Resistance and Resilience to Natural Disturbance during Ecological Restoration

Scott R. Abella, Timothy A. Schetter, John F. Jaeger, Lawrence G. Brewer, Karen S. Menard, Timothy D. Gallaher, Jason J. Diver and LaRae A. Sprow

ABSTRACT

An uncertainty in ecological restoration is how natural disturbances occurring during restoration might influence restoration outcomes. The unplanned nature of natural disturbances makes them difficult to study, and their effects hinge on the resistance or resilience of ecosystem components that may change during restoration. In 2010, a tornado struck a 23-year-old oak woodland-savanna restoration site in northwestern Ohio, USA, providing a rare opportunity to determine how a major natural disturbance could influence the course of restoration. Restoration burning had begun at the site in 1988. We monitored tree and understory metrics before restoration, in 10 of the 22 years during restoration before the tornado, and in two of five years after the tornado until 2015. Trajectories in floristic quality and conservation-priority plant species (e.g., state-listed rare species) were resistant to change by the tornado, non-native plants were resilient (which was desirable as they quickly declined to near pre-tornado levels after an initial increase), and the oak overstory was neither resistant nor resilient. Overstory density was halved after the tornado, moved from woodland toward savanna, and then changed little. Forbs and oaks in the understory were the main increasers after the tornado. The tornado disturbance altered the pathway of restoration but remained consistent with restoration goals, given that both woodlands and savannas were part of reference conditions and conservation-priority forbs increased.

Keywords: fire, oak savanna, oak woodland, tornado, understory

Restoration Recap

- The main effects of a tornado striking a 23-year-old restoration site that had received 10 restoration burns was to halve oak overstory density, stimulate an understory layer of small oak stems, and triple forb cover.
- The tornado shifted overstory structure from woodland to savanna. This remained consistent with a restoration goal of reestablishing open-structured oak ecosystems, as both woodlands and savannas occurred historically and offer unique habitat features.
- Non-native plant cover was low throughout the 28-year study. After a slight increase (but still < 1%) two years after the tornado, non-native cover returned to near pre-tornado levels within five years.
- The first post-tornado decade is a key time for management decisions because of a developing layer of dense, small oak stems. During this period, management activities could favor maintaining savanna or instead redeveloping woodland.

Natural disturbances present a potential conundrum for ecological restoration. On one hand, severe natural disturbances such as floods, wildfires, or wind events could negate restoration gains. This could manifest through undesirable outcomes such as loss of restored forest cover, invasion by non-native species, or disruption of habitat recovery (Allison 2008, Densmore and Karle 2009). On the other hand, natural disturbances may act synergistically with restoration activities to promote ecosystem repair. This scenario might occur, for example, via natural

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disturbance favoring native over non-native species or hastening development of desired vegetation structure (Brewer 2016). Another possibility is that the natural disturbance has a neutral influence on restoration success by triggering a different, but still desirable, restoration outcome, such as an alternative ecosystem state (Paine et al. 1998, Suding et al. 2004).

These possibilities can hinge on how resistant or resilient the ecosystems undergoing restoration are compared to unrestored ecosystems when natural disturbance occurs. Resistance is the ability of an ecosystem to incur a disturbance and not change (Lake 2013). If resistance fails, resilience is the ability of an ecosystem to return to its pre-disturbance state. Resistance and resilience can be useful or not useful in ecological restoration (Nimmo et al. 2015). For example, resistance could help a restored ecosystem avoid invasion by non-native species or be unhelpful if a degraded ecosystem is recalcitrant to restoration.

Different components within an ecosystem—such as a forest overstory versus understory—can vary in their resistance and resilience (Kleinman and Hart 2017). This suggests that different restoration metrics indicative of restoration success could respond variably to natural disturbance. Furthermore, it is important to evaluate for which measures and circumstances resistance and resilience are desirable during ecological restoration and natural disturbance (Abella and Fornwalt 2015). For instance, resiliency of non-native species after disturbance could be desirable if it reverses an increase back toward low pre-disturbance levels. Resiliency in non-native species could instead be undesirable if post-disturbance reductions revert back toward high pre-disturbance levels.

Severe wind storms, such as tornados, are natural disturbances with effects on restoration sites dependent on ecosystem resistance and resilience, influencing trajectories of restoration metrics (Cannon et al. 2017). Tornados, consisting of rotating vertical columns of air that touch the ground, are Earth's most locally severe storms with wind speeds that can exceed 480 km/hour (Foster et al. 1998). The severity of tornados is ranked by an Enhanced Fujita Scale ranging from EF0 (least severe) to EF5 (most severe). With 30,747 EF1-5 tornados recorded from 1950 through 2013 in the lower 48 states, the United States incurs more tornados than any country in the world (Guo et al. 2016). While associations between contemporary warming and tornado activity are being examined (Guo et al. 2016), severe winds have long been part of North America's disturbance regime and reference conditions (Everham and Brokaw 1996). For example, surveyors during 1800s General Land Office appraisals recorded windfalls and tracks of fallen timber, and Burley and Waite (1965) noted that written descriptions of tornados in Wisconsin appear by 1843.

In this study, we examined how a tornado affected the trajectory of a long-term (28-year) restoration project in a Midwestern USA oak woodland-savanna that we monitored for 23 years before the tornado and for five years after. The unique, long-term pre-tornado data enabled evaluating resistance and resilience of ecosystem components undergoing restoration, compared to an unrestored area struck by the same tornado. We addressed the following question: what were temporal trajectories in tree structure, understory plant cover, species richness, floristic quality, and non-native species under 28 years of restoration and tornado influence?

Methods

Study Area

We performed this study in northwestern Ohio in the 40,000–ha Oak Openings region, which formed on beach sands deposited by glacial lakes during the Wisconsin glaciation. U.S. Government land surveys from 1817–1832 indicated that the region supported wet prairies on poorly drained soils and oak savannas or woodlands on well-drained soils (Brewer and Vankat 2004). The fire-dependent savannas and woodlands, dominated by *Quercus alba* (white oak) and *Quercus velutina* (black oak), likely fluctuated in tree density both spatially and temporally. Along a continuum of overstory density, woodlands generally contained more than 43 trees/ha (> 13 cm in diameter) and savannas from 1–43 trees/ha (Brewer and Vankat 2004). It is possible that tree density fluctuations were linked with droughts, variable fire frequencies and severities, or other disturbances such as wind (Ziegler et al. 2008). Based on descriptions in early land surveys, botanical inventories, and contemporary reference sites, understories in the savannas and woodlands are believed to have been dominated by woody plants (e.g., shrubs such as *Vaccinium* spp., and seedlings and sprouts of tree species) and mixtures of forbs and graminoids, partly contingent on tree canopy cover (Schetter and Root 2011).

Within the Oak Openings region, our study site was the 40-ha Mary's Savanna (41°32′15″N, 83°51′00″W), in the southern part of the 1497-ha Oak Openings Preserve, managed by the Metroparks of the Toledo Area. A weather station 10 km northeast of the site reported long-term (1955–2015) averages of 85 cm of annual and 34 cm of summer (May through August) precipitation (Toledo Express Airport; Midwestern Regional Climate Center, Champaign, IL, USA; Figure 1). Soils in Mary's Savanna are classified as mixed, mesic Aquic and Typic Udipsamments of the Ottokee and Oakville series (Stone et al. 1980). Before restoration in 1988, vegetation structure of the site was typical of sites throughout Midwestern North America that were formerly open savanna or woodland and converted to mixed-species forests (with both oak and non-oak tree species) without fire (Knapp et al. 2015). Vegetation physiognomy consisted of an overstory of *Q. velutina* and *Q. alba*, originating after the late 1800s, and a mid-story

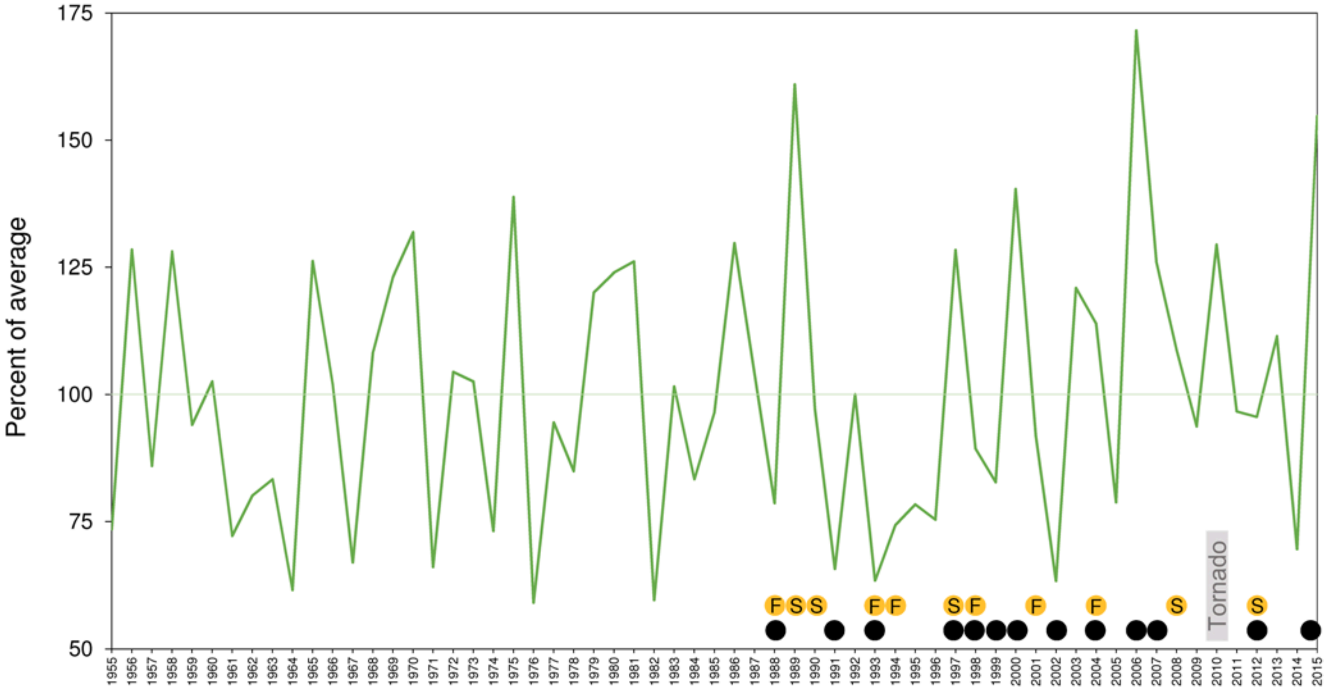

Figure 1. Summer (May through August) precipitation during a 1988–2015 restoration project relative to long-term (1955–2015) variability and average of 34 cm/year summer precipitation measured at the Toledo Express Airport, northwestern Ohio (Midwestern Regional Climate Center, Champaign, IL). Black circles note the years in which we measured vegetation. Orange circles signify prescribed burns, including the season (S = spring, F = fall). A tornado struck the site in 2010.

and understory of primarily non-oak stems of *Acer rubrum* (red maple), *Sassafras albidum* (sassafras) and *Prunus serotina* (black cherry; Figure 2).

In the western half of the site, a restoration burning program between the fall of 1988 and 2015 included 11 burns (Figure 1). The goal of restoration burning was to reinstate fire as a natural process in the evolutionary development of oak savanna-woodland ecosystems, re-establish open-structured oak ecosystems and herbaceous layers by decreasing the mid-story and understory stems of non-oak tree species, and reduce thickness of the O horizon. The O horizon decreased by 39% in the restoration area from before restoration in 1988 to 14 years later in 2002, compared to a 25% increase in the control (Abella et al. 2004). The prescribed fires occurred during the dormant season in fall (November) or spring (March) and occurred every four years or more frequently. Relative humidity at ignition times typically ranged from 30–70%, with winds < 16 km/hr. The burns were surface fires with flames typically < 2 m high. Separated by a dirt road/trail 4 m wide serving as a fire break, the eastern half of the site, within the same soil unit and with similar vegetation physiognomy as the western half, served as an unrestored control.

Twenty-three years into the restoration program on June 5, 2010, a tornado categorized as EF1 (wind speeds 138–177 km/hour) developed southwest of the restoration site. The tornado traveled on a southwestern-northeastern 6-km path, passing directly through the restoration and control areas (National Oceanic and Atmospheric Administration, Cleveland, OH). This tornado was one of 53 on June 5–6, 2010 in the central and eastern United States and Ontario, Canada. At our study site during the subsequent year, Metroparks of the Toledo Area staff performed some cleanup around our study plots using chain saws to fell damaged, hazard trees near the road/trail. The restoration burning program continued after the tornado, with the first post-tornado burn in spring 2012 (Figure 1).

Data Collection and Analysis

In the summer of 1988 before restoration, three 20 × 25 m (0.05 ha) permanent plots were established in the restoration area and two plots in the control. Plots were systematically arranged approximately 50 m from each other. In a 28-year period from 1988 (before restoration) through 2015, restoration plots were sampled in 13 of the years and the two control plots in all of the same years except 1991. To balance the study design, a third control plot (similar in physiognomy and equidistant to the other control plots) was established in 1998 and thereafter sampled on the same schedule as the other plots. Near the peak of the growing season in June–August, we categorized the areal cover of each vascular plant species rooted in plots as trace (assigned 0.1% cover), 0.5%, 1% increments to 10% cover, and 5% increments above 10% cover. Stems of tree species < 1 cm in diameter at 1.4 m were included in these understory cover measurements. Cover, when summed

Figure 2. Examples of repeat photos in 2002 (top row) and in the same locations in 2015 (bottom row) during an oak woodland-savanna restoration in Oak Openings Preserve, northwestern Ohio. The left and middle photo pairs were taken on restoration plots, while the right-side pair was taken on a control plot not receiving restoration burning. Restoration began in 1988 and by the project mid-point in 2002, restoration plots had received eight prescribed fires. The 2015 photos were five years after a tornado struck all plots, sharply reducing overstory tree density. *Photo credits: S.R. Abella.*

for all species, could exceed 100%, reflecting overlapping layers of low herbaceous plants (e.g., *Carex pensylvanica* [Pennsylvania sedge]) below taller woody plants. Stems of tree species larger than 1 cm in diameter were tabulated by species and diameter was measured to the nearest cm. Nomenclature, classification of life span (e.g., annual, perennial), growth form (e.g., forb, shrub), and nativity to the U.S. followed Natural Resources Conservation Service (2018). We recorded *Pinus strobus* (eastern white pine), native to the U.S. but not to the Oak Openings region, as a non-native species because its seedlings occasionally found on plots likely spread from plantations (Abella et al. 2018).

The 2010 tornado striking the long-term restoration site was unreplicated in the region, so scope of inference was this unique event. As a result, we mainly used descriptive statistics, instead of inferential statistics, to assess trends through time including means and standard errors of means from plots for the restoration and control areas. We calculated these descriptive statistics for the restoration metrics of tree density (small and large oaks and non-oak species) and basal area, species richness (per 500 m^2), floristic quality, number of species with coefficients of conservatism from 7–10 and Ohio rare species, and cover of natives and non-natives, plant growth forms, and major taxa. We categorized oak trees as small ($1 \leq$ stem < 40 cm in diameter) or large (≥ 40 cm in diameter), with the 40-cm cutoff generally distinguishing overstory dominants from smaller sub-canopy stems. Coefficients of conservatism express the fidelity of species to natural habitats (compared with affinity to recent anthropogenic disturbances) within states or regions (Andreas et al. 2004). The coefficients rank native species from 0 (typifying widely distributed species associated with disturbed habitats) to 10 (species mainly restricted to natural habitats). We used coefficients developed for Ohio (Andreas et al. 2004) and considered species with coefficients of 7 and above to be of conservation-priority characterizing natural habitats. We calculated floristic quality for each plot as the sum of native species coefficients of conservatism divided by the square root of native species richness (i.e., excluding non-native species from the index), following the standard formula for Ohio (Andreas et al. 2004). Non-native species are traditionally excluded from the index, which we followed, and in our study where non-native plants were sparse to absent, floristic quality indices calculated with only native and with all species were similar. We tabulated the number of Ohio rare species on each plot as the number of species listed by the Ohio Division of Natural Areas and Preserves (Columbus, OH, USA) as state threatened, potentially threatened, or endangered. To provide some inferential statistical perspective for the last three measurement years of the study representing three years before (2007), two years after (2012), and five years after (2015) the tornado, we used two-tailed *t* tests in SAS 9.3 (SAS Institute, Cary NC) to compare restoration metrics between the treatment and control for each year.

Results

Tree Layers

Restoration metrics exhibited different trajectories of change during 28 years of restoration and variable resistance and resilience to the 2010 tornado disturbance. The density of small oaks (1 ≤ stem < 40 cm in diameter) initially sharply declined in the time between before restoration in 1988 and five years into restoration in 1993 in both the restoration and control areas, then gradually declined overall for the next 20 years (Figure 3A). Between 2012 and 2015, after the tornado, small oak density tripled in the restoration area while continuing to decline in the control. Density of large oaks (≥ 40 cm in diameter) and oak basal area were nearly unchanging in the restoration area from 1988 to 2007 during the first 20 years of restoration, before both metrics decreased by over half within two years after the tornado (Figure 3B, C). These overstory metrics then

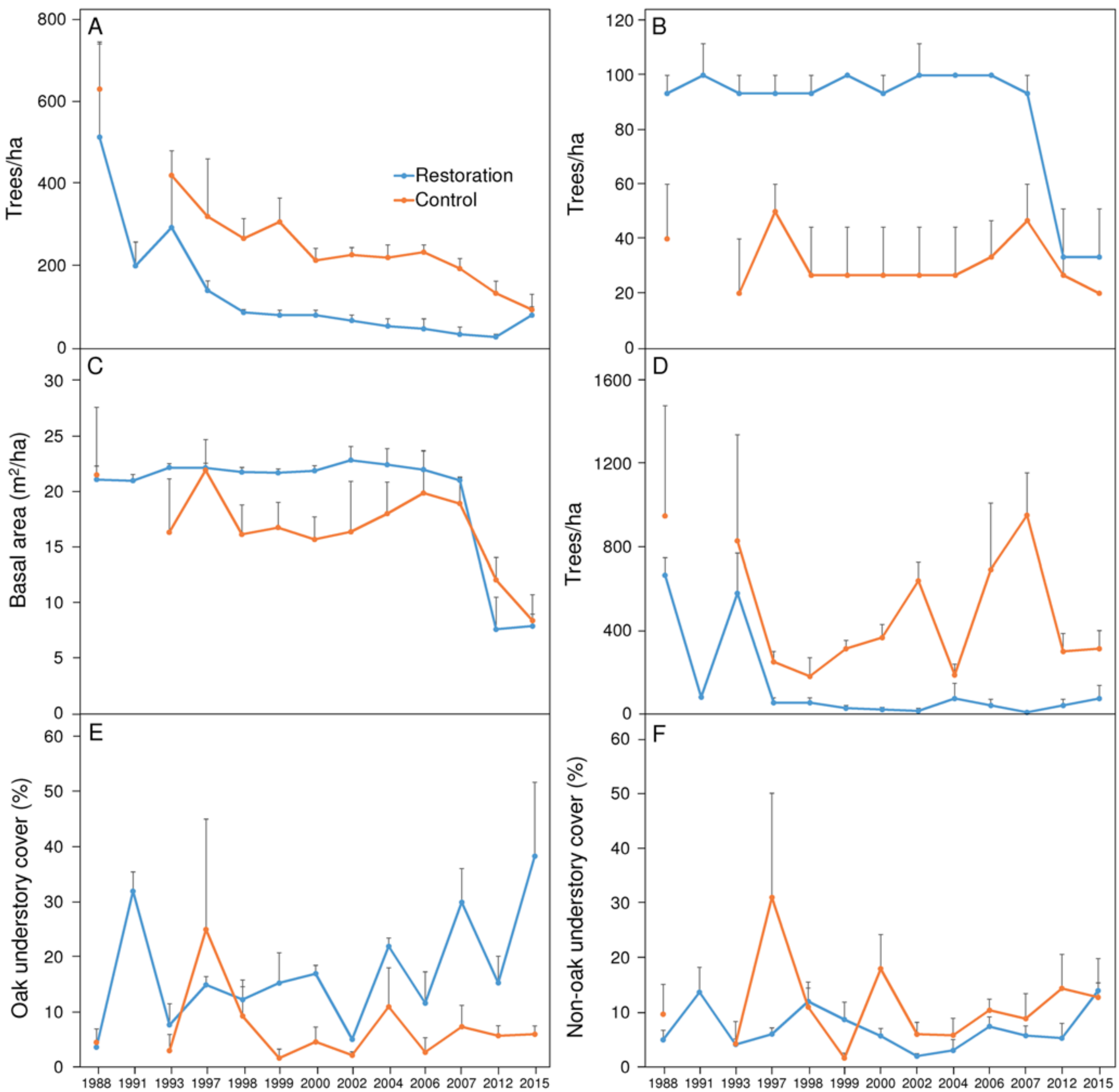

Figure 3. Dynamics of tree species during an oak woodland-savanna restoration in Oak Openings Preserve, northwestern Ohio. Data include: A) small sub-canopy oak trees (*Quercus velutina* and *Q. alba*), 1 cm ≤ stem < 40 cm in diameter at 1.4 m, B) large oak trees ≥ 40 cm in diameter, C) oak basal area, D) non-oak trees (all of which were 1–29 cm in diameter), and E, F) understory cover by tree species < 1 cm in diameter. Error bars are 1 standard error of the mean.

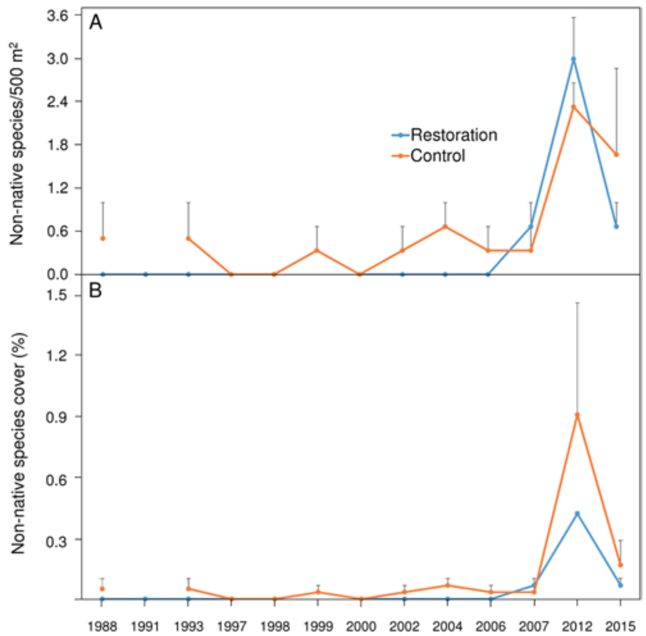

Figure 4. Changes in non-native species during an oak woodland-savanna restoration in Oak Openings Preserve, northwestern Ohio. Non-native species increased following a 2010 tornado, then declined. Error bars are 1 standard error of the mean.

stabilized and changed little between 2012 and 2015. A similar post-tornado decrease in large oak density and basal area occurred in the control. Density of non-oak trees (all < 30 cm in diameter) fluctuated widely during the first decade in both the restoration and control areas, but then non-oak density remained low in the restoration area while fluctuating but being higher in the control area for the remainder of the study (Figure 3D). The cover of understory oaks < 1 cm in diameter fluctuated in the restoration and control areas, remaining highest in the restoration area after 1998 and in 2015 was the highest recorded during the study (Figure 3E). Following a different trajectory, the cover of understory non-oak tree species was nearly identical between the restoration and control areas by 2015 (Figure 3F). Supporting these descriptive statistical results, a main finding of the inferential statistical analysis was that tree-layer metrics that differed between the restoration and control areas in 2007, before the tornado, became more similar between the areas after the tornado (Supplementary Table S1).

Non-Native Plants

Non-native plants were sparse throughout the study, absent from plots in many years (Figure 4). Species richness and cover of non-natives rose in 2012 after the tornado in both the restoration and control areas, then quickly declined by 2015. Even at their peak in 2012, non-natives averaged < 1% cover.

Richness, Floristic Quality, and Rare Species

Native species richness and floristic quality generally increased during the study and displayed resistance or resilience to the tornado. Native species richness gradually increased overall in the restoration area until sharply increasing after the tornado, then showed resiliency by apparently trending back toward pre-tornado levels by 2015 (Figure 5A). In the control, native species richness fluctuated more than in the restoration area, but similarly sharply increased after the tornado then decreased. Trends in floristic quality were more variable, but similar to native richness, there was an increase (largest in the control) after the tornado, then a decrease (Figure 5B). The number of species with high coefficients of conservatism fluctuated in both treatments, and the trends seemed resistant to change after the tornado (Figure 5C). There were more state-listed species per plot in the restoration than control area at the start of the study, but an overall trend for rare species to increase in the restoration but not the control area (Figure 5D). Temporal trends in rare species appeared resistant to the tornado. The inferential statistical analysis further supported these trends, with differences between the restoration and control generally being maintained from before to after the tornado for native species richness, floristic quality, and rare species richness. However, increased variability within the restoration area after the tornado in some cases weakened statistical differences by 2015 (Supplementary Table S1).

Plant Groups and Cover

Trends in total native species cover in the restoration and control nearly mirrored each other for the first 25 years until they diverged in 2015, with a sharp increase in the restoration area five years after the tornado, compared to minimal change in the control (Figure 6). An earlier substantial increase in cover in the restoration area occurred in 1991, three years after restoration commenced. This rise was driven by major increases in all plant growth forms, except forbs, which still increased but attained < 8% cover. The next major change was not until 25 years later in 2015 when total cover tripled in the restoration area. This time, however, forbs increased in cover five-fold and fern cover did not increase, while the other plant groups increased sharply as they had in 1991.

Dominant taxa (those with the greatest cover) responded differently after the tornado (Figure 7, Supplementary Table S1). The shrubs *Vaccinium* spp. and *Gaylussacia baccata* (black huckleberry), and the sedge *C. pensylvanica*, declined in 2012 after the tornado then rebounded by 2015. *Pteridium aquilinum* (bracken fern) generally declined after the tornado. In contrast, the forb *Lupinus perennis* (wild lupine), a state-listed species present on restoration plots in some pre-tornado years but often not abundant, increased after the tornado to the highest cover the species attained in 28 years.

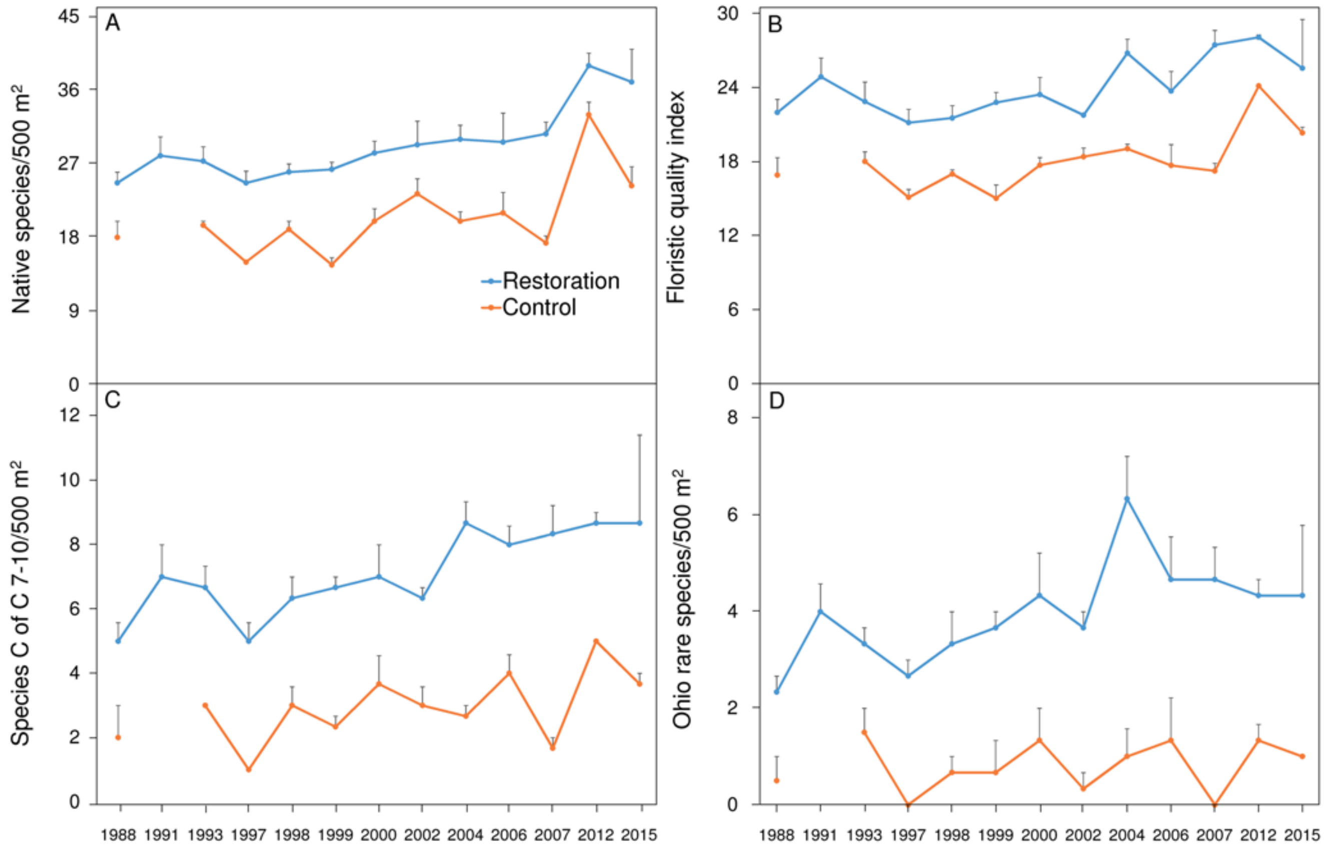

Figure 5. Native species richness and floristic quality measures during an oak woodland-savanna restoration in Oak Openings Preserve, northwestern Ohio. Graph C shows the number of species with coefficients of conservatism from 7 to 10, representing species typifying high-quality natural habitats. Error bars are 1 standard error of the mean.

Discussion

Twenty-three years of restoration before the tornado had two main effects: 1) nearly eliminating a dense understory and mid-story layer of tree stems; and 2) increasing conservation-priority rare native plant species. Additionally, some of these rare plants, such as *L. perennis*, the sole larval host plant for federally endangered Karner blue butterflies (*Lycaeides Melissa samuelis*), are linked with conservation-priority wildlife (Walsh 2017). Restoration, however, minimally affected the density and basal area of the oak overstory. Before the tornado, the site resembled a woodland more than a savanna. In 2007 before the tornado in the restoration area, the density of oak trees ≥ 13 cm in diameter (the targeted minimum size selected as witness trees in historical surveys) remained three times more than the upper limit of 43 trees/ha for 1817–1832 savannas in the region reconstructed from General Land Office survey records (Brewer and Vankat 2004). The tornado moved the site near the tree density occurring in historical savanna with 53 trees/ha (≥ 13 cm in diameter) by two years after the tornado.

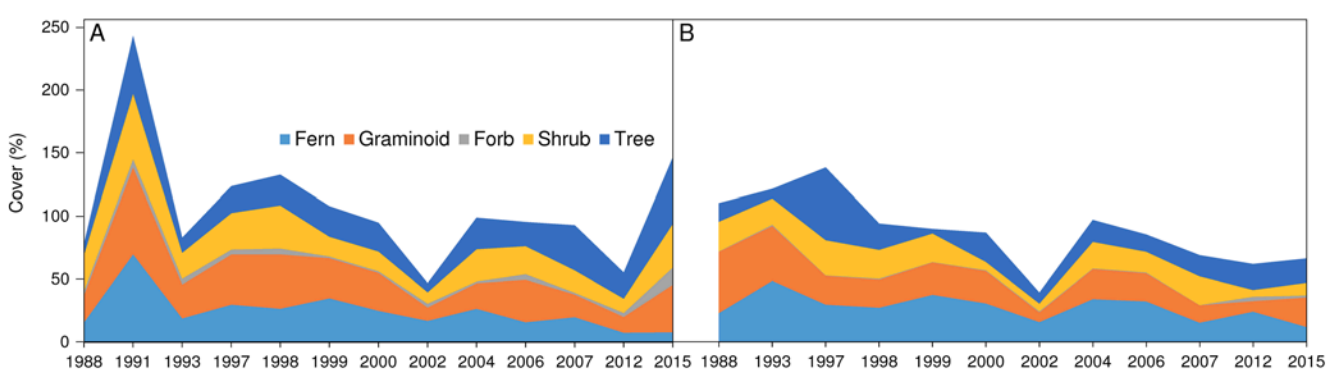

Figure 6. Trends in cover by plant growth forms for A) restoration and B) control areas during an oak woodland-savanna restoration in Oak Openings Preserve, northwestern Ohio. Data were not collected in 1991 for the control.

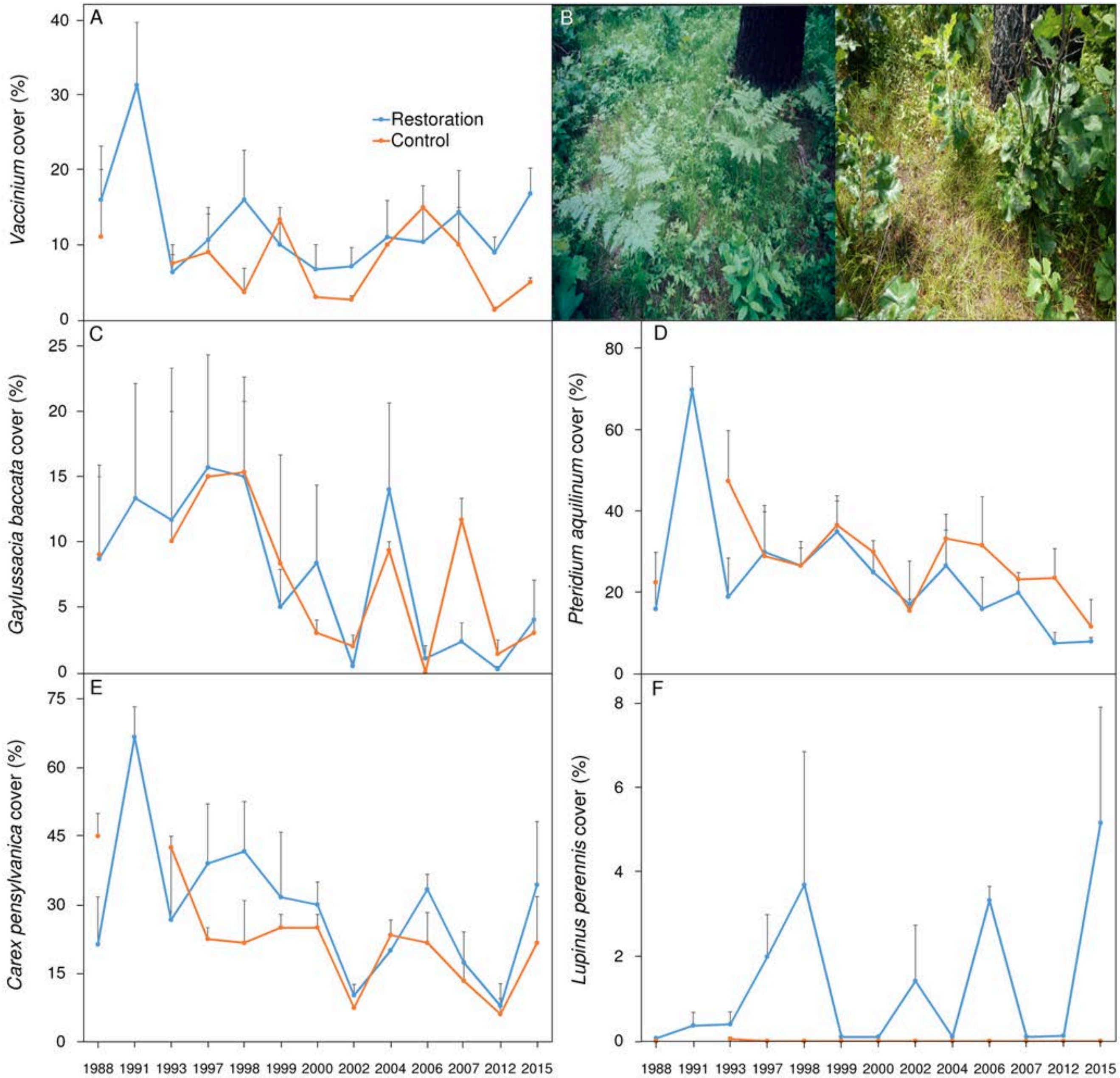

Figure 7. Cover of major taxa during an oak woodland-savanna restoration in Oak Openings Preserve, northwestern Ohio. *Vaccinium* cover in A) includes *V. angustifolium* and *V. pallidum*. The paired photos in B) from the same location within a restoration plot in 2002 (left side) and 2015 (right side) show persistence of groundlayer *Carex pensylvanica* and some *V. pallidum*, a decline in *Pteridium aquilinum*, and an increase in cover of *Quercus velutina* seedlings or sprouts. The trunk of a *Q. velutina* is in the top right. Error bars are 1 standard error of the mean. *Photo credits: S.R. Abella.*

The tornado damage may be an example of a natural disturbance producing simply a "different" restoration outcome than would have occurred with continued restoration in the absence of the disturbance, by selecting for an alternative ecosystem state still within the range of reference conditions. Current understanding is that many sites on pre-settlement Midwestern savanna landscapes supported a dynamic continuum of oak savanna to woodland, via tree densities fluctuating through time with variations in factors such as fire frequency and weather events (Ziegler et al. 2008, Abella et al. 2017). For example, denser woodlands could have formed during long (> 10 years) fire-free intervals, enabling oak recruitment and survival to fire-resistant sizes. It is possible that droughts, wind events, or severe fires reduced overstory density for various time-periods (Arthur et al. 2012). The details of this temporal dynamic are an uncertainty for restoration, such as how much density might have fluctuated and on what time scales, and which factors were paramount when and where in the dynamic. It is possible that this study's tornado event provides an analog to how tree density fluctuated on a site through time in past frequently burned and wind-disturbed woodlands (Cannon and Brewer 2013).

The tornado's aftermath likely represents a management pivot point toward a trajectory for savanna formation versus re-development of woodland (Liu et al. 1997). Small oaks responded vigorously during a three-year, fire-free period after the tornado, probably via release of seedlings or sprouts that had been kept small by dense overstory canopies and frequent fires (Peterson et al. 2007). Given *Q. alba* and *Q. velutina*'s ability for ascension to the canopy under open conditions, especially if the stems have become established before those of competing species (Brudvig and Asbjornsen 2008), it seems likely that if fires are discontinued for over a decade, oak woodland will re-develop. While the size and age structure of historical woodlands are poorly understood, a management strategy of allowing woodland to re-develop after the tornado would likely diversify structure (relative to the pre-tornado woodland) by forming woodland with large and old remnant trees that survived the tornado plus a post-tornado cohort of new recruits. Once the new recruits attain fire-resistant sizes (often > 5–10 cm in diameter; Bowles et al. 2007), burning could resume to maintain open understories to limit the formation of closed-canopy forest. Alternatively, another management strategy could be continuing burning as frequently as every four years to suppress the developing understory tree layer, keeping density closer to savanna structure and perhaps favoring herbaceous layers (Knapp et al. 2015).

Given that post-tornado overstory and many understory metrics were similar between the restoration and control areas, it is reasonable to ask what was gained by doing restoration before the tornado, including how restoration positioned the ecosystem to be resistant or resilient to natural disturbance. First, for two decades before the tornado, state-listed rare plant species, many of which depend on open-structured ecosystems (Walsh 2017), increased in the restoration area while remaining sparse in the control. Second, forb and oak understory cover responded more positively after the tornado in the restoration than in the control area. Many of the forbs were of conservation-priority, typified high-quality natural savannas, and had been sparse in both the restoration and control areas before the tornado. The oak understory layer facilitated by restoration could enhance post-tornado management flexibility (Abella et al. 2017). For example, a passive management option in the post-tornado restoration area could likely sustain an oak ecosystem, while in the control area lacking an oak understory layer, passive management would likely continue a trend for non-oak forests to develop (Holzmueller et al. 2012).

Results highlight the differential resistance and resilience of ecosystem components and in what circumstances resistance or resilience may be desirable in restoration. The fluctuating trends at decadal and yearly time scales before the tornado made it hard to pinpoint resistance or resilience for some variables, while trends were clearer for other variables. With respect to before the tornado and the five-year aftermath, we considered Ohio rare species, floristic quality, and conservative species to be resistant to change; non-native species richness and cover to be resilient; and oak overstory density, basal area, and forb cover to be neither resistant nor resilient. Resiliency of non-native species is desirable in this case, because non-natives quickly returned to near pre-tornado levels after a small post-tornado increase. Oak overstory and forb cover metrics changed substantially and showed no trend within five years to return to pre-tornado levels, so were neither resistant nor resilient. This response remained consistent with restoration goals.

It is unclear to what extent our findings hinged upon particular contingencies of weather and timing, the severity of the tornado, and site conditions. Both annual (103% of average) and May through August summer (102% of average) precipitation were near average during the 1988–2015 study period, and with half of the study years below and half above average (Figure 1; Toledo Express Airport, Midwestern Regional Climate Center, Champaign, IL). However, within this near average period, some notable precipitation years occurred at key points that may have correlated with vegetation patterns. The year the experiment started—1988—was not especially dry for the year (85% of average precipitation) or overall for the summer (79%, May through August), but a three-month April through June period received only 7.8 cm (31% of average) of precipitation. This spring and early summer in 1988 was so dry that during a 1955–2015 available climatic record, the next driest year (1962) for April through June received nearly twice as much precipitation with 15.1 cm (59% of average). The rest of the summer in 1988 received above average precipitation, and this was followed by the exceptionally wet summer of 1989 (161% of May through August precipitation, second wettest on record) and near average (97%) summer of 1990. The rise in total understory plant cover in 1991 (Figure 6) could thus result from recovery after the 1988 drought, coupled with the 1988–1990 annual burns stimulating layering of understory vegetation at high cover following reduction of a mid-story tree layer. Twelve years later, in 2002, summer was the driest during the 28-year study period and fourth driest of the past 60 years with only 63% of average May through August precipitation. Understory plant cover that year was the lowest during the study (Figure 6). With 155% of average summer precipitation, the summer of 2015 was the third wettest on record. Understory plant cover that year in the restoration area was the second highest (with 1991 being the highest) during the study. We hypothesize that combined influences of burns, climate, and the tree overstory were dominant drivers of temporal fluctuations in understory cover.

Atmospheric scientists ranked the 2010 tornado's wind speeds as "moderately damaging," consistent with the frequent breakage of canopies and occasional uprooting of trees, but avoidance of complete destruction of the overstory (National Oceanic and Atmospheric Administration, Cleveland, OH). The understory response, time-frame, and outlook for savanna or woodland restoration could have been different if the tornado had been more severe (Peterson 2000). If the overstory was completely destroyed, it is unclear whether communities typifying dry prairies would have developed (Brewer and Vankat 2006). Greater tornado severity and corresponding damage might have triggered more resprouting by trees, potentially further expanding woody plant dominance (Cannon and Brewer 2013).

Based on trends during the study, we surmise that if not frequently burned, the post-tornado restoration area will be dominated by woody plants along with the sedge *C. pensylvanica*. If the at-least-every-four-year restoration burning continues, we anticipate that forbs could be maintained at a higher cover under a more open overstory than they attained before the tornado. By deflecting a restoration woodland toward a savanna, effects of the tornado remained consistent with restoration goals within reference conditions and by stimulating the herbaceous layer.

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References

Abella, S.R., J.F. Jaeger and L.G. Brewer. 2004. Fifteen years of plant community dynamics during a northwest Ohio oak savanna restoration. *Michigan Botanist* 43:117–127.

Abella, S.R. and P.J. Fornwalt. 2015. Ten years of vegetation assembly after a North American mega fire. *Global Change Biology* 21:789–802.

Abella, S.R., T.A. Schetter, K.S. Menard, E.D. Ziegler, L.A. Sprow, T. Gallaher et al. 2017. Conserving large oaks and recruitment potential while restoring Midwestern savanna and woodland. *American Midland Naturalist* 177:309–317.

Abella, S.R., T.A. Schetter and T.L. Walters. 2018. Testing the hypothesis of hierarchical predictability in ecological restoration and succession. *Oecologia* 186:541–553.

Allison, S.K. 2008. Differences in the effects of drought upon restored and remnant prairies (Illinois). *Ecological Restoration* 26:95–97.

Andreas, B.K., J.J. Mack and J.S. McCormac. 2004. *Floristic Quality Assessment Index (FQAI) for Vascular Plants and Mosses for the State of Ohio*. Ohio Environmental Protection Agency.

Arthur, M.A., H.D. Alexander, D.C. Dey, C.J. Schweitzer and D.L. Loftis. 2012. Refining the oak-fire hypothesis for management of oak-dominated forests of the eastern United States. *Journal of Forestry* 110:257–266.

Bowles, M.L., K.A. Jacobs and J.L. Mengler. 2007. Long-term change in an oak forest's woody understory and herb layer with repeated burning. *Journal of the Torrey Botanical Society* 134:223–237.

Brewer, J.S. 2016. Natural canopy damage and the ecological restoration of fire-indicative groundcover vegetation in an oak-pine forest. *Fire Ecology* 12:105–126.

Brewer, L.G. and J.L. Vankat. 2004. Description of the vegetation of the Oak Openings of northwestern Ohio at the time of Euro-American settlement. *Ohio Journal of Science* 104:76–85.

Brewer, L.G. and J.L. Vankat. 2006. Richness and diversity of oak savanna in northwestern Ohio: proximity to possible sources of propagules. *American Midland Naturalist* 155:1–10.

Brudvig, L.A. and H. Asbjornsen. 2008. Patterns of oak regeneration in a Midwestern savanna restoration experiment. *Forest Ecology and Management* 255:3019–3025.

Burley, M.W. and P.J. Waite. 1965. Wisconsin tornadoes. *Transactions of the Wisconsin Academy of Sciences, Arts and Letters* 54:1–35.

Cannon, J.B. and J.S. Brewer. 2013. Effects of tornado damage, prescribed fire, and salvage logging on natural oak (*Quercus* spp.) regeneration in a xeric southern USA coastal plain oak and pine forest. *Natural Areas Journal* 33:39–49.

Cannon, J.B. C.J. Peterson, J.J. O'Brien and J.S. Brewer. 2017. A review and classification of interactions between forest disturbance from wind and fire. *Forest Ecology and Management* 406:381–390.

Densmore, R.V. and K.F. Karle. 2009. Flood effects on an Alaskan stream restoration project: the value of long-term monitoring. *Journal of the American Water Resources Association* 45: 1424–1433.

Everham, E.M. and N.V.L. Brokaw. 1996. Forest damage and recovery from catastrophic wind. *Botanical Review* 62:113–185.

Foster, D.R., D.H. Knight and J.F. Franklin. 1998. Landscape patterns and legacies resulting from large, infrequent forest disturbances. *Ecosystems* 1:497–510.

Guo, L., K. Wang and H.B. Bluestein. 2016. Variability of tornado occurrence over the continental United States since 1950. *Journal of Geophysical Research Atmospheres* 121:6943–6953.

Holzmueller, E.J., D.J. Gibson and P.F. Suchecki. 2012. Accelerated succession following an intense wind storm in an oak-dominated forest. *Forest Ecology and Management* 279:141–146.

Kleinman, J.S. and J.L. Hart. 2017. Response by vertical strata to catastrophic wind in restored *Pinus palustris* stands. *Journal of the Torrey Botanical Society* 144:423–438.

Knapp, B.O., K. Stephan and J.A. Hubbart. 2015. Structure and composition of an oak-hickory forest after over 60 years of repeated prescribed burning in Missouri, U.S.A. *Forest Ecology and Management* 344:95–109.

Lake, P.S. 2013. Resistance, resilience, and restoration. *Ecological Management and Restoration* 14:20–24.

Liu, C., J.S. Glitzenstein, P.A. Harcombe and R.G. Knox. 1997. Tornado and fire effects on tree species composition in a savanna in the Big Thicket National Preserve, southeast Texas, USA. *Forest Ecology and Management* 91:279–289.

Natural Resources Conservation Service. 2018. The PLANTS database. plants.usda.gov.

Nimmo, D.G., R.M. Nally, S.C. Cunningham, A. Haslem and A.F. Bennett. 2015. Vive la résistance: Reviving resistance for 21st century conservation. *Trends in Ecology and Evolution* 30:516–523.

Paine, R.T., M.J. Tegner and E.A. Johnson. 1998. Compound perturbations yield ecological surprises. *Ecosystems* 1:535–545.

Peterson, C.J. 2000. Catastrophic wind damage to North American forests and the potential impact of climate change. *Science of the Total Environment* 262:287–311.
Peterson, D.W., P.B. Reich and K.J. Wrage. 2007. Plant functional group responses to fire frequency and tree canopy cover gradients in oak savannas and woodlands. *Journal of Vegetation Science* 18:3–12.
Schetter, T.A. and K.V. Root. 2011. Assessing an imperiled oak savanna landscape in northwestern Ohio using Landsat data. *Natural Areas Journal* 31:118–130.
Stone, K.L., E.H. McConoughey, G.D. Bottrell and D.J. Crowner. 1980. *Soil Survey of Lucas County, Ohio*. U.S. Department of Agriculture, Soil Conservation Service.
Suding, K.N., K.L. Gross and G.R. Houseman. 2004. Alternative states and positive feedbacks in restoration ecology. *Trends in Ecology and Evolution* 19:46–53.
Walsh, R.P. 2017. Microclimate and biotic interactions affect Karner blue butterfly occupancy and persistence in managed oak savanna habitats. *Journal of Insect Conservation* 21:219–230.
Ziegler, S.S., E.R. Larson, J. Rauchfuss and G.P. Elliott. 2008. Tree establishment during dry spells at an oak savanna in Minnesota. *Tree-Ring Research* 64:47–54.

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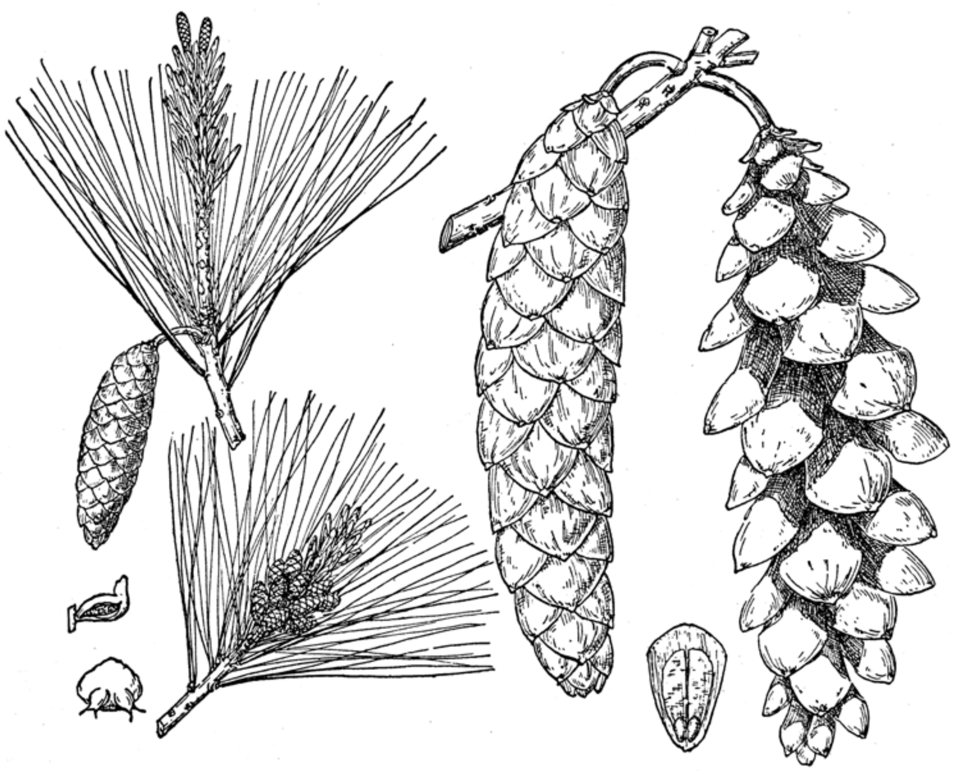

***Pinus strobus*. Sgt. C. Sprague. 1905. *Manual of the Trees of North America*. Boston, MA: Houghton Mifflin Company. The Florida Center for Instructional Technology, fcit.usf.edu.**

Supplementary Materials

Table S1. Raw data, means, and statistical results for the last three measurement years of the study representing three years before (2007), two years after (2012), and five years after (2015) the 2010 tornado. We used two-tailed *t* tests to compare means of restoration metrics between the three restoration and three control plots for each year. Data correspond with Figures 3-7 of the paper. Data are ordered as a list of the raw values for each of the three plots within treatments for each year, followed by treatment means in bold.

Figure 3A. Density of small oaks ≥ 1 < 40 cm in diameter (trees/ha)

Restoration	Control	*t* -statistic	*p* -value
2007			
0	180		
40	160		
60	240		
33	**193**	-5.4	0.006
2012			
20	140		
20	80		
40	180		
27	**133**	-3.6	0.023
2015			
180	100		
20	100		
40	80		
80	**93**	-0.3	0.806

Figure 3B. Density of large oaks ≥ 40 cm in diameter (trees/ha)

Restoration	Control	*t* -statistic	*p* -value
2007			
100	60		
100	60		
80	20		
93	**47**	3.1	0.035
2012			
60	20		
40	40		
0	20		
33	**27**	0.4	0.742
2015			
60	20		
40	20		
0	20		
33	**20**	0.8	0.492

Figure 3C. Oak basal area (m^2/ha)

Restoration	Control	*t* -statistic	*p* -value
2007			
20.7	17.1		
21.4	23.7		
21.0	16.0		
21.0	**18.9**	0.9	0.431
2012			
12.0	8.2		
8.7	13.5		
2.1	14.6		
7.6	**12.1**	-1.3	0.274
2015			
12.2	8.2		
9.0	7.5		
2.5	9.5		
7.9	**8.4**	-0.2	0.869

Figure 3D. Non-oak tree density (trees/ha)

Restoration	Control	*t* -statistic	*p* -value
2007			
0	560		
0	1060		
20	1240		
7	**953**	-4.7	0.009
2012			
100	320		
0	440		
20	140		
40	**300**	-2.8	0.048
2015			
200	380		
20	420		
0	140		
73	**313**	-2.2	0.091

Figure 3E. Understory cover of oaks < 1 cm in diameter (%)

Restoration	Control	*t* -statistic	*p* -value
2007			
25	15		
20	5		
40	2		
30	**7**	3.1	0.036
2012			

15	9		
7	5		
25	3		
15	**6**	1.9	0.137
2015			
25	5		
25	9		
65	4		
38	**6**	2.4	0.074

Figure 3F. Understory cover of non-oak species of trees < 1 cm in diameter (%)

Restoration	Control	*t* -statistic	*p* -value
2007			
9	5		
5	4		
3	18		
6	**9**	-0.6	0.562
2012			
2	25		
3	6		
11	11		
5	**14**	-1.3	0.251
2015			
10	10		
5	9		
25	20		
14	**13**	0.2	0.862

Figure 4A. Non-native species richness (500 m^2)

Restoration	Control	*t* -statistic	*p* -value
2007			
1	1		
0	0		
1	0		
0.7	**0.3**	0.7	0.519
2012			
4	2		
2	3		
3	2		
3.0	**2.3**	1.0	0.374
2015			
0	1		
1	4		
1	0		

0.7	**1.7**	-0.8	0.468

Figure 4B. Non-native species cover (%)

Restoration	Control	*t* -statistic	*p* -value
2007			
0.1	0.1		
0.0	0.0		
0.1	0.0		
0.1	**0.0**	0.7	0.519
2012			
0.5	2.0		
0.5	0.5		
0.5	0.5		
0.5	**0.9**	-0.9	0.426
2015			
0.0	0.1		
0.1	0.5		
0.1	0.0		
0.1	**0.2**	-0.9	0.442

Figure 5A. Native species richness (500 m^2)

Restoration	Control	*t* -statistic	*p* -value
2007			
31	19		
28	17		
33	16		
31	**17**	7.8	0.001
2012			
41	31		
40	36		
36	32		
39	**33**	2.8	0.049
2015			
33	25		
45	28		
33	20		
37	**24**	2.7	0.052

Figure 5B. Floristic quality index

Restoration	Control	*t* -statistic	*p* -value
2007			
28.6	16.5		
25.1	16.7		
28.7	18.5		

27.5	**17.3**	7.7	<0.001
2012			
27.8	24.1		
28.5	24.3		
28.0	24.0		
28.1	**24.1**	18.2	<0.001
2015			
22.6	20.6		
33.4	21.0		
20.7	19.5		
25.6	**20.3**	1.3	0.258

Figure 5C. Number of species with coefficients of conservatism from 7-10 (500 m^2)

Restoration	Control	*t* -statistic	*p* -value
2007			
10	2		
7	1		
8	2		
8.3	**1.7**	7.1	0.002
2012			
9	5		
9	5		
8	5		
8.7	**5.0**	11.0	<0.001
2015			
7	4		
14	4		
5	3		
8.7	**3.7**	1.8	0.143

Figure 5D. Number of Ohio rare species (500 m^2)

Restoration	Control	*t* -statistic	*p* -value
2007			
6	0		
4	0		
4	0		
4.7	**0.0**	7.0	0.002
2012			
4	2		
5	1		
4	1		
4.3	**1.3**	6.4	0.003
2015			
4	1		

7	1		
2	1		
4.3	**1.0**	2.3	0.083

Figure 6A,B. Total plant cover (%)

Restoration	Control	*t* -statistic	*p* -value
2007			
90	75		
70	71		
119	56		
93	**67**	1.7	0.169
2012			
51	80		
41	70		
74	33		
55	**61**	-0.3	0.762
2015			
140	38		
83	56		
216	101		
147	**65**	1.9	0.130

Figure 7A. *Vaccinium* (*V* . *angustifolia* + *V* . *pallidum*) cover (%)

Restoration	Control	*t* -statistic	*p* -value
2007			
10	20		
6	5		
25	5		
14	**10**	0.5	0.657
2012			
7	1		
7	1		
15	2		
10	**1**	3.6	0.023
2015			
10	5		
20	4		
20	6		
17	**5**	3.4	0.027

Figure 7C. *Gaylussacia baccata* cover (%) [note: no data for photo Figure 7B]

Restoration	Control	*t* -statistic	*p* -value
2007			
0	10		

2	15		
5	10		
2	**12**	-4.2	0.013
2012			
0.0	0.5		
0.0	4.0		
0.5	0.1		
0.2	**1.5**	-1.0	0.355
2015			
0	4		
2	4		
10	1		
4	**3**	0.3	0.771

Figure 7D. *Pteridium aquilinum* cover (%)

Restoration	Control	*t* -statistic	*p* -value
2007			
25	20		
25	25		
10	25		
20	**23**	-0.6	0.561
2012			
9	25		
10	35		
2	10		
7	**23**	-2.1	0.101
2015			
7	5		
10	5		
7	25		
8	**12**	-0.5	0.615

Figure 7E. *Carex pensylvanica* cover (%)

Restoration	Control	*t* -statistic	*p* -value
2007			
15	5		
7	15		
30	20		
17	**13**	0.5	0.646
2012			
3	4		
3	15		
20	1		
9	**7**	0.3	0.792

2015			
55	5		
8	20		
40	40		
34	**22**	0.7	0.502

Figure 7F. *Lupinus perennis* cover (%)

Restoration	Control	*t* -statistic	*p* -value
2007			
0.1	0.0		
0.1	0.0		
0.1	0.0		
0.1	**0.0**	No variance	
2012			
0.1	0.0		
0.1	0.0		
0.1	0.0		
0.1	**0.0**	No variance	
2015			
5	0		
1	0		
10	0		
5	**0**	2.0	0.110