncut controls. Means without shared letters differ at $P < 0.05$ in separate comparisons for native and non-native species. Error bars are one standard error of means for total species richness or cover.

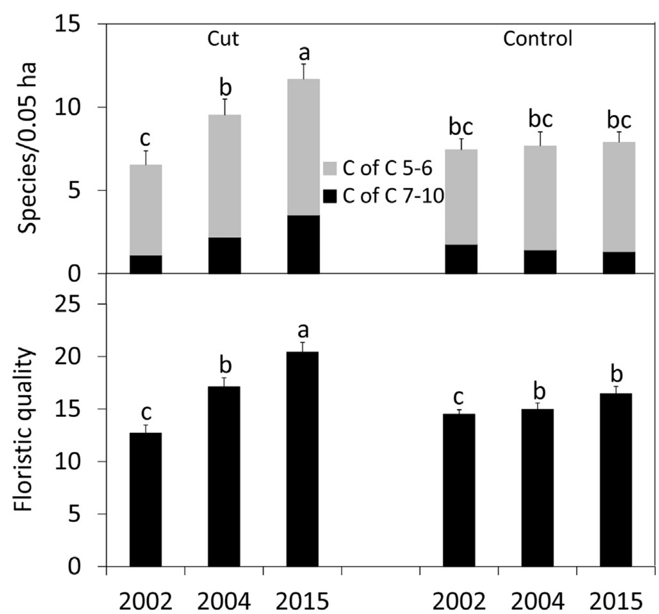

Fig. 5. Mean plant species richness for species with high coefficients of conservatism and mean floristic quality during a pine plantation removal experiment to restore native oak savanna-prairie ecosystems in northwestern Ohio, USA. Data are from one (2002), three (2004), and 14 years (2015) after pine cutting, as compared to uncut controls. In the top graph, the number of species is partitioned into those with moderate (5–6) and high (7–10) coefficients of conservatism (C of C). C of C values range from 0 to 10, with higher values for specialist species typical of minimally disturbed habitats. The floristic quality index in the bottom graph is unitless, with higher values indicating higher floristic quality typified by native, conservative species. Means without shared letters differ at $P < 0.05$ in both graphs, and in the top graph, represent comparisons of total mean richness including species with coefficients of 5 to 10. Error bars are one standard error of means.

the total plant cover on control than on cut plots at year 14.

Several major species dominated plots at different times during the experiment (Table S3). Within the first three years after cutting, the native perennial forb American pokeweed (*Phytolacca americana*), annual forb pilewort (*Erechtites hieraciifolius*), and shrubs *Rubus* spp. dominated cut plots, along with the non-native perennial forb sheep sorrel (*Rumex acetosella*) and non-native shrub common buckthorn (*Rhamnus cathartica*). These non-natives nearly disappeared by year 14, when cut plots were dominated by native *Rubus* spp., deertongue (*Dichanthelium clandestinum*), wrinkleleaf goldenrod (*Solidago rugosa*), and big bluestem (*Andropogon gerardii*). In the first three years of the experiment, the minimal cover on control plots was mainly tree seedlings, a trend continuing in year 14 when black cherry, sweetgum (*Liquidambar styraciflua*), and eastern white pine seedlings formed half the cover. *Rubus* spp. and pilewort were primary increasers in year 14 on control plots mainly where some pines died.

3.3. Specialist, rare, and wetland species

Richness of conservative specialist species and the floristic quality index increased through time on cut plots, and were significantly higher by year 14 on cut than control plots (Fig. 5, Table S1). Conservative species and floristic quality did not change through time on control

Table 1
Percent frequency of the most conservative species, with coefficients of conservatism ≥ 8, during a pine plantation removal experiment to restore native oak savanna-prairie ecosystems in northwestern Ohio, USA. Pines were cut in 2002 in the cutting treatment, while control plots remained untreated.

			Cut			Control		
Species[a]	C of C[b]	Growth form	2002	2004	2015	2002	2004	2015
			Frequency (0.05 ha, %)					
Carex bicknellii (T)	9	PG[c]		7	7			
Carex lucorum (E)	9	PG		7				
Carex tenera	8	PG		7	13	11		
Carex tonsa var. *rugosperma*	8	PG		13	27			
Comptonia peregrina (E)	8	shrub	7		7			
Dichanthelium depauperatum	8	PG		7	7		11	
Dichanthelium spretum	9	PG			20			
Hypericum kalmianum (T)	8	shrub			7			
Krigia virginica (T)	8	annual forb			20			
Liatris squarrosa (P)	8	perennial forb			7			
Opuntia humifusa	8	cactus			7			
Polygala polygama (T)	10	biennial forb		33	13			
Symphoricarpos albus	8	shrub	7			11		
Triplasis purpurea	9	AG[c]			7			
Vernonia missurica	8	perennial forb			7			

[a] Letters in parentheses note state rarity status: P, potentially threatened; T, threatened; E, endangered.
[b] Coefficient of conservatism, ranging from 0 to 10, with higher values for specialist species typifying minimally disturbed habitats.
[c] PG, perennial graminoid; AG, annual graminoid.

plots, except for a statistically significant, but small, increase in floristic quality between years 1 and 3. Including only the most conservative non-tree species, with coefficients 8 to 10 (thereby excluding seedlings of native tree species all with coefficients 5 to 7), differences between cut and control plots became even more pronounced. The number of species with coefficients ≥ 8 on cut plots increased from two in the first year after cutting, to 13 by year 14 (Table 1). No species with coefficients higher than 7 were detected on control plots in year 14.

State-listed rare plant species increased each year on cut plots, while no state-listed species inhabited control plots. The total number of state-listed species on cut plots doubled from one inventory to the next throughout the experiment (Fig. 6). Half of cut plots contained at least one state-listed species by the third year, which increased to 60% by year 14. In year 14, six of the state-listed species were also species with high coefficients of conservatism of 8 to 10 (Table 1). The remaining four state-listed species, with coefficients of 5 to 7, were arrowfeather threeawn (*Aristida purpurascens*), Canadian St. Johnswort (*Hypericum canadense*), wild lupine (*Lupinus perennis*), and whorled mountainmint (*Pycnanthemum verticillatum* var. *pilosum*).

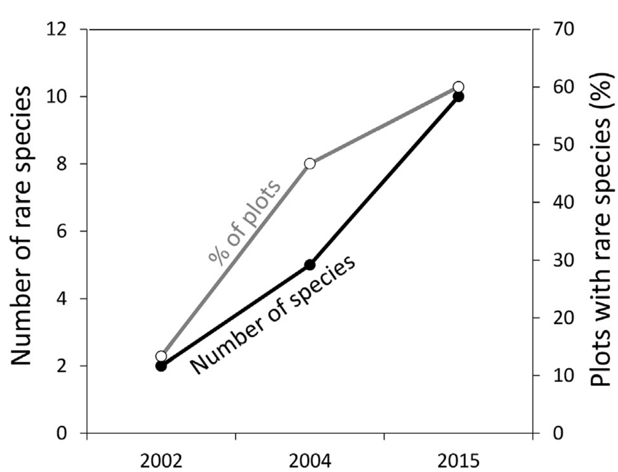

Fig. 6. Total number of state-listed rare plant species, and percent of 0.05-ha cut plots in which at least one state-listed species was detected, during a pine plantation removal experiment to restore native oak savanna-prairie ecosystems in northwestern Ohio, USA. Data are from one (2002), three (2004), and 14 years (2015) after pine cutting. No state-listed species were detected on uncut control plots.

There were totals of 57 facultative wetland and 14 obligate wetland species detected during the experiment, collectively comprising 19% of the 370 total species recorded. The most frequent obligate wetland species were swamp smartweed (*Polygonum hydropiperoides*), hop sedge (*Carex lupulina*), stiff marsh bedstraw (*Galium tinctorium*), Canadian rush (*Juncus canadensis*), and royal fern (*Osmunda regalis*). A wetland-upland biophysical community gradient formed among cut plots but not among control plots. Three years after cutting, the number of wetland species per plot was related to soil loss-on-ignition (a surrogate for organic matter and drainage) on cut plots, while no relationship existed for control plots (Fig. 7).

3.4. Floral resources for conservation-priority invertebrates

Estimated minimum potential floral resources for federally endangered Karner blue butterflies and bee communities were orders of magnitude higher on cut compared to control plots (Fig. 8). On cut

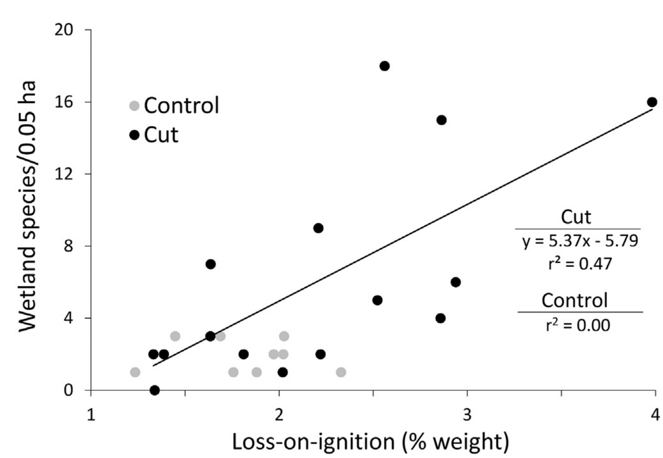

Fig. 7. Relationship between soil loss-on-ignition and the number of facultative wetland + obligate wetland plant species during a pine plantation removal experiment to restore native oak savanna-prairie ecosystems in northwestern Ohio, USA. Data are from 2004, three years after pine cutting, as compared to uncut controls. The regression line is for cut plots only, as there was no relationship for control plots. Loss-on-ignition, measured for a mineral soil depth of 0–15 cm, is a surrogate for organic matter with higher values on poorly drained soils.

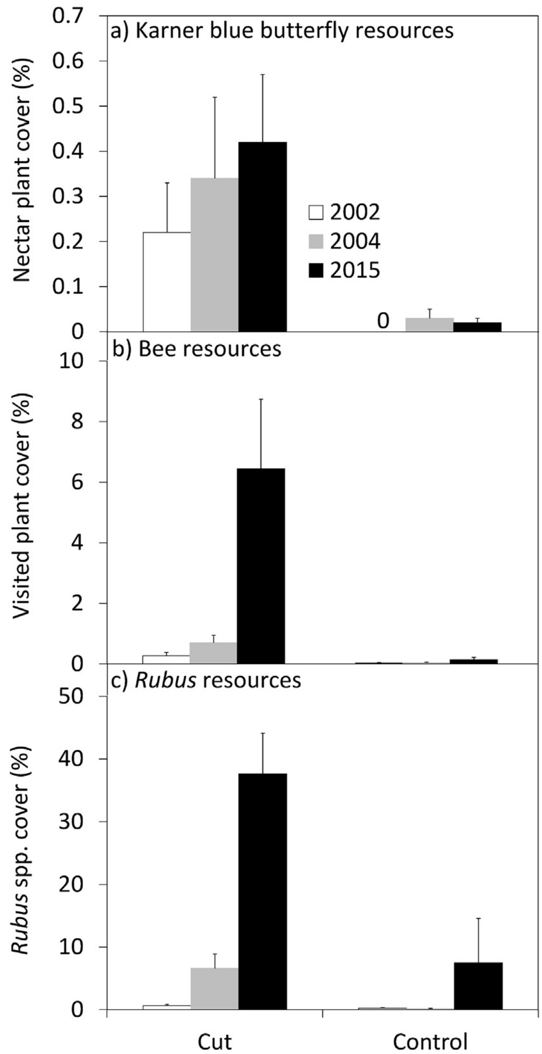

Fig. 8. Estimated potential nectar plant resources for federally endangered Karner blue butterflies and bee communities, with *Rubus* spp. utilized by both, during a pine plantation removal experiment to restore native oak savanna-prairie ecosystems in northwestern Ohio, USA. Data are from one (2002), three (2004), and 14 years (2015) after pine cutting, as compared to uncut controls. Error bars are one standard error of means. Nectar plant utilization was based on Grundel et al. (2000) for Karner blue butterflies and Arduser (2010) for bees.

plots, the cover of Karner blue nectar plants doubled between post-treatment years 1 and 14. During this time, the cover of plants utilized by bees increased by 24 ×. Cover of *Rubus* spp., important floral resources for both Karner blue butterflies and bee communities, was five times higher on cut compared to control plots in year 14.

4. Discussion

4.1. Factors in conservation benefits of plantation removal

Cutting non-native conifer plantations rapidly and persistently benefited native species for at least 14 years. Our findings, combined with those of previous studies, highlight the circumstances in which plantation removal (as opposed to passive management) can be most effective for restoring native communities. The natural vegetation type displaced by a plantation is a key variable. Deciduous forests were desired vegetation types to restore via plantation removal in most previous studies (e.g., Artigas and Boerner, 1989; Hirata et al., 2011; Atkinson et al., 2015), rather than the desired savannas and prairies that plantations were replacing in our study. Shade tolerance of understory species is generally greater in deciduous forests than in savannas and prairies (Leach and Givnish, 1999), so shade-tolerant species of natural forests can more readily become established within plantations than can shade-intolerant species of savannas-prairies. This may be why some studies in deciduous forest biomes found little difference in conservation-priority native understory species between plantation removal sites and unmanaged plantations, which already contained developing native understories (Artigas and Boerner, 1989; Jonášová et al., 2006; Atkinson et al., 2015; Brown et al., 2015). In contrast, as in our study, conservation-priority savanna and prairie species – growing only in semi-shaded or open habitats and absent from plantation understories – increased after plantation removal in a previous study in southern Ontario (Catling and Kostiuk, 2010).

Additionally, previous studies have noted that conditions of a plantation's understory at the time of treatment affect whether plantation removal benefits native species more than simply allowing a plantation to senesce. For example, 40-year-old pine plantations studied by Artigas and Boerner (1989) in southern Ohio contained over 7000 seedlings and saplings/ha of 11 deciduous tree species, and the authors concluded there was little benefit to deciduous forest species of removing plantations. Similarly, in the United Kingdom, Atkinson et al. (2015) found that species of natural deciduous forests already inhabited plantations, and cutting plantations did not further increase these species. At the beginning of our experiment, plantation understories uniformly lacked saplings of deciduous trees and conservation-priority savanna and prairie species. All 24 plantation sites in our experiment had the same land use – agricultural fields – before plantations were established. While the specific details of the fields might have differed in unknown ways (e.g., type of last crop), general land use was identical across all of our sites. Root structures and soil seed banks could have been destroyed during conversion to agriculture (e.g., via plowing) and unable to recover under the subsequent plantations, potentially accounting for why desired species were absent from plantation understories when our experiment began. However, a benefit of these sparse understories was that non-native plants were rare and they remained subordinate after plantation removal, despite the intensive disturbance. In comparison, intact plantations in a southern Ontario study were dominated by non-native species, which formed a legacy effect by also dominating after plantations were thinned (Parker et al., 2001).

Another important factor in the suitability of plantation removal as a restoration strategy is the growth and recruitment dynamics of the plantation trees. In some studies where plantations were only thinned and not removed, tree thinning only temporarily benefited the understory because canopies of residual trees quickly filled gaps (Harrington, 2011; Hu et al., 2016). This could be especially true for light thinnings that remove few trees (Harrington, 2011). The idea that native species can recover through passive management by allowing plantations to senesce is not necessarily viable if the plantation trees are non-native and regenerate within or around plantations. For instance, Scots pine (*Pinus sylvestris*) spread from plantations to invade remnant prairies in Ontario (Catling and King, 2007). In our study area, eastern white pine has spread from plantations to oak forests and prairies (Abella and MacDonald, 2002). In these circumstances of expanding plantation trees, completely removing plantations might most benefit understories and curtail invasion by plantation trees via eliminating seed sources.

4.2. Early colonizing species

The disturbance-associated pilewort, American pokeweed, and several *Rubus* spp. were among the most important species during the first three years after plantation cutting and have traits that confer rapid colonization of openings (Artigas and Boerner, 1989; Leck and Leck, 1998; Keyser et al., 2012). These species form persistent soil seed banks and are readily wind- (pilewort) or bird-dispersed (American pokeweed and *Rubus* spp.). Seed burial experiments revealed that pilewort can persist at least eight years in seed banks (Baskin and Baskin, 1996). In natural deciduous forests, all three species colonize treefall gaps (Hyatt and Casper, 2000). In addition to providing initial plant cover, American pokeweed and *Rubus* provide berries utilized by birds and small mammals, likely contributing to greater food availability for wildlife on plantation removal sites compared to unmanaged plantations (Greenberg et al., 2007).

4.3. Specialist and rare species

One of the largest conservation benefits to the plant community was that plantation cutting triggered colonization by numerous conservative, specialist species, which were absent from uncut control plots in 2015. There was no consistent particular assemblage of conservative or rare species among cut plots, with the maximum frequency of any species being only 27% (*Carex tonsa* var. *rugosperma*), but there was usually (73% of plots) at least one rare or highly conservative (coefficients 8–10) species on cut plots. A commonality among the 15 highly conservative species on cut plots was that they require abundant sunlight and are associated with oak savannas and prairies in natural habitats of the region (Brewer and Vankat, 2004).

In an example of the "reclaiming" of habitat for these species by removing plantations, the most conservative species (with a coefficient of 10) on cut plots, the state-threatened biennial racemed milkwort (*Polygala polygama*), was found at only 12 locations after 1960 in Ohio (Burns, 1986). As of 2008, the species inhabited only four counties in Ohio that had suitable sandy, open habitat (Ohio Division of Natural Areas and Preserves, Columbus, OH). Habitat for this species was apparently suitable within three years after plantation removal on cut plots, as the species had already colonized 33% of cut plots and persisted on 13% of cut plots by year 14. This was the only rare species to decline in frequency on cut plots from year 3 to 14, and it is unclear whether this relates to shading from expansion of large plants (e.g., *Rubus*, perennial grasses), climate, or fluctuations in other factors interacting with the biennial longevity of individual plants of this species. Overall, the number and frequencies of conservative and rare species increased on cut plots each year, compared to no change or declines on control plots.

4.4. Development of biophysical gradients for landscape diversity

Biophysical gradients from dry uplands to wet prairies add landscape-scale diversity to Midwestern oak savannas (Annen and Lyon, 1999; Brewer and Vankat, 2006). In the study area, a decrease in elevation from uplands of only a few meters results in finer-textured soils, an increase in soil organic matter, and water tables near the surface (McCormack and Wilding, 1969). In natural ecosystems, this physical gradient is accompanied by a shift from dry-site oaks and understory species such as lowbush blueberry (*Vaccinium angustifolium*), to nearly treeless wet prairies with mixtures of herbaceous plants and shrubs such as swamp dewberry (*Rubus hispidus*; Brewer and Vankat, 2004). These biophysical gradients were not apparent within the set of control plots, while half of cut plots contained ≥ 4 wetland species (one more than the maximum found on control plots) and the other half were dominated by upland species. The plantations likely suppressed upland-wetland community differentiation, and when plantations were removed, soil and topographic factors resumed filtering community composition.

4.5. Floral resources for conservation-priority invertebrates

Projected floral resources for federally endangered Karner blue butterflies and bees were up to 24 × higher on cut than control plots. This is probably only a minimum estimate, because our projections only included cover of plant species specifically on published utilization lists for the published study sites (Grundel et al., 2000; Arduser, 2010). Thus, we excluded similar plant species found on our study plots that probably are also utilized by the invertebrates.

The Karner blue butterfly became extirpated in Ohio between 1975 and 1998, until it was reintroduced in 1998 (Ohio Karner Blue Recovery Team, Toledo, OH). One reintroduction site was in the southern part of the study area, and while Oak Openings Preserve has no known current population of Karner blue butterflies, plantation removal could contribute to increasing potentially suitable habitat. In addition to nectar plants required by adults, larvae feed only on the legume wild lupine (Shuey et al., 1987). This plant species is state potentially threatened and restricted to dry, open prairies and oak savannas (Plenzler and Michaels, 2015). Wild lupine colonized one cut plot by 14 years after cutting in 2015. Its low abundance might be more limiting to Karner blue habitat quality than availability of floral resources on cut plots.

Bee assemblages are species-rich in Midwestern oak savanna-prairie landscapes and of conservation interest amid global concern for pollinators (Grundel et al., 2010). In a 280-ha preserve just north of our study area, Arduser (2010) recorded 124 species of bees (97% native) in 24 h of sampling in restored savanna-prairie habitats. While no comparative data exist for bee or pollinator diversity in intact plantation and removal sites, many of the bee-utilized plant species Arduser (2010) found in restored oak savannas (reestablished through thinning and burning oak forest) are now abundant on our cut plots. *Rubus* was the most frequently visited genus by bees in the Arduser (2010) study, and this genus had nearly 40% cover on our cut plots by year 14. Another most-visited genus, *Solidago* spp., had 559 × more cover on cut plots, averaging 6.15% cover on cut plots compared to only 0.01% on control plots. Furthermore, the increase in conservative plants over time on cut plots could promote bee diversity. At least some of the conservative plant species on our plots, such as dwarf dandelion (*Krigia virginica*), appear linked with certain specialist bees (Arduser, 2010). Future research on comparing invertebrate and animal use among plantations, cut plots, and restored prairies and savannas could benefit long-term planning for integrating plantation sites into the conservation landscape.

4.6. Conclusion

In evaluating what was gained by removing plantations compared to no management, plantation removal increased plant diversity and cover, benefited conservation-priority native species, stimulated landscape diversity through development of a wetland-upland biophysical gradient, and enhanced potential floral resources available to invertebrate species. Oak trees (≥ 1 cm in diameter) also only became established on cut plots, crucial to meeting a long-term goal of encouraging a native landscape of oak savanna-prairie. These benefits accrued with minimal increase in non-native plants compared to uncut plantations.

Additional management strategies could be evaluated in the future. The plantations are considered a historical cultural feature of the park, and some plantations could be strategically maintained in priority locations. This may require periodic thinning or re-planting of pines, and monitoring to ensure the non-native pines are not spreading into natural ecosystems (Catling and King, 2007). Certain plantations could also be heavily thinned (and not removed entirely) to create open pine savannas, which may offer unique habitat structure until oaks become established. However, this strategy has the disadvantage of sustaining pine seed sources which have invaded native prairies and savannas (Abella and MacDonald, 2002), and eastern white and red pine can live for centuries (Paton et al., 1944). At plantation removal sites, prescribed burning treatments could be compared to evaluate effects of reintroducing fire as a process structuring natural oak savannas and prairies (Plenzler and Michaels, 2015). It may be important to compare different burn timings and frequencies, such as to avoid killing new oak recruits and slowing development of oak savanna. Our results combined with those of previous studies suggest that plantation removal is most consistently effective as a conservation action for native species when: 1) there is a desired vegetation type with shade-intolerant species, 2) desired species are absent in intact plantations and there are few non-natives, and 3) undesired plantation trees are recruiting and spreading.

Acknowledgements

This study was funded by a grant from the Metropolitan Park District of the Toledo Area to Natural Resource Conservation LLC. We thank John Jaeger for organizing initial treatments; Karen Menard, Jenny Finfera, and Denise Gehring for help sampling six plots; and Romaike Middendorp and an anonymous reviewer for helpful comments that improved the manuscript.

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Table S1. Summary of means, variability, and statistical results for response variables analyzed using a two-factor (treatment and time) repeated measures analysis of variance during a pine plantation removal experiment to restore native oak savanna-prairie ecosystems in northwestern Ohio, USA. Pines were cut in 2002 in the cutting treatment, while control plots were uncut plantations.

	Cut			Control					
	2002	2004	2015	2002	2004	2015	Treatment (T)	Year (Y)	T × Y
	Mean ± standard error of mean						Degrees of freedom/*F*-statistic/P-value		
Pine trees/ha[a]	249±54	219±49	53±20	900±155	951±169	751±111	1,22/21/<0.001	3,66/18/<0.001	3,66/11/<0.001
Pine basal area (m^2/ha)[a]	21±4	21±5	9±4	59±3	63±3	64±8	1,22/50/<0.001	3,66/12/<0.001	3,66/17/<0.001
Oak trees/ha[b]	0±0	0±0	87±44	0±0	0±0	0±0	–[b]	–	–
Native species/0.05 ha	35±3	44±3	41±3	24±2	23±2	25±3	1,22/21/<0.001	2,44/2/0.145	2,44/3/0.067
Non-native species/0.05 ha	5±1	9±1	9±1	2±1	3±1	4±1	1,22/13/0.002	2,44/10/<0.001	2,44/2/0.139
Cover native species (%)	21±4	27±5	73±8	8±1	4±1	33±11	1,22/16/<0.001	2,44/26/<0.001	2,44/2/0.097
Cover non-native species (%)	2±1	8±2	2±0	1±0	1±0	2±1	1,22/10/0.005	2,44/6/0.006	2,44/9/<0.001
Conservative species/0.05 ha[c]	7±1	10±1	12±1	7±1	8±1	8±1	1,22/2/0.184	2,44/13/<0.001	2,44/9/<0.001
Floristic quality (unitless)	13±1	17±1	21±1	15±1	15±1	17±1	1,22/2/0.171	2,44/34/<0.001	2,44/13/<0.001

[a] Pine tree density and basal area were measured in 2001, before cutting, so the repeated measures model included four years.

[b] Oak trees present were 1 to 15 cm in diameter at 1.4 m. There were no oak trees ≥ 1 cm in diameter in 2002 or 2004 in any plot, and in 2015, they only occurred in cut plots. The 87 oak trees/ha on cut plots in 2015 was significantly greater than the zero oak trees on control plots based on a one-tailed *t* test (14 degrees of freedom, *t*-statistic = 2.0, P = 0.035).

[c] Includes species with coefficients of conservatism from 5 to 10, representing specialist species with restricted distributions.

Table S2. Frequency, density, and basal area for 16 species of trees recorded in the tree layer (> 1 cm in diameter at a height of 1.4 m) during a pine plantation removal experiment to restore native oak savanna-prairie ecosystems in northwestern Ohio, USA. Pines were cut in 2002 in the cutting treatment, while control plots were uncut plantations.

	Cut			Control			Cut			Control			Cut			Control		
	2002	2004	2015	2002	2004	2015	2002	2004	2015	2002	2004	2015	2002	2004	2015	2002	2004	2015
	Frequency (%)[a]						Trees/ha[b]						Basal area (m^2/ha)[b]					
Acer rubrum	13	7	13	11	11	11	7	1	96	13	11	9	0.01	0.01	1.27	0.71	0.73	0.76
Amelanchier arborea			7						7						0.01			
Betula populifolia			7						3						0.01			
Cornus florida				11	11	11				2	2	2				0.01	0.01	0.01
Fraxinus americana		7						1						0.01				
Pinus resinosa	33	33	13	56	56	56	141	113	8	702	740	538	7.14	6.18	0.58	36.1	37.5	32.6
Pinus strobus	40	47	27	44	44	44	108	105	45	198	211	213	14.3	14.5	8.63	23.3	24.9	31.1
Pinus sylvestris			7						1						0.01			
Populus deltoides			7						4						0.01			
Prunus serotina	7	7	27	22	33	44	1	1	196	4	7	31	0.14	0.14	0.41	0.31	0.32	0.39
Quercus alba			20						8						0.03			
Quercus ellipsoidalis			7						3						0.01			
Quercus imbricaria			7						3						0.01			
Quercus palustris	7		27				1		19				0.07		0.09			
Quercus velutina			40						55						0.07			
Sassafras albidum			7						3						0.02			

[a] Percentage out of 15 cut or 9 control plots in which a species occurred. Plots were 0.05 ha.
[b] Values are means based on 15 cut and 9 control plots.

Table S3. Average percent cover of the 28 understory species (including tree seedlings < 1 cm in diameter at a height of 1.4 m) with the highest cover during a pine plantation removal experiment to restore native oak savanna-prairie ecosystems in northwestern Ohio, USA. Pines were cut in 2002 in the cutting treatment, while control plots were uncut plantations. Species are arranged by growth form.

		Cut			Control		
Species	Growth form[a]	2002	2004	2015	2002	2004	2015
Erechtites hieraciifolius	annual forb	2.1	2.6	0.1	0.1	0.1	2.9
Alliaria petiolata	annual-biennial forb*	0.6	0.1	0.1	0.2	0.2	0.1
Polygonum virginianum	annual-perennial forb	0.2	0.2	0.1	0.2	0.1	0.3
Dryopteris carthusiana	fern	0.6	0.9	0.1	0.1	0.2	0.3
Phytolacca americana	perennial forb	4.3	0.8	0.1	0.1	0.1	0.6
Solidago rugosa	perennial forb	0.1	0.1	4.7	0	0	0.1
Parthenocissus quinquefolia	perennial forb	1.2	1.1	0.1	0.3	0.1	0.2
Solidago canadensis	perennial forb	0	0.1	1.1	0	0	0
Rumex acetosella	perennial forb*	0.3	2.6	0.2	0	0	0.1
Cirsium arvense	perennial forb*	0.2	0.9	0.1	0	0	0
Dichanthelium clandestinum	perennial graminoid	0.1	0.5	7.2	0.1	0.1	0.6
Andropogon gerardii	perennial graminoid	0	0	3.4	0	0	0
Carex swanii	perennial graminoid	0.1	0.1	0.5	0	0.1	0.9
Agrostis perennans	perennial graminoid	0	0.1	1.0	0	0	0.1
Eragrostis spectabilis	perennial graminoid	0	1.0	0.1	0	0	0
Dryopteris carthusiana	fern	0.6	0.9	0.1	0.1	0.2	0.3
Rubus spp.	shrub	0.7	6.6	37.6	0.2	0.2	7.5
Toxicodendron radicans	shrub	1.1	1.5	0.1	0.5	0.2	0.3
Spiraea tomentosa	shrub	0	0.1	1.3	0	0	0.1
Rhamnus cathartica	shrub*	0.2	1.7	0	0.1	0.1	0.1
Elaeagnus umbellata	shrub*	0.2	0.6	0.2	0.1	0.1	0.6
Berberis thunbergii	shrub*	0.1	0.2	0.2	0.1	0.1	0.8
Prunus serotina	tree	0.7	0.8	1.5	1.2	0.4	11.5
Acer rubrum	tree	1.3	1.8	0.3	1.5	0.4	0.8
Liquidambar styraciflua	tree	0	0.1	0.1	0	0	2.8
Quercus velutina	tree	0.2	0.3	1.6	0.2	0.2	0.2
Betula populifolia	tree	0	0	2.1	0	0	0
Pinus strobus	tree	0.2	0.3	0.1	0.3	0.1	0.7
Quercus palustris	tree	0.1	0.2	0.6	0.1	0.1	0.1
Portion of total cover (%)[b]		62	72	86	64	55	90
Cover of all species (%)[b]		23	35	75	8	4	35

[a] Asterisks note non-native species.

[b] The portion of total cover represents the 28 species in the table out of the 370 total species recorded during the study. The cover of all species is the average cover per plot including all 370 species.