OAK SAVANNA RESTORATION STRATEGIES AND THEIR EFFECTS ON LIGHT, VEGETATIVE COVER, FLOWERING FORBS, AND POLLINATOR COMMUNITIES

By

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ABSTRACT

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Oak savannas are rare natural communities characterized by scattered oak trees, a rich continuous understory containing many flowering plants, high levels of biodiversity, and frequent fires. The rarity of remnant oak savannas not converted to agriculture or settlement is further exacerbated by widespread fire-suppression. Lack of fire has allowed fire-sensitive woody plant species to rapidly grow and fill in formerly open oak savannas to the detriment of oak trees, understory plants, and other biota. I chose to explore the effect of two current oak savanna restoration methods designed to reverse this process, on light availability, vegetative cover, pollinator communities, understory flowering forbs, and pollinator communities. I found that after two seasons, the “burn only” restoration method achieved increased light, floral abundance, floral richness, and bee abundance relative to unmanaged reference areas. The “thin and burn” restoration method achieved all of the aforementioned effects as well as decreased cover and increased bee richness. Restoration methods stimulated both native savanna and exotic understory plant species, highlighting the benefits and drawbacks of reintroducing disturbances to remnant oak savannas. Overall, repeated burns may be required to achieve the more substantial shift in habitat, forb, and pollinator communities realized by the thin and burn method. I conclude that although there are variable effects from each restoration method, each one can be appropriate under different financial, logistical, and ecological scenarios.

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LITERATURE REVIEW

Background

Savannas, ecosystems generally characterized by scattered overstory trees and a dense herbaceous understory, are found throughout the world in both temperate and tropical climates. Temperate savannas, while once common, are today one of the rarest global biomes. These savannas were readily converted for agriculture and settlement and today have the highest recorded Conservation Risk Index, with 45.8% of the original biome area converted for human use, yet only 4.6% of the remaining un-converted biome area receives any sort of protective status (Hoekstra et al. 2005). Furthermore, with degradation of savannas from sources like invasive species, grazing, and alteration of ecological processes, high-quality intact savannas are exceedingly rare. In the Midwestern United States, a region with formerly abundant oak savanna ecosystems (i.e. temperate savanna), less than 1% of the former area of intact savanna exists, and much of what remains is highly degraded, principally through a disruption of historical disturbance regimes (Nuzzo 1986). In an effort to conserve and restore these rare and declining ecosystems, it is pertinent to explore their definitions, ecological context, processes, and importance.

Definitions

The word ‘savanna’ was coined when Spanish explorers in the Caribbean heard the term used by the Carib Indians, referring to the striking tropical savanna landscape of abundant grasses with scattered shrubs and mature trees. The term is now extended to ecosystems in temperate regions with a similar structure, but differ in their composition of biota with their presence and distribution being more dictated by climate than tropical savannas (Curtis 1959).

Some of the earliest scientific investigation into midwestern savannas occurred in the mid-20th century (Cottam 1949, Curtis 1955, Bray 1958, Curtis 1959, Bray 1960), when an effort was made to describe and define these ecosystems quantitatively. These early studies were important contributions to the field of ecology and had a lasting impression on the modern perception of savannas. The most notable of these impressions was the designation of savannas as ecotones, acting as intermediaries between grassland and forest, rather than standing alone in their own right as unique communities. From this viewpoint, savannas were simply "prairies with trees" (Packard 1988, Henderson 1995, Leach and Givnish 1999). Savanna sites from these studies were selected based on being devoid of selective cutting (Cottam 1949), having a dominance of understory grasses known to occur in prairies, and without a recent history of burning. Furthermore, forb-rich sites where prairie grasses had been reportedly reduced by grazing were rejected for study (Bray 1958, 1960). This combination of factors resulted in a view of Midwestern oak savannas as largely ecotonal, and grass-dominated. However, observations later emerged from restoration practitioners (Packard 1988) and were subsequently supported (Pruka 1994, Bowles and McBride 1998, Leach and Givnish 1999), which led to a new perception of savannas. A notable feature of this new perception was the dominance and importance of forbs, as opposed to grasses, in the understory layer. This dominant forb community is a remarkably diverse one (Leach and Givnish 1999), containing species found in both prairies and forests. Other species are relatively unique to savannas, deemed "savanna specialists" or "true savanna species"

(Packard 1988, Pruka 1994, Henderson 1995). These savanna specialists are described as reaching their peak abundance in savanna microsites along a range of conditions (Leach and Givnish 1999, Pruka 1994), and can also be described as indicators of savannas where they don’t fit neatly into other nearby natural communities (e.g. tallgrass prairie, forest) (Vestal 1936, Packard 1988). In light of these findings, although savannas or ‘forblands’, do have many ecotonal properties, they may also be viewed as distinct natural communities, and deserve definitions and classifications that reflect this uniqueness.

The fact that savannas gradate into other communities such as woodlands makes it difficult to put concrete boundaries on them, and has led to a somewhat arbitrary definition for these ecosystems. Several metrics have been proposed for defining savannas, and the range of those metrics varies among authors. Those metrics often involve the characteristics of the overstory trees of the system and include their ratio of crown height to crown diameter (Bray 1955), density (Curtis 1959), and most often canopy cover percentage (e.g. Curtis 1959, Kost et al. 2007). In general they can be described as relatively open areas with scattered trees, usually oak, a variable shrub component, and a well developed understory containing proportionately more forbs than grasses.

Community classifications

Several community types exist within the definition of a temperate savanna ecosystem. These natural community types can be separated by ecological variables such as soil moisture, soil texture, and topography/aspect (Chapman and Brewer 2008).

A common defining ecological variable for savannas in Michigan is soil moisture (Table 1). With increasing moisture from dry to wet-mesic, subsequent changes in the plant community are evident. Along with position in the landscape, latitude, and disturbance regime, characteristic savanna community types result (O'Connor 2006).

According to Michigan Natural Features Inventory (2007), there are seven savanna community types in Michigan, each with a distinct set of environmental conditions, flora and fauna, ecological processes, and distribution. For example, the dry oak barrens found in southern Michigan are characterized by a large range of black and white oak canopy cover, from 5-60%, with coarse textured, well-drained soil, and characteristic dryland species, while bur oak plains are characterized with canopy cover 10-30%, with mesic soil containing a higher organic matter content and plant species characteristic of a more fertile habitat. These defining community attributes are helpful in general for identifying and inventorying remnant savannas, and are particularly useful for management and restoration purposes. However, our perception of savanna communities should remain flexible, especially given the dearth of high-quality remnant savanna communities in Michigan (Chapman and Brewer 2008) and the larger Midwest (Nuzzo 1986) from which to draw defining data and observations.

Landscape context and distribution

Savanna communities were historically widely distributed across the Midwestern United States. Moving from the dry shortgrass prairies east of the Rocky Mountains, to the lush deciduous forests of eastern North America, there is a gradual increase in the amount of annual precipitation and primary productivity, which is reflected in the dominant vegetation. In the center of this gradation lies the North American Midwest, where a large region historically supporting temperate savannas is found (Bray 1955, 1958, 1960, Curtis 1959). Midwestern savannas are representative of this gradual change, being essentially co-dominated by the herbaceous understory of the west and the woody overstory of the east (Chapman and Brewer 2008).

Historically savannas would have been part of a matrix of ecosystems along with prairie, woodland, forest, and wetlands, which were dynamic and changing in size depending on the disturbance regime and variation in climate (Grimm 1983). In Michigan, the southern part of the lower peninsula lies in the northeastern portion of the distribution of tallgrass prairie and savanna biomes (Gleason 1917; Transeau 1935; Curtis 1959), and contained relatively high levels of oak-dominated savanna types. Northern Michigan contained scattered oak-pine and pine barren savanna communities, with forested ecosystems increasing in dominance as latitude increases in the state.

Glacial process and oak savanna formation

While savannas occur broadly across this region, factors like hydrology, topography, and glacial history influence the local occurrence of savannas and other natural communities. Many landforms and soils in Michigan are the result of multiple historical glaciation events, depositing substrate and contouring the land, resulting in a great variability in the features of local soil and topography. This phenomenon is pronounced in the ‘Interlobate region’ of Southern Michigan (Figure 1), where glacial lobes from multiple Great Lakes met, creating a complex of glacial deposits, landforms, and water features. This resulted in a geologically and ecologically diverse landscape, with natural communities such as oak openings, dry-mesic prairie, and prairie fen wetland closely adjoining one another (O'Connor et al. 2009). Deposition of coarse substrates such as sand and gravel, at times in combination with local increases in elevation (e.g. esker ridges), tended to lead to more well drained, droughty, and fire-prone habitat than the surrounding vegetation, and often resulted in the formation of savannas or prairies (O'Connor 2006); communities adapted to these conditions.

Local water features sometimes affected the presence of savannas on this landscape as well. Lakeplain oak openings were found in close proximity to large water bodies, and due to their fluctuating water levels (Kost et al. 2007) they kept an open canopy cover due to the mortality this temporary inundation caused to many individual trees. Near rivers, several savanna community types in Michigan were more frequently found on the west side than the east, as these water bodies acted as natural firebreaks for burns pushing eastward due to the prevailing winds (Gleason 1913, Kost et al. 2007). The aforementioned Jackson interlobate region of Michigan holds the largest area of former savanna in the state, but significant areas of savanna existed in the lakeplain regions in southeast and east-central lower Michigan, near Lake Erie and Saginaw Bay respectively, as well as the scattered dry savanna communities of the sandy plains of northern Michigan (Figure 1) (O'Connor 2006).

Ecological processes

Savannas are disturbance-dependent systems, requiring ecological processes to retard woody growth and maintain their patchy heterogeneous character. These multiple disturbances acted in concert to maintain savanna structure and ecology, and the biota of savannas have a suite of adaptations which make them well suited to thrive amidst those disturbances. Arguably the single most important factor in defining savannas is fire, cited by many authors as a critical component of savanna maintenance (Cottam 1949, Curtis 1959, Nuzzo 1986, Grimm 1983, Leach and Givnish 1999, O'Connor 2006, Chapman and Brewer 2008). Other disturbance factors can also be important such as grazing by North American and European ungulates (Curtis 1959, Karnitz and Asbjornsen 2006), drought (Cottam 1949, Faberlangendoen and Tester 1993, Abrams 1996), and windthrow (Kost et al. 2007). Fire in the past, occurring in oak savannas would have been relatively frequent, low intensity, and taken place on a landscape level throughout the Midwest region, carrying over to, or initiating in, plant communities surrounding these savannas (e.g. tallgrass prairies) (Curtis 1959, Wolf 2004). Fires would have been promoted by the flammable litter found in savannas, consisting of desiccated forbs, grasses, and oak leaves (Kost et al. 2007), all readily combustible.

Oak adaptations to fire

Given their defining presence in oak savannas, the unique set of characteristics of many oaks (*Quercus spp*.) rendering them fire-adapted is not surprising. The ability to sprout and resist rot after fire scarring, their thick, tough, insulating bark, and the deep roots protect the vital parts of the tree from low intensity ground fires and drought, while the propensity of acorns to germinate in close contact with mineral soil, provided by the burning of leaf litter, illustrates the favorable conditions for many oak species found in savannas (Abrams 1996). However, oak species vary in their bark thickness and resistance to fires as mature trees, and young size classes of all oak species are somewhat susceptible to aboveground dieback from burns if intensity is great enough. Many oak species in the fire-prone Midwest formed “grubs” (Figure 2), often resulting from frequent (annual to semiannual) fires which continually top-kill young oaks that form a hard woody callus over the fire scar and continue to develop roots. Large mature oaks could also form oak grubs if a rare high-intensity fire occurred, or if they were of a less fire resistant species (e.g. *Quercus velutina* & *ellipsoidalis*), being top-killed, yet re-sprouting from mature root systems (Curtis 1959). This phenomenon could occur on a nearly annual basis, resulting in root systems hundreds of years old with aboveground growth that would suggest an oak of only a few years (Muir 1913). Oak grubs can be formed from many oak species associated with savannas, but would be formed most frequently with less fire resistant species like *Q. velutina*, and would be most prominent in communities where those species dominated, such as oak barrens.

Oak seedlings also tend to grow very slowly in a shaded and competitive situation (Abrams 1996), but can exhibit increases in height and girth when such shade is removed (Brudvig and Asbjornsen 2005), which could be accomplished by various disturbances associated with savannas such as fire, grazing, or drought. Many other woody species in the surrounding Midwestern landscape are susceptible to disease and direct mortality following a fire, and in fact fires can reduce overall woody stem density in savannas, including smaller size classes of oaks (White 1983). Some individual oaks in savannas overcome this mortality by reaching a fire tolerant size (White 1983) which could be achieved during periods or locations of fire scarcity, caused by disruption of fire ignition and spread, and/or variability of weather (e.g. increases in precipitation). These individuals could then likely survive the damage caused by burning when optimal bark thickness and/or root development is reached. Young oaks and fire-intolerant plant species found in savannas may find fire protection in sheltered microsites in the savanna landscape such as areas with relatively high moisture levels like shaded or low-lying areas, both being promoted by the heterogeneity of savanna ecosystems and the patchy nature of savanna fires (Anderson and Brown 1986). By generally restraining woody growth, fire and other disturbances also allow established oak trees to grow in a distinctive form found in open sunny environments, with broad spreading crowns, and low sprawling branches (Bray 1955, Curtis 1959), similar to the open grown landscape trees of neighborhoods, parks, and orchards.

Herbivory

Grazing and browsing made up another major disturbance factor of the Midwest savanna region, and would have been accomplished by three principal ungulate species, the American bison (*Bison bison* Linnaeus, 1758), Eastern forest elk or wapiti (*Cervus elaphus canadensis* Erxleben 1777), and white-tailed deer (*Odocoileus virginianus*, Zimmerman 1780). Of these herbivores, *B. bison* was nearly driven into extinction and was recently reintroduced into small parts of its historical range (Knapp et al. 1999), the subspecies *C. elaphus canadensis* is thought to be extinct (Polziehn 2000), while *O. virginianus* remains common throughout the Midwest and has reached exceptionally high population levels in much of this area (Roseberry and Wolf 1998).

Although studies of large herbivorous ungulates in Midwestern savannas are relatively few, many ecological studies of these animals have illustrated their role in natural systems. The collective herbivory by large herds of these native North American ungulates would have suppressed woody plant growth (Ritchie et al. 1998, Knapp et al. 1999), acted as vectors of seed dispersal (Urbanek et al. 2012), influenced nutrient cycling and distribution (e.g. nitrogen inputs through urination and carcasses) (Ritchie et al. 1998, Knapp et al. 1999), and created soil disturbances which provide opportunities for establishment of certain plants (Knapp et al. 1999), serving to further diversify the savanna plant community. Also, these large mammal populations, which were abundant historically, in part supported American Indian tribes who frequently used prescribed fire to maintain favorable grazing conditions to encourage these populations, which were highly valued culturally, nutritionally, and economically.

Introduction of domestic livestock broadly coincided with the time of European settlement, the extinction of the Eastern forest elk, the extirpation of the American bison, and the forced removal of American Indian tribes. Grazing by these European ungulates in savannas was common and still would maintain the open character and original spacing of overstory oaks, but was also associated with introduction of exotic weeds and overgrazing, which “destroyed the understory” (Curtis 1959) in many cases. Due to this fact, in his scientific exploration of plant communities of Wisconsin in the mid 20th century, Curtis went so far as to say “Beyond question, an oak savanna with an intact groundlayer is the rarest plant community in Wisconsin today.”

Drought

Much of the North American Midwest was prone to periodic drought, which would have suppressed the vigor of woody growth in general and prevented the development of forests (Faber-Langendoen and Tester 1993), exacerbated fire (Grimm

1986), and given a competitive advantage for oaks relative to other tree species (Abrams 1996), all creating a favorable situation for the persistence of oak savannas.

Windthrow

Windthrow, as in the uprooting of overstory trees by wind, is noted for creating canopy gaps in forested regions of eastern North America (Rentch 2010). Windthrow would have created and maintained canopy openings that promoted higher levels of light, favoring understory growth and oak establishment in savannas. Considering the relatively low tree density of savannas compared to closed canopy forests of the region, wind would be particularly forceful to individual overstory trees lacking an abundance of other trees nearby to buffer the wind, and is noted to be an appreciable ecological process important for many savanna community types (Kost et al. 2007). Overall, a combination and complex interaction of disturbance factors are crucial for the persistence of oak savanna communities in the North American Midwest.

Biodiversity and conservation

Due to the widespread impacts oak savannas faced before they were properly documented, our knowledge of their characteristic flora and fauna is limited to somewhat vague historical accounts, early scientific accounts of altered savannas, small remnants, species' responses to ongoing restoration, and ecological guesswork. Yet in spite of this, we have learned much from these sources, which have proved to be useful in laying a foundation for contemporary ecological investigation into oak savannas. It seems evident that savannas today are host to a large diversity of plants and animals, many of which are rare and/or declining, and seem to parallel the rarity of oak savannas today.

Plants

Plants were a more well documented group by early scientific investigations into oak savannas (Gleason 1913, Cottam 1949, Curtis 1951, 1955, 1959, Bray 1958, 1960), and given that one or two tree species usually dominate the overstory, the bulk of the plant diversity is found in the understory layer (Bray 1960, Leach and Givnish 1999). By their nature, savannas contain both forest and prairie plant species, each persisting in its preferred microsite among the wide gradient of conditions savannas create, like moisture, light, aspect, soil organic matter, temperature, and effective rainfall (Henderson 1995, Leach and Givnish 1999). Yet they also contain specialist species, which are apparently uniquely adapted to the intermediate conditions savannas provide (e.g. dappled light) (Henderson 1995), which may explain why they are considered to be “unusually diverse” (Leach and Givnish 1999), in regard to their plant community. Pruka (1994) found that plant richness was highest in savannas along a prairie-forest gradient, and Leach and Givnish (1999) found that in groundlayer plant communities in 22 savanna sites totaling <50 ha, ~ 27% of the entire flora of Wisconsin was present among these handful of sites. In Michigan, nearly 32% of all the “plant species of greatest conservation need” and greater than one third of all wildlife species listed as endangered, threatened, or special concern, occur in savannas and prairies (O’Connor et al. 2009). These occurrences are more impressive when taken in light of the fact that savanna and prairie communities are thought to only have occupied a mere 7% (5.8% savannas, 1.2% prairies) (Figure 1) of the total land area in Michigan circa 1800 (O'Connor 2006).

Insects

Insects are notoriously abundant and among the "hyperdiverse" groups of global fauna (Colwell and Coddington 1994), and many, such as Lepidoptera, are highly specific in their habitat requirements (Shuey 1997, Gutierrez et al. 2001). Thus, given the exceptional heterogeneity of conditions found within savanna ecosystems (Leach and Givnish 1999), the resultant insect community could be expected to be similarly diverse. Many insect species have distinct relationships with specific plant taxa or communities, many of which require discrete conditions (e.g. well-drained soil and relatively high light levels) provided by savannas, and thus insects depending on these plants are also dependent on the same conditions provided to the plants by savannas. The Karner blue (*Lycaeides melissa samuelis* Nabokov), a federally endangered butterfly, is one such species, as its larvae require the leaves of wild lupine (*Lupinus perennis* L.) to complete its development into an adult. *L. melissa samuelis* is susceptible to mortality from fire, yet fire is required in the maintenance of oak-pine barrens, an open sunny savanna community with dry soils where its only host plant, *L. perennis,* thrives (Rabe 2001). Thus, this butterfly indirectly requires the burns that maintain its host plant. Although the majority of insect species found in savannas are poorly known and studied, it can be expected that many other similar ecological relationships existed between insects and savannas and it is reasonable to expect that many insect species formerly associated with savannas are extinct or scarce (Henderson 1995), like the savannas themselves.

Birds

Midwestern savannas also play host to a variety of bird species, many of which are uncommon or rare and associated with the decline of early successional habitats in the region. Red-headed woodpeckers (*Melanerpes erythrocephalus* Linnaeus, 1758) are one such species, and despite their broad range throughout the Central and Eastern U.S., they have been on a marked decline for decades, up to a 50% overall reduction since 1966 (Smith et al. 2000). Although the decline of *M. erythrocephalus* can be attributed to a variety of reasons, several of the noted stressors on their populations parallel the decline of oak savannas. These include widespread reductions in masting trees (e.g. oaks) and overall declines in open disturbance-mediated habitats, owing at least in part, to fire suppression (Smith et al. 2000). These broad long-term changes have greatly altered the availability of preferred food resources of this species. *M. erythrocephalus* is a behaviorally unique species among woodpeckers in that in addition to feeding on mast crops like acorns, they capture insects while in flight and thus require a certain degree of open space (like that of an oak savanna) to feed effectively. Contemporary restoration efforts have corroborated this relationship between *M. erythrocephalus* and oak savannas and woodlands. Several studies have confirmed this association, documenting an abundance or increase of *M. erythrocephalus* with frequently burned areas reminiscent of remnant savanna as compared to closed canopy forests (Davis et al. 2000, King et al. 2007, Au et al. 2008). Brawn (2006) also noted this increase and additionally offered that, based on point count surveys, *M. erythrocephalus* was the only bird species documented in the study that could be labeled as an “oak savanna bird” due to its near fidelity to oak savanna tracts in the study. In addition to supporting the declining *M. erythrocephalus,* modern studies of bird communities in savannas reveal that there is a greater diversity, abundance, and even nesting success of bird species in savanna tracts than in closed-canopy forests (Davis et al. 2000, Brawn 2006, Au et al. 2008). Many of the species documented in these savannas are also species associated with open-country habitats, both of which are in a notable decline, highlighting the conservation importance and potential of oak savannas.

Reptiles

Savannas are also frequently utilized by reptiles, including a number of species of concern, likely due to several key features of the ecosystem. As ectothermic animals, reptiles often require a combination of exposed and sheltered areas to manage their body temperature. As such, the scattered distribution of shady and sunny microsites within a savanna would seem to provide ideal conditions for a reptile to maintain an ideal body temperature while expending minimal energy reserves to find sites that would passively raise or lower that temperature.

Most of Michigan's savanna communities have well-drained coarse-textured soil with a large component of sand (Kost et al. 2007), and this feature makes them important nesting areas for many turtle species. Particularly in the Jackson interlobate region in southern Michigan, savannas are often found bordering various types of wetlands (e.g. prairie fen, wet prairie), which often hold an abundance of turtles. Despite aquatic or semi-aquatic habits, many turtle species (including Michigan state special concern Blanding's turtle) residing in these wetlands are known to prefer open sandy upland sites like savannas for nesting, and may travel several hundred meters in search of them (Harding 1997).

The decline of the Eastern Massasauga rattlesnake, a Michigan state special concern and federal candidate species, has been noted to be associated in part with the decline in savanna (Henderson 1995). Although this ‘swamp rattler’ is generally associated with prairie fens and similar wetlands, in summer many individuals (often gravid females) will venture into adjacent open habitat such as oak savanna (Lee and Legge 2000). Neglecting to include adjacent uplands in Massasauga conservation efforts will fail to preserve the species (Harding 1997), and alteration of open habitats such as savanna through vegetative succession has reduced habitat availability (Lee and Legge 2000) for these snakes. Both nesting turtles and the Eastern Massasauga rattlesnake highlight the importance of connectivity between savannas and other communities and their ecological interdependence.

“Conservation efforts aimed at savannas may pay rich dividends in terms of plant and insect conservation, generally” (Leach and Givnish 1999). Furthermore, heterogeneity of an ecosystem has been frequently recognized as an important correlate of biodiversity of multiple taxonomic groups (Tews et al. 2004), and the heterogeneity of savanna ecosystems is notably exceptional (Leach and Givnish 1999), thus it is likely this prominent heterogeneity of structure, conditions, biota, and disturbance gives savannas their remarkable biodiversity and underscores their conservation importance.

Impacts

Based on historical accounts, General Land Office Surveys, and in part the existing structure and composition of vegetation on the ground today, it is thought that savanna communities once were spread across 11-13,000,000 acres of the North American Midwest (Minnesota, Iowa, Missouri, Illinois, Wisconsin, Michigan, Indiana, and Ohio), and as of 1985 were thought to have been reduced to just 6,442 acres of high quality intact savannas (Nuzzo 1986). The vast majority of these remnant intact savannas are found on poor soils, as savanna communities on richer soils were disproportionately impacted (Curtis 1959, Nuzzo 1986). This severe degradation and overall 99.98% reduction in Midwestern savanna area since European settlement has been driven through both direct and indirect factors such as agricultural production and disruption of the historical fire regime.

Direct impacts

> "*In my first drive through the oak-openings of our peninsula, which I recall with infinite delight, frequent glimpses of deer were caught, through the open park-like timber*."
>
> -Bela Hubbard, 1887, *Memorials of a half-century*

> "*The oak openings were perfectly beautiful, being from June a perfect flower garden*."
>
> -Ephraim Williams, 1886, *Personal Reminiscences, Mich. Historical Collection*

It is clear from the many casual historical accounts from American settlers and explorers, that people of this time period found the oak savannas of the Midwest inspiring, beautiful, and inviting. Their frequent comparisons of oak savannas to parks, orchards, and gardens emphasize what seems to be an innate human attraction to these areas. There is even modern research that suggesting that the way we design and prefer our parks and neighborhoods today is reminiscent of the structure, tree age, and tree distribution of Midwestern oak savannas (Gobster 1994). How is it then, that such a prominent natural system with so much appeal and charm to humans could be practically wiped out of the Midwestern landscape in a relatively short amount of time? The answer seems to lie in this innate appeal of savannas as well as their practical combination of multiple resources in one area, and it has been suggested that "Our culture almost lost the oak grasslands as a result of liking them so much." (Packard 1988).

Settlement

As populations in the eastern settlements of North America continued to grow through the 1800s, settlers that pushed westward seeking opportunity entered the Midwest. The open nature of the prairies and savannas of the region would have facilitated travel of large groups of people using wagons and horses, and this relative openness would have made these areas more ideal for cultivation and grazing than the surrounding forests, and as a result many pioneers chose to settle in these regions. A typical account of land settlement from Kalamazoo County, in southern Michigan, is a particularly representative example of the ideal setting this landscape provided. Apparently areas lying on the border of mesic prairie and bur oak plains were especially sought after and relatively common in Kalamazoo County at that time, as settlers could cultivate the fertile prairies with no removal of trees necessary, yet could also utilize the mature oaks in adjacent savannas for their fences, lumber, and firewood, as well as the abundant acorn crop for feeding their pigs (Peters 1970, as cited in Chapman and Brewer 2008). It is noted that this unique high value land of Kalamazoo County was thought to be occupied by pioneer land settlements in only a couple of years, and is likely a representation of many other cases of settlement of savanna throughout the Midwest. Commenting on the burr and white oaks of Wisconsin oak openings in 1845, Bayley (1954) said "The roots of both these strike down so that they are not in the way of the plough, and it is no uncommon thing to see large fields of heavy wheat, with the trees all standing, but girdled to prevent the foliage shading the ground." However, not all of these mature oaks were destroyed and a short drive through parts of the agricultural Midwest today is sure to produce one of these grand old oaks in the middle of a cornfield or along a fencerow, and is perhaps a lasting glimpse into the former savanna landscape of the region.

Logging

In addition to harvesting wood for practical purposes on a homestead, many mature oaks in savannas were also harvested for shipbuilding, barrel-making, and other commercial purposes, and these industries would have encouraged the removal of the high-valued mature oaks in savannas, the cornerstones of that ecosystem. Although the white pine (*Pinus strobus* L.) was the primary target of the logging era in Michigan, the sturdy and rot-resistant wood of the white oak (*Quercus alba* L.) was especially sought after for the construction of wooden ships. The white oaks were the chief overstory tree of the oak openings in Michigan, and in this setting would have been able to attain great sizes given relatively little competition with other trees in such an open landscape. Geologist and explorer Bela Hubbard (1887) wrote of the remarkable size of some of these savanna trees in the Detroit region, one of the foremost areas at that time for coastal commerce, which would have fueled the removal of many white oaks for various nautical applications. In an area just south of modern day Detroit, Hubbard writes of one white oak felled by a group of ship builders that measured ~18 feet in circumference, yielding one piece of lumber that measured 3 feet across by 55 feet in length. Hubbard goes on further to take note of one 300+ year old white oak that would have sprouted when Columbus landed, and another awe inspiring specimen growing between a forested area and “the openings” that attained a nearly 12 foot diameter and was 35 feet in circumference, a “very respectable tree to be found out of California.” he commented, referring to the legendary redwoods (*Sequoia spp.*) of that state. Large, open grown oaks such as these in such an open, high visibility landscape would have been conspicuous targets for harvesting, and thus represented one of the first direct steps in the destruction of the Midwestern oak savannas.

Indirect impacts

Although direct impacts from agriculture, logging, and settlement converted a major portion of Midwestern savannas for human uses in somewhat obvious ways, a shift to a European-type resource and land use also created other less obvious alterations to the remaining savannas. The primary indirect effects of this type on savannas were from the introduction of exotic organisms and disrupted regimes.

Exotic species

Many introductions of exotic animals and plants to the savanna landscape were made, both intentionally and unintentionally by settlers of European origin. The new Euro-American populations of people in North America were living in a relatively unfamiliar environment, and as such, used familiar land practices from Europe, most of which required introductions of European plants and animals.

Perhaps the most obvious introductions were those of various domesticated livestock, which would have been a staple of an early homestead, producing meat, milk, and fiber. Given the pasture-like nature of savannas and prairies, it would have been natural for settlers to select these areas for grazing due to the abundance of herbaceous vegetation. Native ungulate herbivore species (i.e. elk, bison, and white-tailed deer) would likely have complemented one another in their herbivory, as they differ in their foraging preferences (Romme et al. 2005, Towne et al. 2005, Urbanek et al. 2012) among woody plants, forbs, and grasses which are all found in savanna plant communities. Also, plant consumption by native grazers would have been kept in check by top predators, such as wolves, that were eradicated from the majority of the Midwest throughout the period of European settlement (Chavez et al. 2005). However, having a group of the same type of domestic herbivore feeding in an unchecked fashion in a confined area undoubtedly resulted in a decrease of many native plant populations and often shifted the community to an abundance of toxic, spiny, or otherwise unpalatable species of plants. In addition to shifting the plant community in this way, natural areas often suffered from soil erosion due to the continual impact of trampling from the overstocking of grazing animals (Trimble and Mendel 1995), often followed by introductions of weedy exotic species taking advantage of this newly disturbed ground, such as Kentucky bluegrass (*Poa pratensis* L.) (O'Connor 2006). In fact, many times exotic plants like Kentucky bluegrass were intentionally sown by settlers to improve the forage quality for their animals, often at the expense of the native savanna understory.

Aside from use for forage, plant introductions were made by European settlers for a variety of other applications including agricultural, culinary (e.g. seasonings), ornamental (e.g. hedgerows), and medicinal purposes (Mack 2003). A number of these plant species escaped into natural areas such as oak savannas, where many of them still adversely affect the ecological health of those systems today. A particularly problematic group of those invasive plants in savannas today are a number of shrubs of Eurasian origin, originally planted for ornamental purposes (Mack 2003), or for reputed wildlife value (O'Connor 2006). These shrubs include but are not limited to, common buckthorn (*Rhamnus cathartica* L.), honeysuckles (*Lonicera spp.*), autumn olive (*Elaeagnus umbellata* Thunb.) and multiflora rose (*Rosa multiflora* Murray). The fruits of these species are all readily consumed, dispersed (Knight et al. 2007, Gleditsch and Carlo 2011), and even sometimes preferred over native fruiting shrubs by frugivorous birds (Lafleur et al. 2007). These birds often preferentially perch in open grown oaks, like those found in oak savannas, and disperse their fruits upon takeoff, thus facilitating invasion by these exotic shrubs into Midwestern savannas (O'Connor 2006). Other traits such as rapid growth, a tolerance of a wide range of environmental conditions, allelopathy, high germination rates, and success in disturbed habitats may exacerbate this plant invasion in Midwestern savannas (Knight et al. 2007), which are particularly vulnerable to invasion given the high edge to size ratio of many remnants (Apfelbaum and Haney 1991). Many ecologists have documented the presence of these invasive shrubs in remnant Midwestern savannas today (Packard 1988, Bowles and McBride 1998, O'Connor 2006, Hedtcke et al. 2009, Abella 2010), which, along with a shift in environmental conditions caused by succession of the plant community, have gone so far as to disrupt the very ecological processes that are characteristic of, and critical to the persistence of savannas.

Disruption of ecological processes

The fires that were ubiquitous across much of the Midwest prior to European settlement were not only necessary to maintain savannas by restraining woody encroachment, but layers of oak pollen have been associated with layers of charcoal in lake sediments (Cole and Taylor 1995, Abrams 1996), suggesting the existence of a positive relationship between fire and oak-dominated plant communities, such as savannas. Furthermore, periods of increased frequency of fire in the Midwestern landscape often correspond to episodes of drought (Clark 1988), a condition where characteristic oak species in savannas have been shown to be highly competitive and prevalent (Abrams 1996, Faber-Langendoen and Tester 1993). However, a combination of shifting patterns of land use and negative attitudes towards fire following European settlement has taken away these conditions under which oak savannas prevail, creating important physical and ecological changes within remaining savanna remnants to the detriment of those communities.

Fire history and suppression

American Indian tribes of the Midwest not only co-existed with fire, but in fact they frequently used fire to their advantage for a multitude of reasons including security (i.e. increased visibility), communication, travel (i.e. creating more easily traversable open areas) agricultural management, hunting, and maintenance of ideal habitat for game (Abrams and Nowacki 2008). In fact, it has been suggested that American Indians were almost entirely responsible for the historical pattern and frequency of wildfires across most of the Eastern United States, and many of the fire-dependent species or communities in this region during the pre-settlement period can be explained by fire-related activities of indigenous peoples. In contrast to other regions of the country (e.g. The Great Plains), annual periods of peak lightning activity in the Midwest are observed during a period with green vegetation, high humidity, and complementary rainfall, all of which would impede the spread of lightning ignited fires. Thus barring major drought episodes, this type of ignition would have been relatively infrequent (Nowacki and Abrams 2008). Conversely, American Indian tribes frequently took advantage of conditions in early spring and early fall (i.e. 'Indian summer') during rain-free periods when most of the vegetation was either still dormant or senescing, and thus highly flammable. Furthermore, without a means to effectively extinguish fires after ignition, burns were carried over large areas (Nowacki and Abrams 2008), thus any effects observed from fire on the landscape were widespread.

While fire was a common and indispensable tool among American Indian tribes and critical to numerous practices that sustained many of their populations, burning was not crucial to a Euro-American way of life in North America. While there are cases of fire frequency temporarily increasing following European settlement (Cole and Taylor 1995), settlers did not rely on indigenous flora and fauna to the same degree that American Indians did, instead using more domesticated European plants and animals to provide for themselves, and thus would not be invested in maintaining ideal habitat or hunting for those native species through the use of fire. Furthermore, the forced removal of American Indian tribes by the federal government also removed the source of ignition for the nearly annual fires. In Michigan the Potawatomi Indians, a prevalent tribe historically found in the savanna region in the southern part of the state, were mostly removed by 1840 (Chapman and Brewer 2008). It is interesting to note that Potawatomi roughly translated means "people of the land of the fire." In the near absence of these and other native keepers of the fire, any fire that did manage to become established in the Midwest would be short lived due to both overt suppression of fire from Euro-Americans of the region in part to protect property, or due to one of the numerous firebreaks found in this increasingly fragmented landscape in the form of roads, railways, tilled agricultural soil, etc. (Nuzzo 1986, O'Connor 2006, Brewer and Chapman 2008).

Mesophication

> *"…though the rural beauty of the country is still unrivaled, little remains of the original character of the openings. This is a result partly of the progress of civilization, and partly of the thick growth of small timber that has covered all the*

uncultivated portions since the annual fires have ceased, which kept down the underbrush."

Bela Hubbard, 1872, *A Michigan geological expedition in 1837*.

Given the many adaptations of the oak savanna flora to fire, and the historical prevalence and frequency of burning throughout the Midwestern oak savanna region, it is easy to imagine how an abrupt cessation of fire would result in dramatic changes in this vegetation over time. Oak grubs with little aboveground biomass that were constantly set back by frequent fire, were released from this pressure and finally allowed to realize their aboveground potential supplied by substantial underground root systems. Due to these mature root systems, an oak grub could reach a fire resistant size aboveground faster than an oak seedling originating from the germination of its acorn (Chapman and Brewer 2008), which led to a rapid transformation from savannas of an open nature to a great density of oak saplings (Bowles and McBride 1998). As these saplings in fire-suppressed savannas continued to grow and increase their overall leaf surface area, less light reached the understory, and leaf litter began to accumulate in greater quantities than in the past where it would be continually burned off. This created unfavorable conditions for savanna understory plant species requiring relatively high light levels, contact with mineral soil for proper germination of seeds, and with small seeds that have little in the way of starchy reserves to aid in pushing through leaf litter following germination before sufficient light levels could be reached. As this phenomenon progressed, an associated decrease in overall temperature and increase in soil moisture would have also been observed, resulting in an overall shift towards forest-like conditions, called “mesophication” (Nowacki and Abrams 2008). This change in environmental conditions of savannas facilitated or coincided with a second level of woody invasion by fire intolerant trees and shrubs from surrounding mesic forests, like *Prunus serotina* Ehrh., which was said to be rare in savannas by early studies (Curtis 1959). No longer suppressed by fire, these species could capitalize on the relatively high light levels, more mesic conditions, and little competition (oaks are slow-growing by comparison) the remnant oak savannas offered and rapidly transformed their character, structure, and biota.

Curtis (1959) commented on the astonishingly rapid rate at which this change took place after fire suppression, suggesting that “within a decade, the openings became filled by saplings and brush and within twenty-five to thirty years, dense oak forests were present.” This conversion is thought to be most rapid on mesic savanna sites where soils are the most ideal for woody plant growth and fire is the major restriction to establishment, while sites with wet or dry moisture conditions are already less ideal for woody growth, and invasion would occur less rapidly (O’Connor 2006). Cottam (1949) documented many of these successionary changes when he sampled the vegetation of a remnant oak opening (“Stewart’s Woods”) in southwestern Wisconsin and compared those data with land surveyor’s notes 100 years earlier. He documented substantial increases in tree density and basal area relative to historic data at ten and eight times respectively, as well as an 89% decrease in the frequency of *Quercus macrocarpa* Michx. (a particularly shade intolerant oak), and dramatic decreases in major savanna understory species. It is interesting to note in this study, that although *Quercus spp.* and *P. serotina* (a mesophytic invader) made up ~96% and ~2% of the composition of tree species found there respectively, the reverse is true when looking at a smaller size class (1-1.39 in.) alone, with *P. serotina* dominating and *Quercus spp.* being in the minority, and *Quercus* regeneration seems restricted to the relatively higher light of canopy gaps. This dearth of oak regeneration is a widespread observation by ecologists and foresters across much of the Eastern United States (Russell and Fowler 1999, Nowacki and Abrams 2008, DeSantis et al. 2011, Kern et al. 2012). This lack of regeneration parallels the decline of many savanna understory communities (Curtis 1959, Abella et al. 2001, Pavlovic et al. 2006), and seems to be attributed largely to the lack of fire, elevated shading and competition associated with shade tolerant and/or fast growing tree and shrub species, and intense preferential deer browsing associated with their widespread overpopulation.

Given the vast amount of former Midwestern savanna area directly converted for human use that is now under agricultural production or settlements, and the forested conditions found in the vast majority of remaining savannas, understanding how to reverse this trend of mesophication in existing remnants today represents our greatest opportunity to restore these unique communities and increase the overall area of high quality oak savannas in the region.

Restoration

Most remnant oak savannas today are not high-quality intact systems, but exist in an almost unrecognizable state where mesic forest trees dominate much of the plant community and little light reaches the depths of a litter-laden understory. Simply identifying remnant oak savannas is a difficult task, yet a combination of tools of different scales and methodologies can signify where potentially restorable oak savannas exist. Methods broad in scope can indicate regions in which to focus conservation efforts, while methods fine in scope can identify individual savanna remnants and reveal where the greatest potential for restoration of those remnants exists. Ecological changes within these remnants related to the degradation oak savannas have been occurring for decades to centuries. Understanding how to reverse these changes in order to rehabilitate savanna ecosystems in a relatively short time presents a logistical and ecological challenge to the conservation community.

Identification of fire-suppressed remnants

Identifying the extent and distribution of natural communities is a useful first step towards their conservation. Most Midwestern oak savanna remnants are relatively small (<50 ha) (Nuzzo 1986, Apfelbaum and Haney 1991, Brawn 2006), and exist throughout a landscape characterized by agricultural and urban fragmentation. Thus, simply identifying remnant oak savanna communities in this region is a difficult preliminary task in their restoration, yet conservation planners have a set of tools at their disposal to address this challenge. These tools include historical data such as presettlement vegetation maps and written records, remote data such as aerial photos or satellite imagery, as well as remnant biotic, abiotic, and structural factors associated with oak savanna communities.

Records and remote data

Identification of a targeted natural community of conservation importance (e.g. oak savanna) should begin with the location of the broad geographical region where communities of interest are likely to exist. Pre-settlement vegetation maps can facilitate this process, and are one of the most useful resources for conservation planners in the Midwestern United States. In the early to mid 1800s extensive and relatively detailed land surveys were conducted throughout the Midwest by the General Land Office (GLO) in an attempt to determine the extent of viable agricultural lands. This information helped the National Government inform and promote subsequent migration and agricultural settlement of the area. Surveyors typically collected biological data every half mile (quarter sections) in a grid pattern, taking note of size (dbh) and species of witness (those at section corners) and line (those in between corners) trees. Soil characteristics, namely its suitability for agriculture, as well as general notes on other natural features (e.g. water features, dominant vegetation, landscape features) were also collected throughout this process (Anderson et al. 2006). Although this information was intended to inform agricultural settlement, it has also proved to be a lucrative dataset for restoration ecologists and conservation planners nearly 200 years later. Combining natural and geographical information from land surveyor’s notes with contemporary knowledge of high-quality remnant communities, ecologists have created statewide maps illustrating an interpretation of natural land cover prior to much of the ecological degradation that coincided with widespread European settlement of the region. These maps are often available at the county level (Figure 1), providing a more resolved picture of historical plant communities.

This ecological interpretation of historical data typically fails to capture fine-level biological information (e.g. understory flora and faunal communities) however, and represents a snapshot in time of a dynamic landscape (Grimm 1983, Packard and Mutel 2005). Still, these maps provide an invaluable resource in defining reference information for ecological restoration and identification of natural communities. Use of presettlement vegetation maps can serve as the first step in the identification of a region where a targeted community of conservation importance may exist.

Although they are available inconsistently depending on historical exploration and documentation of a region, written records can provide a unique form of information regarding the historical presence of natural communities. These sources generally lack the fine detail necessary for technical restoration plans and to form clear pictures of historical communities. They can however, provide an important piece of reference material for time periods generally lacking in formal scientific investigations and aid in community identification. These records sometimes originate from formal descriptions of a region's natural features by trained individuals (e.g. State Geologists), but other times are available from general historical recordkeeping. Two examples of qualitative oak savanna descriptions from Michigan include written records from 19th century State Geologist Bela Hubbard, and early pioneer of the Saginaw Valley region, Ephraim Williams. In *Memorials of a half-century* (1887) Hubbard makes specific mention of the species of overstory trees that characterized oak savannas, along with some detailed description of various plant and animal species. Here he provides insight into some of the savanna biota that lack proper scientific documentation prior to widespread human impacts. In 1832 he regards the open grown burr oaks (*Quercus* macrocarpa Michx.) as being among the largest trees of the southwest portion of the state. He mentions the distinctive outline of these oaks and the prevalence of the now extirpated burr oak plains communities characteristic of the rich mesic soils (O'Connor et al. 2009) of St. Joseph, Cass, and Kalamazoo counties. Documenting his general experiences in Eastern Michigan, Williams in his *Personal Reminiscences* (1886) writes of Genessee County:

"Next morning we rode to Flint River, seven miles, (where the city now is), crossed the river on the rapids where the dam and mills now are; explored the surroundings, which were beautiful, being an open oak forest like an orchard. We could see for miles around, having been burned over, and could see the wild deer feeding on the acorns in from twos to droves of often a dozen."

While Williams' description lacks the specific naturalist detail of the biota often provided by Hubbard's descriptions, combining this record with other sources such as a presettlement vegetation map of Gennessee county could provide a more clear and powerful view into the historical landscape composition of the region.

Landscape and site level information useful in identifying oak savannas can be provided or enhanced by remote sensing techniques utilizing both historical and contemporary imagery. While historic imagery is not typically available for periods prior to human-induced ecological degradation, aerial photographs taken several decades prior to present day can still be useful when they are available. These early aerial landscape photos lack the color and resolution of contemporary images, yet they may provide important coarse-level structural information of a particular landscape. Following European settlement, many oak savannas served as grazing areas for livestock, which often disrupt the understory plant community (Curtis 1959, O'Connor 2006). In some cases however, light grazing may viewed as a positive influence in that it can prevent or reduce the natural succession process once fire and other disturbances have ceased (Curtis 1959, Nuzzo 1986). In the latter scenario, canopy structure and distribution may be preserved as long as grazing is maintained, and thus may be captured through historical aerial photography. Not only can this imagery be useful in identifying savanna remnants at a local and landscape scale, but can provide useful reference information for ecological restoration. Percentage of canopy cover is often a main focus of oak savanna restoration projects and used as a target metric through reduction of the overstory (Faber-Langendoen and Davis 1995, Asbjornsen et al. 2005, Peterson et al. 2007, Bowles et al. 2011). Careful interpretation of these aerial photographs can yield historical canopy coverage estimates and serve as a relevant benchmark for canopy reduction in modern oak savanna restoration. One recommended source of historical aerial photographs (www.oaksavannas.org/recognition.html) is the National Archives and Records Administration (www.archives.gov) located in College Park, Maryland.

Contemporary aerial images of landscapes of interest are widely available today. Sources for contemporary aerial images include the National Aerial Photography Program provided by the United States Geological Service (USGS), and the Natural Resources Conservation Service (NRCS) under the United States Department of Agriculture (USDA). This information can be used in a conservation context to assess current structure and distribution of vegetation types or used in conjunction with historical aerial photos to provide useful qualitative and quantitative information regarding land or canopy cover change (Faber-Langendoen and Davis 1995). For example, Schetter and Root (2011) utilized the orthorectified Landsat imagery database provided by USGS in order to assess the current distribution of oak savannas and associated plant communities in the Oak Openings region of Ohio. Using an USGS-based platform, ER Mapper, and ArcGIS the authors found that >96% of the former area of savannas and prairie had been converted since European settlement. They also successfully identified oak openings, prairies, and oak barrens, and determined that nearly all of these remaining communities were already in some sort of land protection. Although this study demonstrates the ability of Landsat imagery to successfully identify rare plant communities remotely, verification found that the accuracy of this identification varied from 60-79%. This suggests that coarse-level remote techniques should be combined with other methods of vegetation classification, such as ground verification. Drawing on historical imagery, Simpson et al. (1994) used four sets of aerial photos from 1940-1988 to assess patterns of landscape-scale vegetation change in a region of Central Ohio with formerly prevalent oak savanna. Comparison of land conversion patterns between two landscape types (moraine and till plain) was conducted using GIS. Historical areas of oak savanna as small as eight hectares were identified, and a similar pattern of savanna conversion of 67% and 62% was found over 48 years on moraine and till plain respectively. While this contemporary study further underlines great losses in savanna communities to agriculture, this style of historical aerial photo comparisons could identify conversion of savanna to other land cover types as well.

A geographical area where conversion from savanna to forest was found could parallel the widespread mesophication process, identify a fire-suppressed remnant not yet known to the conservation community, and create opportunities for future ecological restoration. This process of aerial identification of remnant oak savanna, can be further supported or enhanced by a more precise identification on the ground using distinctive structural and biological indicators.

Structural features

Historically, with frequent fires and grazing limiting encroachment from competing woody species, the overstory oak trees so characteristic of oak savanna ecosystems would have been able to attain great sizes and longevities. The open nature of savannas provided high levels of light to these individuals, allowing them to take on a characteristic spreading shape. The branches of these “wolf trees” were able to effectively invest more growth in a horizontal direction, in contrast to the investment in vertical growth a comparable oak would have to make in a more forested environment where high light levels are limited to the upper reaches of the canopy. Dramatic changes in structure, biotic composition, and abiotic conditions of the ecosystem surrounding these distinctively shaped oaks parallel the woody succession that has since occurred there. Yet the very presence of mature open-grown oaks amidst an abundance of young vertically oriented trees belies a shaded state of dense woody vegetation. As succession from woody vegetation progresses around these overstory oaks, the light-deprived branches begin to die starting from the lower portion of the tree and progressing upwards, paralleling the sequence of shading associated with vertical woody succession. Given enough time in the absence of disturbance, these shade-intolerant oaks may suffer from outright mortality once light levels are sufficiently depleted and insufficient energy stores exist in the roots to maintain health and vigor in the tree. The rate of this woody succession and concomitant oak mortality is influenced by multiple factors such as sources of propagules from mesophytic trees, local climate, soil type, and disturbance patterns. If savanna remnants are identified before overstory oak health is too severely compromised, reintroducing disturbances can reduce woody competition and therefore increase light availability to these oaks. This process, sometimes referred to as “daylighting”, can effectively create conditions necessary for healthy oak growth and act to retain mature overstory trees; major components of a successful savanna restoration. Although the specific bounds of savanna communities may be difficult to discern in a fire-suppressed state, the presence of open-grown oaks is a strong indicator of formerly open conditions; like that of a savanna.

Biotic features

Due to their short stature relative to the tall fast-growing woody species responsible for savanna mesophication, understory plants would have been one of the first components of oak savanna vegetation to be diminished following fire suppression. Reduced light availability, high levels of litter, increased soil moisture, and increased competition from fire-intolerant species resulted from fire suppression in oak savannas (Nowacki and Abrams 2008) and collectively contributed to the decline of the understory (Cottam 1949, Brudvig and Mabry 2008). Despite this substantial and widespread decline of the understory, circumstances exist where understory flora characteristic of oak savannas still persist. The presence of these remnant understory populations can serve as another important biotic factor in the identification of former oak savannas.

The abiotic changes to oak savannas from mesophication are widespread (Nowacki and Abrams 2008), yet microsites may exist within fire-suppressed remnants that retain a subset of the historical conditions expressed there. Examples of these microsites include canopy gaps caused by windthrow or tree harvesting, intentional reductions of woody vegetation for power line corridors, partial retention of fire regimes from trains or other human activities (Wolf 2004, Considine 2013), and forest edges. It is in these microsites within a fire-suppressed savanna remnant where the potential to find relic understory populations is perhaps highest. Our knowledge of the historical floral composition of oak savanna understories is somewhat debated and limited (Leach and Givnish 1999), and thus begs the question of what species in these microsites would be most indicative of former savanna. One way to address this question is through our knowledge of historical documentation and habitat preferences of individual understory plant species. This information can help to assess the likelihood that a plant growing at a microsite is descended from a historical population of savanna plants.

Although they are scarce, historical studies documenting savanna understories have produced a number of local plant lists. John T. Curtis produced one such list in his extensive documentation of the vegetation of Wisconsin (1959). His work in several oak savanna sites in Southern Wisconsin generated a list of plant species along with associated frequency and presence data. Much of the overall degradation of oak savannas had already occurred by the 1950s, and Curtis’s list is based on a small region of the Midwest. However, this seminal work is important to conservation of oak savannas today and many plants in the list have fairly widespread distributions and thus can be applied to a wider range of sites than were actually documented in the study. Stephen Packard (Stevens 1995) used a combination of historical documentation in the literature and anecdotal observations to create another local savanna understory plant list. By observing the response and emergence of understory plants in response to restoration activities, Packard generated a list of "oddball species" (1988) that he postulated were unique savanna plants. The profiles of these species in Swink and Willhelm's *Plants of the Chicago Region* (the area of Packard's research) included botanical associates; plant species often found growing at the same site that seem to prefer similar conditions. Many of these species were not recorded as outright savanna species, yet description of the habitat they were found in often referenced open woodlands, canopy gaps, and forest edges which reflect conditions provided by savannas. Thus, Packard utilized a combination of existing literature, ecological detective work, and experimental approaches to developed an understory plant list. This list can further serve the conservation community in subsequent savanna identification and provides a useful model for restorationists in other regions to develop local understory plant lists.

Consideration of habitat preferences of plant species documented in potential savanna remnants is also an important factor in their identification. A plant species that typically prefers higher light levels than those actually expressed at the site could be found in a closed canopy forest or otherwise shaded area. This phenomenon could be observed either at a lighted microsite (e.g. forest edge) or under a more completely shaded canopy. Documenting such a situation could signify that at some point in the past, this small population of sun-loving plants were more widespread at the site, yet are now simply relegated to microsites where high light conditions still exist. It could also signify that the population was documented in the context of a decline from a formerly larger population that existed while canopy cover was sparser, and adverse conditions are simply not yet severe enough to cause a local extirpation of the species. Another tool in distinguishing which plant species are indicative of savannas is to consider species with fidelity to high-quality intact habitats, which can be expressed through the use of "Coefficient of

Conservatism" (C) values. These values range from 1-10. A plant species assigned a value of 10 is found in habitats with minimal degradation from human activities, and is thought to closely reflect its pre-settlement habitat preferences. A species with a value of zero has little fidelity to habitats that are comparable to its pre-settlement habitat, and thus are generally widespread and found in many habitats spanning a range of human disturbances. This distinction of conservativeness for plant species was developed for the flora of the Chicago Region (Swink and Willhelm 1994), and subsequently adopted in Michigan (Herman et al. 1996), Missouri, and Wisconsin. A plant species inventory and subsequent application of locally appropriate C values can be used to develop a Floristic Quality Index. This is a holistic assessment of the botanical quality of a site. Use of C values in documentation of understory plant species can be a supporting consideration used in potential savanna remnant sites. The floral composition of an oak savanna understory is likely made up of a combination of species spanning a range of C values. Plant species found in oak savannas with low C values are likely found at a variety of habitats where similar conditions are found and are likely to be as common as those respective habitats. Plant species with high C values are likely to be more constrained to growing in intact oak savannas, and are likely to be as rare as that savanna community type. Therefore, the presence of a number of plant species in a potential savanna remnant with high C values can provide a strong indication of a remnant oak savanna of high conservation value. If nearby high quality oak savannas exist, either of a restored or remnant nature, the understory plant species composition of these sites can serve to further support designation of plant species as oak savanna flora at a more degraded site. Despite the fact that it is desirable to classify a remnant community prior to initiation of restoration activities, these criteria of designating understory plant species as savanna indicators, and thus identifying a remnant savanna, can be applied to plant species which are newly documented in response to restoration. In this way, small experimental restoration areas, which require a relatively low amount of resources invested in them, can serve as helpful sites for defining a remnant. They can also further inform land managers about what to expect in the future restoration of larger areas on the site.

Identification of remnant oak savanna communities is the first step in their conservation. Tools of savanna identification include landscape-scale presettlement vegetation maps and aerial imagery, historical records (scientific or otherwise), and local-scale structural and biological features of a site. No one method of oak savanna identification described here should be used on its own. A combination of methods using information spanning time periods, spatial scales, and scope should be utilized and collectively inform the land manager.

Restoration methodology

Over the past several decades there has been an increasing recognition among the conservation community of the importance of oak ecosystems (savannas, woodlands, and forests), and the ecological restoration that many of them require (Leach and Ross 1995). Ecological restoration is fast growing, yet is relatively young as an academic field and practice (Brudvig 2011). While tallgrass prairie restoration in the Midwest has an uncommonly long history in the field, dating back to the 1930's, much less is known in the way of Midwestern oak savanna restoration. Recent work has shown great promise for oak savanna restoration in regards to the resiliency of many disturbance-deprived remnants and the positive response of biodiversity to restorative actions (Leach and Givnish 1999, Brudvig and Asbjornsen 2009). Despite the preliminary promise of oak savanna restoration, the need for resilient Midwestern oak ecosystems in the future requires that we carefully assess proposed restorative methodology against the overall goals of the recovery of these oak ecosystems. Certain elements will be essential in oak savanna restoration (e.g. disturbance), yet given the diversity of oak savanna community types, landscape contexts, site histories, and restoration goals, variability exists in potential and appropriate restoration schemes, and gaps remain in our knowledge of the ecosystem effects of these schemes. Two restorative variables that exist for developing an oak savanna restoration scheme are fire and mechanical thinning of woody vegetation.

Prescribed fire

Historically, reoccurring fire was a ubiquitous disturbance present during the development of mixed-oak ecosystems of Eastern North America, which included the Midwest (Nowacki and Abrams 2008, McEwan et al. 2007). Also, the successional process of mesophication that is degrading many savanna remnants today is thought to be the direct result of the absence of fire and other disturbances (Nowacki and Abrams 2008). As such, fire should be considered an essential part of an oak savanna restoration scheme wherever possible. Given that controlled burning is feasible at a restoration site, when and how often should we burn? This question is influenced by the sensitivity of biota to seasonality of burning, historical fire frequency in oak savannas, and restoration goals.

Timing of prescribed fire is a frequent subject of discussion and research among restoration ecologists and land managers. Individuals are faced with selecting a window of timing for burning that satisfy 1) the physical requirements for a burn to be successfully carried out (e.g. low litter moisture), 2) safety concerns both for individuals directly involved in the burn and for individuals in the surrounding area (e.g. smoke management for surrounding residential areas), and 3) restoration objectives. Many more fires in the Eastern North America, including the Midwest, were of human origin and not initiated by lightning like many western fires (Abrams and Nowacki 2008). These fires were somewhat variable in season and used to accomplish a diverse set of tasks that include cropland preparation, maintenance of masting and fruiting trees, and enhancement of game habitat. The reasons and context of human-induced fire differ greatly today. Today, burns carried out by land managers in the Midwest are most often conducted in early spring due to a relatively timeframe of appropriate conditions for physically carrying out a burn, and due to physical conditions that generally limit the risk related to keeping burns under control. However, burning repeatedly at the same time of year indefinitely could ultimately compromise restoration objectives. Although burning is necessary to maintain light levels and other conditions necessary for oak savanna-dwelling biota, there can be a short-term cost to these organisms depending on their vulnerability to fire damage at that time of year. For example, insects that may yet be dormant (e.g. in early spring) in the upper reaches of the leaf litter could suffer high levels of mortality following a burn. Various species of cool season grasses or early flowering forbs, that have most of their biomass above ground in early spring, are more vulnerable to early season fire than plant species with differing phenologies. Pavlovic et al. (2011) found that early spring burns reduced the number of flowering stems in early flowering shrubs one season after burning, with the negative effect diminishing with time. The authors also documented several shifts in bloom time from various plant functional groups, either delaying or hastening flowering in response to particular fire timings. This suggests that plant species impacted by the occurrence of burning at a vulnerable time of the season may recover if given time, but the authors warn that repeated burning at a particular time of year could ultimately affect the reproduction and plant community composition. Furthermore, certain functional groups of plants may be less susceptible to a particular burn timing, as the majority of their biomass may be underground and insulated from the effects of fire. These groups may actually benefit from consistent timing of burns, taking advantage reductions in sensitive plant species from burning, and shifting species abundances and composition over time. Burn timing clearly has to satisfy physical and safety requirements of using prescribed fire as a management tool. Yet this timing should be variable where possible to allow vulnerable biota sufficient time to recover following a burn, and avoid favoring particular species or functional groups that are capable of taking advantage of this effect. In this way, variable timing and frequency of prescribed fire can help to promote a diversity of species and functional groups in savanna restoration, a frequently cited restoration objective.

Historical fire frequency, or return interval, can be thought of as a reference disturbance regime for developing modern savanna restoration practices. These rates can be generated by examining fire scars on cross sections of mature trees that were present at the time of historical burning, and is expressed as the average number of years between fires. Mature oak trees found locally in remnant Midwestern savannas whose age predates European settlement are uncommon, and thus fire frequency studies (especially local studies) that document fire-return interval and may be used as a reference for determining modern-day return intervals are also uncommon (Wolf 2004). However, regional studies can help to inform this gap in knowledge. Two tree ring analyses conducted in oak ecosystems in Missouri indicate that fire return interval varied widely, from 2 to 24 years, but mean fire return intervals prior to European settlement in two particular oak ecosystems were 2.8 and 4.3 years (Guyette and Cutter 1991, Cutter and Guyette 1994). Mean fire return intervals from 1-10 years are generally thought to have pervaded the Midwestern tallgrass prairie and oak savanna regions (Cottam 1949, Pyne 1983, Axelrod 1985, Abrams 1992, O’Connor 2006). Furthermore, we know that temporal changes in climate, landscape context, and fire activity by indigenous peoples, and fire suppression all further influenced fire frequency and vegetation change in the oak savanna landscape (Grimm 1983, Abrams 1992). Not only was fire return interval affected by human activity, but stand structure and tree species composition of oak ecosystems was actively managed through silvicultural practices conducted by indigenous peoples. These practices were so influential to the distribution of oak ecosystems that forest types (e.g. oak savanna) and particular tree species persisted in periods and regions that according to climatic and abiotic conditions and should otherwise support a later successional, less fire-dependent forest type (Abrams 2006, Nowacki and Abrams 2008). As such, we should view historical fire return intervals as a reasonable benchmark for modern reintroduction of fire into oak savannas, yet acknowledge that ecological factors, including humans, can significantly alter this critical disturbance. In this way, the restoration community can use prescribed fire at particular frequencies to achieve various oak savanna restoration goals.

Given that we have a general idea of how often fires occurred historically, but also recognizing fire as a restoration and modern management tool, how often *should* we burn to achieve our restoration goals (e.g. tree species composition and canopy cover)? Different oak savanna community types are thought to inherently burn at different frequencies depending on factors related to moisture levels, fuel accumulation, and landscape position (O’Connor 2006), and this can help determine fire frequency for a particular savanna restoration. However, individual sites differ in their site history, restoration goals, burning feasibility, and importantly, their level of woody encroachment that further influences modern fire return intervals. Examination of fire frequency on overstory tree composition and distribution has revealed that choosing a particular fire return interval can determine the level of canopy cover and species composition of the resulting woody plant community. A higher frequency of fire could logically be expected to lead to a lower canopy cover, and a lower abundance of fire-sensitive mesic forest species. Fire frequency in oak savannas has been associated with rates of change in canopy cover and basal area (Faber-Langendoen and Davis 1995, Peterson and Reich 2001), and Bowles et al. (2011) found that a moderate fire return interval of 3 fires/decade with no additional management significantly reduced canopy cover in an Eastern sand savanna. The latter study cited canopy reductions as high as 55%, corresponding to canopy levels associated maximum heterogeneity; a metric proposed to support high levels of biodiversity in oak savannas (Leach and Givnish 1999). Conversely, Abella et al. (2004) and White (1983) found that treatments receiving only burns in fire-suppressed oak savannas did not affect overstory oak density over 15 and 13 years, where seven and 13 burns were applied respectively. Restoration goals of tree density were not met in the former study, where further reductions of 33-50% would be required to achieve target tree densities observed historically.

In addition to structural goals, reducing abundances of encroaching mesic tree and shrub species through introduction of fire are often cited, yet results can be mixed in this these restoration goals as well. For example, Alexander et al. (2008) found that in Kentucky oak forests, fire successfully lowered survival of *Acer rubrum* seedlings, an encroaching “fire-sensitive” tree species targeted by oak savanna restoration, and this effect has been cited in other studies as well (Glasgow and Matlock 2006). However, seedling density of other mesic invader species (i.e. *Sassafras albidum*) were unaffected by fire, and larger size classes of the effected *A. rubrum* were unaffected by fire. There are several potential explanations for these mixed results of burning on canopy cover as well as effects from fire on encroaching woody species.

As highlighted by Haney et al. (2008), the intensity, in addition to the frequency of fires, offers one explanation for these discrepancies of outcomes in oak savanna restoration metrics. By measuring scorch height on tree trunks after controlled burns, researchers correlated fire intensity to overstory characteristics to determine its effects on canopy cover. At a return interval of only three fires per decade, high intensity burns successfully reduced canopy cover to targeted levels that matched historical tree density. Furthermore, somewhat longer fire return intervals may allow for greater fuel accumulation, and by extension allow for burns of greater intensity, where greater tree mortality could occur. This highlights a potential tradeoff for land managers between fire return interval and burn intensity in that, burning more frequently (e.g. annually) could be ineffective at reducing woody vegetation if fuel accumulation and the resulting fire intensity is not great enough to kill encroaching woody species.

A second explanation for mixed results of burn only approaches to oak savanna restoration would be the increased fire resistance achieved through increases in girth by both overstory oaks and “fire sensitive” tree species after long periods of fire exclusion. This phenomenon is further expressed through species-specific life history traits related to physiological responses to burning, as discussed by Peterson and Reich (2001). Tree species that would be considered fire-adapted could achieve this adaptation through being a “resister” or an “endurer,” while tree species considered ill-suited to survive after burns are called “avoiders.” Avoiders (e.g. *Prunus serotina*, *Acer rubrum*) can tolerate shady conditions, and are fire-sensitive; being killed directly by one or more fires, or being indirectly killed through facilitation of secondary infection from burn damage. These species are generally not found in great abundance in fire-prone oak savannas, but fire suppression has allowed these species to gradually fill in formerly open areas from surrounding savanna margins. Endurers are tree species that can survive after fire, generally owing to thick bark that insulates vital underlying tissues. Resisters are species that can resprout after fire, replacing damaged aboveground growth from extensive underground carbohydrate stores. Various oaks that persist in savannas can be generally though of as both endurers (e.g. *Quercus macrocarpa*) and resisters (e.g. *Quercus velutina*), depending on the species. Given enough time to develop extensive root systems, bark thickness, and girth, tree species traditionaly classified as avoiders, like *P. serotina*, can become endurers or resisters. In this case, the negative physiological effects from fires that would typically kill avoider species outright, are now ineffective at doing so due to the more fire-resistant growth form these individuals have taken during large lapses in fire. Therefore, in cases where fire-sensitive species have attained fire resistant sizes and/or ages, reintroducing the disturbance that historically marginalized them in oak savanna communities may no longer be sufficient to reduce or limit their encroachment.

Lastly, fire return interval in remnant oak savannas may change over time due to the changing short-term goals of the particular restoration scenario. Prescribed fire regimes can take different forms, moving from restoration phase to maintenance phase. The restoration phase would likely be driven by major structural goals such as target levels of canopy cover, overstory species composition, and woody vegetation reduction. This phase would be characterized by a more aggressive disturbance regime where higher fire frequency and/or woody vegetation removal (e.g. mechanical reduction) are used to make major short-term changes to remnant stands. Results from restoration research (e.g. Faber-Longendoen and Davis 1995) suggest that biennial fires produce the most rapid reductions in tree density, and would be an appropriate fire regime for a restoration phase. The maintenance phase acknowledges success of the restoration phase, or an already desirable state of a remnant savanna. This phase could be driven by finer level goals such as maintenance of understory plant community restoration, continued suppression of woody encroachment, and conserving canopy cover levels. A lower intensity disturbance regime characterizes this phase, where fire return intervals are longer and/or more variable. This will ensure that fire-sensitive oak seedlings receive a long enough fire-free window for unmolested growth to become fire resistant and ensure oak regeneration for future canopy recruitment and to allow diversification of stand structure. Additionally, the lower intensity of the maintenance phase ultimately brings financial costs and investment of resources into restoring a site to more sustainable long-term levels.

Overall, land managers and restoration ecologists have a suite of factors to take into account to determine fire frequency and timing in a particular oak savanna restoration scenario. Species-specific seasonal effects, historical fire frequency, burn intensity and fuel accumulation, restoration goals and phase, site level constraints, and burning feasibility are all factors that should be accounted for when developing a fire-regime for an oak savanna remnant. Furthermore, we know that simply reinstating the historical fire return interval may not be sufficient to bring species composition and canopy structure to historical levels, and the effects of fire alone on canopy cover and species composition is contextual. As such, fire should be combined with other management techniques (e.g. thinning or grazing) when necessary.

Mechanical thinning

Where reduction of encroaching woody vegetation through fire alone is not possible because it is “unacceptably slow” (Peterson et al. 2007), ineffective, or is not logistically feasible at a site, selective mechanical thinning may be utilized in order to meet objectives. This is a widely used practice in the restoration field, can increase understory light levels, promote understory plant growth, develop targeted stand structure, and alter woody species composition, but also faces certain biological and financial limitations in practice.

Researchers highlighting the limitations and the benefits of prescribed fire alone in oak ecosystem management point out that using mechanical thinning in conjunction with burning could have an overall greater benefit to oak regeneration and understory development than just fire (Hutchinson et al. 2005). In fact, the inability of burning alone to accomplish restoration objectives, and the call for overstory thinning to enhance this process are widespread in the literature (Considine 2013, Dey 2004, Karnitz and Abjornsen 2006, McCewan et al. 2007, Abella et al. 2004, White 1983, Wolf 2004). Nielsen et al. 2003 considered thinning followed by burning the best way to restore fire-suppressed savannas, as burning alone produced modest changes in understory plant functional groups, but failed to incur sufficient mortality of overstory trees. In this study, thinning allowed land managers to have direct control of canopy cover, and resulted in increased understory plant richness and evenness. Brudvig and Asbjornsen (2009) found that overstory thinning alone promoted abiotic gradients (e.g. moisture) characteristic of the heterogeneous nature of oak savannas, when examining physical factors potentially related to the understory plant community between overstory trees and canopy gaps. This study demonstrated the positive effects of overstory thinning irrespective of fire, showing increases in forb, graminoid, and woody cover as well as increasing plant species richness after thinning. The authors then continue to suggest that including fire in addition to thinning would likely further enhance these gradients and subsequent biodiversity.

Although positive results of mechanical thinning of woody vegetation in fire-suppressed oak savannas have been demonstrated, there are a number of cases where its practice may produce negative effects related to restoration. Brudvig and Asbjornsen (2007) found that oak regeneration, another frequently cited savanna restoration goal, was not significantly greater in oak savannas plots that had undergone mechanical thinning compared to un-manipulated control plots. Authors point out that, the initial resiliency and resprouting of targeted woody mesophytic species, may outcompete adjacent slow-growing oaks. It is also suggested that, again, introduction of fire in conjunction with thinning may be required to enhance oak regeneration. Many original overstory oak trees have persisted for decades in savanna remnants, amidst high densities of newly recruited overstory trees since fire cessation. Restoration scenarios of rapid canopy reductions are designed partly to reinstate conditions that are conducive to the growth of these remnant overstory oaks, where neighboring trees are removed to increase light to shade-intolerant oaks. However, sudden removal of neighboring trees may also have the undesirable effect of increasing wind intensity on remaining overstory oaks, which could cause physiological stress or windthrow to these individuals. Given the importance of retaining stand structure and original overstory oaks in savanna restoration, overstory thinning should be carefully evaluated before being carried out and/or conducted gradually to limit negative physiological effects on remnant oaks. Furthermore, the potential drawback of stimulating exotic understory plant species with burning may be further exacerbated by overstory thinning, and promote aggressive species that respond well to rapid disturbances (Hutchinson et al. 2005). In order to facilitate emergence and success of conservative understory plant species, understory vegetation responses should be monitored. Furthermore, overstory thinning should be carried out in stages so that resulting light availability increases gradually to prevent aggressive disturbance-adapted species from rapidly outcompeting conservative native species.

Lastly, mechanical thinning is a costly process in terms of funds, personnel, and time, and may not be an option for every restoration scheme. Thinning may become prohibitively expensive and impractical for restoration of oak ecosystems on a large (e.g. landscape) scale, where burning alone may be the only option. Thinning alone can quickly reduce canopy cover and alter understory conditions, but cannot replace the effects of fire (Peterson et al. 2007). Given the variability in site conditions and history of each oak savanna remnant, thinning practices should be used in conduction with other restoration tools to cater to unique challenges that each site presents, and allow oak savanna restoration goals to be more fully realized.

Given the dearth of high quality oak savanna remnants in the Midwest, restoring fire-suppressed remnants is the best way forward for savanna conservation. Identifying fire-suppressed oak savannas can be accomplished regionally through a combination of presettlement vegetation maps, historical written records, and aerial imagery, while structural and biological indicators can further identify a local remnant. Upon identification of an oak savanna remnant, a number of restoration tools are available to the restoration community, and should be applied in a way that reflects the unique set of conditions present at the site. Timing and frequency of prescribed burning, as well as mechanical thinning practices are several main tools that can be utilized to accomplish specific site-level restoration goals. Yet more research is needed to fully understand the tradeoffs and effects of these management choices, particularly on biological communities, and effects on communities outside of the well-studied plant kingdom.

Oak savannas and pollinators

In general, pollinator communities, and their plant interactions have received very little attention in restoration ecology (Dixon 2009, Menz et al. 2011, Williams 2010). Vegetation-based approaches to ecological restoration are typical given the fundamental function and relative ease of manipulation of the plant community. However, biological communities not directly manipulated by restoration are critical to the persistence and dynamics of the plant community, such as pollinator communities and their vital pollination services. Importantly, 78% of plant species in temperate regions are animal-pollinated, while the remainder of these species use other mechanisms such as wind (Ollerton et al. 2011). Forbs (i.e. non-woody, non-graminoid flowering plants) make up a subset of these animal-pollinated plants, and are particularly obligated to animal pollination as a group. Forbs make up the largest vegetative component of oak savanna understories (Leach and Givnish 1999), and understory plant development is a primary goal of fire-suppressed oak savanna restoration. Knowledge of pollinator communities, of which insects are the primary taxa, of oak savannas and their pollination ecology is critical to the persistence of understory savanna forbs. Although studies of pollinator communities in restoration are increasing (e.g. Williams 2010, Fiedler et al. 2012), studies specifically targeting pollinators in Midwestern oak savannas are particularly scarce (Swengel and Swengel 2001, Summerville 2005, Grundel et al. 2011). Given this gap in our knowledge of oak savanna-pollinator communities and the importance to forb communities in oak savanna restoration, research in this area is greatly needed. A review of the effects of fire and other oak savanna restoration techniques on arthropods in general, in addition to pollinators, may provide much needed insight into this area.

Arthropods and burning

Fire is the most critical tool in oak savanna restoration, yet there is an inherent tradeoff between the benefits gained by use of prescribed burning and its negative impact on biological communities. Hence, these negative effects on sensitive biota from fire need to be considered when conducting ecological restoration that utilizes fire as a tool. The degree to which a particular species is affected positively or negatively by fire depends on the burn seasonality, burn frequency, life history traits of that species, and the ability of those populations of that species to recover after fire.

The seasonality of prescribed fire is limited by the physical ability of an ecosystem to carry fire and the level of risk related to burning at a particular time of year. The sensitivity of an arthropod species to burning is affected by the annual sequence of life stages, and the differential use of habitat of those life stages. The mobility of arthropod species (e.g. mobile adult vs. stationary pupa) and its typical location within the habitat (e.g. canopy vs. leaf litter) also varies. Hence, if an arthropod species dwells in the canopy as an adult it is both mobile and in a safe location, and should escape direct impacts of a ground level burn. If an arthropod species that is pupating in the leaf litter is both immobile and in the direct path of the fire, will likely suffer population decreases. It is this variation among species, along with colonization and recovery ability, which should determine species-specific responses to burning.

Studies of burning in prairie ecosystems cite negative effects on abundance of particular butterfly functional groups, and changes in assemblage of grasshopper species following fire (Evans 1984, Swengel and Swengel 2001). However, it was found that the negative effect of fire on butterfly groups declined over time after a site was burned. Despite short-term negative effects of burning, fire is required to maintain populations of prairie plants that certain butterfly species need for larval development. This tradeoff should be reflected in the fire frequency utilized by land managers, in that burns should occur often enough to maintain long term viability of prairie plants, but infrequently enough to limit direct impacts to butterfly populations. Evans (1984) found that the highest species diversity of grasshoppers in prairie sites occurred at intermediate burn frequencies, which reflect the aforementioned tradeoff. To allow for population stability and facilitate colonization of recently burned cites, Swengel and Swengel (2007) recommend establishing permanent lightly managed refugia for butterfly species, as direct impacts to butterflies in these areas should be greatly reduced.

In a broadly-focused examination of arthropod communities in black oak savanna in Minnesota, Siemann et al. (1997) found that fire did not have negative effects on fauna overall. From this, several major results and their respective implications stand out in their importance related to consideration of arthropod populations in response to fire. First, during the year of a burn, arthropod abundance and richness were significantly decreased, but overall (across 30 years) abundance and richness were not decreased. Furthermore, the short-term and long-term responses of individual arthropod taxa to burning were inversely related. In other words, a species that suffers a short-term population decline after fire will increase over time. Fire has an immediate negative effect on many arthropod groups, yet their required habitat are benefitted from the effects of a burn, and thus the populations of that arthropod species benefit overall. Second, the dominant taxonomic arthropod group varied depending on the experimental fire frequency. This result highlights the variation in response to burning from an individual taxon, and suggests that maintaining a particular fire frequency is also likely to allow species that most benefit from a particular burn interval to dominate the community, while reducing populations of those taxa who are sensitive to that interval.

The immediate effects of burning on arthropod communities in fire-dependent ecosystems may be negative, however the use of fire is critical for these communities' long-term viability. Fire may decrease a population through their direct exposure to flames, while the habitat structure and species composition rendered from the effects of fire, may be maintained. Furthermore, variability exists in species-specific temporal susceptibility to fire, and favorability of a particular fire regime for particular populations. In this way, a consistent management technique and timing (e.g. spring burns) may ultimately eliminate a sensitive species from the community, while allowing a species which benefit to dominate. Therefore, burning should be viewed as critical to the sustainability of fire-dependent habitats, but its use and frequency should be variable to limit its negative effects on biological communities, and allow for the highest possible species diversity.

Effects of restoration on pollinators and function

Although studies of pollinator communities in oak savanna restoration are rare in the literature, an exploration of studies of different taxa in the same ecosystem, or the same taxa in a different ecosystem, can allow for a more well-informed insight into this understudied area. Additionally, the assumed importance of pollinators in restoration is related to their functional effects on flowering plants with obligate animal pollination syndromes. However, studies of restoration and pollinator diversity often fail to actually measure function. Studies addressing pollination function in restoration do exist though, and are important to acknowledge to support assumed significance of pollinators in oak savanna restoration.

Assumptions of resultant benefits to pollinator communities from manipulation of plant communities in restoration are widespread, yet studies that test this assumption are mixed. A study of biological diversity in an oak savanna in the Southwest United States compared patterns of species diversity between various taxonomic groups, to see if metrics of diversity positively co-varied (i.e. diversity begets diversity), as is often assumed (Bock et al. 2007). Flowering plants and butterflies were monitored, as well as diverse taxonomic groups such as lizards and birds. The authors found that across taxa, two metrics of diversity, species abundance and richness, were positively correlated. However, species evenness displayed a weak negative relationship with abundance. These results suggest that increased abundances of species may lead to communities where a few species dominate, leading to reduced evenness. This study both supports and contradicts the assumption that diversity patterns in the plant community result in parallel diversity patterns in higher level taxa, depending on which diversity metric is measured. Grundel et al. (2010) reported mixed results of this assumption where plant community composition did not effectively predict bee community composition along a gradient of canopy cover. However, plant species richness was significantly related to bee community composition along with abiotic factors such as canopy cover and soil characteristics. Panzer and Schwartz (1998) found support for this assumption in their study of plant and insect diversity in Chicago-area prairies. Several of their metrics of plant diversity explained a significant amount of variation of insect diversity, suggesting that manipulation of the plant community in prairie restorations directly relates to diversity patterns in higher level taxa, such as insects. Plant diversity patterns in this study failed to explain variation in rare insect diversity however, and suggests intimate knowledge of biology of particular species and subsequent targeted management are required for restoration of rare insect taxa. The assumption that altering plant diversity and composition will have similar effects on pollinators is likely to be mixed, and depend on the particular diversity metrics measured and specific life-histories of the pollinator taxa.

Studies of non-pollinator taxa in oak savannas may be useful for predicting pollinator community responses to oak savanna restoration in that beneficial adaptations and community patterns may be shared among arthropods responding to the same disturbances found in this natural community. Studies of bark-dwelling arthropods in a fire frequency experiment in remnant black oak savanna share aforementioned patterns of insect responses to burning in that, the highest diversity of fauna was observed at intermediate fire frequency (Nicolai 1991). This again suggests that the positive and negative effects of burning are best balanced by using this tool at moderate frequencies where recovery of populations is allowed, direct mortality is limited, and habitat structure and species composition is maintained. Ryndock et al. (2012) studied spider diversity in an oak woodland restoration experiment in Northern Mississippi, examining spider communities at various intensities of woodland restoration, along with both closed-canopy and open-canopy references. The authors predicted a significantly higher richness in restoration plots than either reference, due to an additive combination of both open canopy and closed canopy adapted spider species in oak woodlands inhabiting forest and open-field niches respectively. Indeed, both spider species that are considered forest specialists and spider species adapted to disturbances contributed to a significantly richer spider community in intensely restored plots. Despite modest structural changes moving closed canopy plots toward a more open nature, there was no decline in forest specialist spider species, yet additional spider species predicted to be attracted to openings from canopy gaps were observed, leading to an overall increase in richness. Less intense restoration methods did not have an increased richness in the spider community than either reference, suggesting that more time, or more intensive management is needed to observe influxes in species adapted open areas.

Studies of pollinators in ecosystems similar in structure and plant species composition to oak savannas may lead to useful comparisons and predictions related to effects of savanna restoration on pollinators. One such study was conducted in ponderosa pine (*Pinus ponderosa*) and gambel oak (*Quercus gambelii*) woodland restoration plots, where researchers monitored butterfly communities, which were compared between restoration and control plots (Waltz and

Covington 2004). This ecosystem is structurally similar to Midwestern oak savannas with fire-resistant overstory trees, and thinning through mechanical means and through fire being utilized as restoration techniques. Understory development and canopy reductions were goals of this study, which are also shared with Midwestern oak savanna restoration. Butterfly diversity in restoration plots increased markedly. Butterfly species richness and abundance were greater in restoration plots relative to controls at a level of two and one and a half times greater in year one, and three and three and a half times greater in year two respectively. Understory floral resource availability and richness was not different among treatments however, but light intensity was significantly greater in restoration plots. This study demonstrates that richness and abundance of a pollinator group can be increased with initial restoration of a closed canopy woodland, and that light availability is an important factor in pollinator communities of pine-oak woodlands. A similar study examined combinations of restoration techniques in oak-hickory forests in North Carolina on diversity of floral-visiting insects (Campbell et al. 2007). Researchers monitored floral visitors through the use of colored pan traps and visual surveys for butterflies in four treatments: control (no management), fire only, woody thinning only, and fire + thinning combination. Overall, a greater species abundance and richness was observed in fire + thinning combination relative to all other treatments, which were statistically equivalent. This supports the aforementioned results from Ryndock et al. (2012) where upon initial restoration of a closed-canopy, fire-dependent ecosystem, a more intensive restoration technique successfully increases diversity of specific arthropod taxa, while the diversity of lower intensity restoration plots fail to achieve this increase.

Ecosystem function related to effective pollination of populations of flowering plants is rarely measured in restoration studies, where more often, diversity metrics of pollinator communities and floral visitation are used as proxies. Pollination function can be a difficult to measure metric, and definitions of pollination function vary among researchers. Williams (2011) measured native bee diversity, a taxa not directly targeted by restoration, in restored riparian sites and compared them to high quality reference sites. Bees were collected in traps and through netting from native flowering plants throughout each season, and community metrics were calculated. An equal species richness and abundance of bees was found in restored and reference plots, suggesting that a restoration targeting vegetation successfully restored a higher level taxonomic community. Community composition however, was distinct among treatments, as relative abundances of shared species was markedly different. Although pollination function was not directly measured, interaction networks examining visitation rates between bee and flowering plant species was generated, and it was found that many flowering plant species received significantly less visitation and less diverse visitation at restored sites. Therefore, ecosystem function (i.e. pollination) could be considered less robust at restored sites because if fluctuation of environmental variables causes one bee species to be drastically reduced, and a flowering plant is only visited by that particular species (which was observed here), pollination would be greatly reduced as well. In a forested ecosystem of a more mesic type, Proctor et al. (2012) measured pollination function through one particular understory flowering plant species (*Claytonia caroliniana*) in the context of silvicultural management techniques. Understory vegetation, light levels, pollinator diversity, and *C. caroliniana* seed set were measured in treatment plots where groups of trees were harvested and canopy gaps were created, as well as unharvested plots. Before leaf-out of the canopy, pollinator levels were equivalent between harvested and unharvested stands. Pollinator abundance after leaf-out, and the number of flowering stems of *Rubus strigosus* were found in treatment plots, where increased light, temperature, and bare soils were speculated to have increased pollinator levels. Furthermore, researchers found that there were more fertilized ovules of *C. caroliniana* in harvested plots, which flowers prior to leaf out. This suggests that canopy thinning through alteration of floral resources can also change pollinator communities as well as measures of pollination function.

Grundel et al. (2010) carried out a comprehensive study of bee communities, and habitat parameters predicted to affect these communities across a gradient of forest cover (including oak savanna) in a natural community-mosaic in Northwestern Indiana, where significant restoration efforts had taken place. Researchers found that plant richness, soil characteristics related to nesting, and canopy cover were the factors most critical to bee community composition. The oak savanna cover type along the forest gradient had a significantly greater abundance and richness of bees than forest, which could be viewed as a pre-restoration ecosystem. Bee community composition differed along this woody gradient, and was attributed to the presence of diet-specialist bees, which were found in forested and open cover types, but not savanna or woodland. This supports one of two opposing hypotheses that savannas and woodlands are ecotones, linking distinctive ecosystem types, rather than representing unique ecosystems themselves. Overall authors report that local habitat factors (e.g. fire frequency, nesting resources) within several hundred meters were key determinants of bee community composition.

In general, fire and other common management techniques of vegetation are mixed in their effects of particular arthropod taxa, and the correlation of the directly manipulated plant community with unmanipulated higher level taxa. A collection of studies examining how restoration techniques affect arthropods (including pollinators), and patterns of pollinator community composition following restoration and in similar ecosystem types, are helpful considerations of pollinator communities in Midwestern oak savanna restoration. However, more direct studies of pollinator community response to oak savanna restoration techniques, pollination function, as well as interactions and patterns in the flowering plant community are still needed for the sustained development of diverse pollinator and understory flowering plant communities in the increasing amount of Midwestern oak savanna restorations.

CHAPTER 2

OAK SAVANNA RESTORATION IN SOUTHERN MICHIGAN: ASSESSING EFFECTS OF DIFFERENTIAL MANAGEMENT ON LIGHT, COVER, AND FLOWERING FORBS

Abstract

Oak savanna communities are rare in the North American Midwest, where fire suppression has allowed fire-sensitive tree species to increase in prevalence, resulting in greater shading, discouraging both oak (*Quercus spp.*) regeneration and diverse herbaceous understory communities. To investigate the best way to restore oak savanna remnants, we designed an experiment in Southern Michigan to examine the effects of 1) unmanaged references, 2) burning only, and 3) thinning and burning, representing a gradient of management intensity, on vegetative cover, light, and flowering forbs in a remnant fire-suppressed oak savanna. We found that increasing management intensity corresponded with increased light availability, abundance of floral resources, diversity of forbs in flower, and decreased vegetative cover. Low management intensity did not significantly increase light availability or decrease vegetative cover relative to unmanaged references, while high management intensity achieved both management goals. Both restoration methods generally increased diversity of flowering forbs, with the greatest diversity found with high intensity management. These increases were particularly exaggerated two seasons after burning, when we saw sharp increases in richness and abundance of flowering forbs. We saw the emergence of forb species of conservation interest as well as weedy species in managed plots, yet overall, average values of plant conservatism of flowering forbs were no different from unmanaged areas. We suggest that both intensities of oak savanna restoration may be appropriate under different temporal, financial, and ecological scenarios. Our work demonstrates the differential efficacy of oak savanna restoration methods currently utilized by land managers, and highlights the potential for restoration of understory forb communities where relict populations and/or viable seedbanks exist.

Introduction

Temperate savanna ecosystems are among the rarest and least-protected biomes on earth today (Hoekstra et al. 2005), and intact remnant oak savanna communities in the North American Midwest landscape have all but disappeared (Nuzzo 1986). The majority of Midwestern oak savannas have been directly converted for agricultural production or residential settlements, while the remaining remnants exist in altered ecological states due to disruption of their historic disturbance regimes (Nuzzo 1986, O'Connor 2006, Nowacki and Abrams 2008). As such, the restoration of remaining remnant savannas is key to their persistence in the Midwestern landscape.

Oak savannas are noted for their exceptionally rich flora and fauna, and host a large number of species of conservation concern (Henderson 1995, Leach and Givnish 1999, Davis et al. 2000, O'Connor 2006). This biotic richness can be attributed in part to the pronounced heterogeneity created by a scattered canopy of mature oaks which creates strong gradients of abiotic factors such as light availability and soil moisture, yielding a diverse set of niches occupied by a variety of organisms. For example, in an oak savanna, plant species more typical of oak-hickory forests may be found under the shade of a cluster of oaks while, species more typical of dry-mesic prairie may be found in intervening openings with high light levels, and savanna "specialist" species may be found in those microsites with intermediate conditions (Packard 1988, Henderson 1995). In support of this phenomenon, understory plant richness was found to peak in savanna microsites along surveyed gradients from open prairie to closed forest, with 27% of the vascular flora of Wisconsin represented among just 42 ha of remnant savanna (Leach and Givnish 1999). Restoration of fire-suppressed oak savannas has been shown to yield the highest bird species richness compared with surrounding habitats, including bird species of conservation concern (Davis et al. 2000, Brawn 2006, Au et al. 2008). In Michigan, prairies and savannas host a higher number of rare and declining plant and animal species than any other terrestrial habitat (Eagle et al. 2005 as cited in O'Connor 2006). Although more documentation of oak savanna biodiversity is needed, it has been suggested that "*conservation efforts aimed at savannas may pay rich dividends in terms of insect and plant conservation*" (Leach and Givnish 1999).

Midwestern oak savannas are disturbance-dependent ecosystems (Heikens and Robertson 1994, Nowacki and Abrams 2008). Among the historical sources of disturbance, fire is arguably the most important in maintaining structure and associated biological communities. Low intensity surface fires with relatively frequent return intervals characterized these ecosystems (Wolf 2004, O'Connor 2006, Nowacki and Abrams 2008). These primarily indigenous fires (Abrams and Nowacki 2008) acted to suppress encroachment of woody vegetation, and promote the high light levels necessary to maintain a dense herbaceous understory (Bowles and McBride 1998, Leach and Givnish 1999, Reich et al. 2001, Pavlovic et al. 2006). European settlement and subsequent cessation of historical fire regimes resulted in a number of key changes in abiotic conditions and biological communities. This successional process, termed "mesophication," includes increased woody plant density and soil moisture, decreased light availability, increased occurrence of mesophytic tree species, and a shift to less-flammable litter (Nowacki and Abrams 2008). Thus, many of our oak savanna remnants today exist in a fire-suppressed state with a closed canopy, dominance by mesophytic tree species, declining prevalence of oaks, a relatively thick, moisture-retaining litter layer, and a greatly reduced understory plant community.

The greatest opportunity for maintaining oak savanna communities in the Midwest lies in reversing the effects of mesophication in fire-suppressed remnants in order to restore historical savanna structure and biological diversity. Given that the cessation of frequent fire from the landscape initiated the dramatic changes that led to the current state of many savannas (i.e. mesic closed-canopy systems), reintroduction of fire is of great importance for the recovery of oak savanna communities (White 1983, Haney et al. 2008).

The use of fire in oak ecosystem restoration can affect nutrient cycling (Reich et al. 2001, Dijkstra et al. 2006), stimulate the understory seed bank (Glasgow and Matlack 2007), reduce canopy and overall woody cover (Faber-Langendoen and Davis 1995, Haney et al. 2008), increase light availability (Kay et al. 2007), and promote a dense herbaceous understory plant community (Nuzzo et al. 1996, Leach and Givnish 1999). Many oak savanna restorations also utilize woody vegetation management, targeting invading mesic trees and shrubs through mechanical removal and subsequent herbicide treatment (Nielsen et al. 2003, Brudvig and Asbjornsen 2007, Abella 2010). This practice can accelerate savanna restoration by increasing light availability, shifting woody species composition and abundance, and facilitating the development of the understory plant community (Brudvig and Asbjornsen 2009). Restoration of flowering understory plants is critical to oak savanna recovery, yet our knowledge of the effects of management on forb flowering is scant (Huffman and Werner 2000, Pavlovic et al. 2011). Woody vegetation management is costly, and if carried out too quickly may facilitate rapid encroachment from invasive exotic or aggressive native plant species. Furthermore, intensively removing large numbers of mesophytic overstory trees adjacent to desirable overstory trees (e.g. *Quercus spp.*) may result in increased wind stress and mortality of remaining overstory oak trees. Therefore, a higher intensity of management may not necessarily result in a more desirable outcome of restoration.

The objective of this study was to measure the effects of management intensity on oak savanna restoration. Specifically, we monitored the effects of burning only vs. thinning woody vegetation in addition to burning on light availability, vegetative cover, and flowering of understory forbs. We focused on forbs in bloom rather than their vegetative state because our overall project goal was to investigate pollinator communities in the context of restoration (Lettow 2013). Flowering is also relevant due to its necessity for sexual reproduction of forbs, and we hypothesize that many light-loving forb species are suppressed vegetatively and/or suppressed from flowering due to decades of mesophication. Overall, we predicted that with increasing management intensity, light availability, floral abundance, and richness of forbs in flower would increase, while vegetative cover would decrease.

Methods

Study site

The study site was located on the MacCready Reserve in Jackson County, MI (42°07’36” N, 84°23’38”), an ~165 ha natural area owned by Michigan State University. The reserve lies in the Jackson Interlobate Region, an area formed at the intersection of three separate glacial lobes (13-16,000 years ago). Glacial landscape features such as outwash plains and moraines, as well as ice-contact topography such as eskers, kettles, and kames characterize the region (Albert 1995). This diversity of landscape features in the region has led to a diversity of natural communities, which are well represented at the study site. These include oak opening savannas, hillside prairies, prairie fen wetlands, and southern wet meadows (Michigan Natural Features Inventory, www.mnfi.anr.msu.edu/communities). These communities span a range of human-induced disturbances including tilling, grazing, hydrological impediments, fire suppression, and encroachment from invasive plant species.

An esker ridge within MacCready Reserve that supports remnant, albeit fire-suppressed, oak savanna communities was the focus of this study. The coarse soil of this esker is dominated by the Boyer-Leoni complex, characterized by sandy loams and gravelly loams in the upper portion of the soil profile with 18 to 40 percent slopes (USDA NRCS Web Soil Survey). Despite the ample precipitation of the area (~79 cm/year), the coarse texture of soil of the esker ridge promotes effective drainage, and is thought to have resulted in relatively low productivity of overstory trees compared to surrounding areas (O'Connor 2006). This relative reduction in productivity, grazing by livestock (evidenced by remnant fencing), and regionally common surface fires frequently conducted by indigenous people in the past (Hubbard 1887, O'Connor 2006), all likely contributed to the structure and species composition of this oak savanna community. In aerial photos from 1938 (Figure 4A), an open canopy structure of scattered mature trees is evident. Site visits confirm the large size and laterally spreading limb architecture of remnant open-grown overstory trees, suggesting that historically relatively open conditions were maintained for long periods of time.

Mesophication (Nowacki and Abrams 2008) resulting from cessation of the historical disturbance regime has altered the canopy composition and increased the density of woody plants in remnant savanna patches on the property (Figure 1B). Overstory trees common on site prior to the initiation of restorative management included white oak (*Quercus alba* L.), black oak (*Quercus velutina* Lam.), northern red oak (*Quercus rubra* L.), pignut hickory (*Carya glabra* (Mill.) Sweet), red maple (*Acer rubrum* L.), and black cherry (*Prunus serotina* Ehrh.). Common understory plants in the pre-management stage included Pennsylvania sedge (*Carex pensylvanica*

Lam.), licorice bedstraw (*Galium circaezans* Michx.), northern dewberry (*Rubus flagellaris* Willd.), Virginia creeper (*Parthenocissus quinquefolia* (L.) Planch.), enchanter's nightshade (*Circaea canadensis* (L.) Hill), black cherry (*Prunus serotina* Ehrh.), red maple (*Acer rubrum* L.), summer grape (*Vitis aestivalis* Michx.), pointedleaf ticktrefoil (*Hylodesmum glutinosum* (Willd.) H. Ohashi & R. R. Mill), sassafrass (*Sassafrass albidum* (Nutt.) Nees), ash (*Fraxinus* sp.), American hogpeanut (*Amphicarpaea bracteata* (L.) Fernald), and roundlobe hepatica (*Hepatica americana* (DC.) Ker Gawl).

Experimental design

In fall of 2010 through spring of 2011, we identified 15 comparable fire-suppressed patches of remnant oak savanna. Criteria for selection of these patches were: the presence of open grown oaks, scattered mature overstory trees present in the 1938 aerial image (Figure 1A), minimal canopy cover of planted pine species, and minimal presence of exotic understory species. We randomly assigned each of the ten fall-selected remnant patches to one of two treatment types receiving management, either "burn only" or "thin and burn" (hereafter referred to as "BO" and "TB" respectively). The BO treatment received a controlled burn in alternate springs, while the TB treatment received controlled burns in alternative springs and three additional stages of woody plant removal. These were compared to five spring-selected reference areas that received no management (hereafter referred to as "UN"). Thus, there were 15 experimental units with five replicates of each treatment (unmanaged, burn only, thin and burn), which span a gradient of management intensity. Experimental unit size ranged from 0.5 acres to 2 acres and was largely determined by the natural distribution of savanna remnants on the property.

During woody plant removal stage one (fall 2010), we cut non-oak woody plant species with diameter-at-breast-height (DBH) ≤ 4” at ground level with chainsaws and applied a glyphosate-based herbicide (Cornerstone Plus) to cut stumps to prevent re-sprouting. During stage two (fall 2011), we cut and applied herbicide to stumps of woody plants of the aforementioned characteristics up to DBH ≤ 7”, and in a future stage three, we will cut and treat any remaining woody plants of the same group with DBH ≥ 7”. Overstory trees ≥ 7” contribute substantially to the surface fuels in experimental plots through leaf litter deposition, and help to carry prescribed burns continuously across the site. Stage three will take place when enough herbaceous cover has developed in the understory so that fire can burn continuously in the absence of this deposition. In spring 2011, two prescribed burns were conducted and encompassed all 10 BO and TB experimental units. The burns were conducted one week apart, under similar weather conditions, and produced similar effects on vegetation and litter.

Downed woody material was removed in TB units where it was found in great excess after cutting, such that all units were visually similar in the amounts of woody litter. Downed woody material was also removed near the perimeters of the experimental units in order to reduce fuel for appropriate prescribed fire control and safety. In the spring of 2012, hand removal of garlic mustard (*Alliaria petiolata* (M. Bieb.) Cavara & Grande) and musk thistle (*Carduus nutans* L.) in the understory was conducted across all experimental units, with the exception of two 10 x 10 m “no removal” plots located near the center of each unit on both the uphill and downhill half of the plot (Figure 5). The purpose of these plots was to understand how, if at all, restoration methods affect *A. petiolata* invasion.

Light

We assessed light availability among treatments in this study using a 1 m long ceptometer (Sunfleck, Decagon Devices Inc., Pullman, WA). Photosynthetically active radiation (PAR) was measured on clear sunny days at three random sampling points per unit (Figure 5) at 1 m height between 10 a.m. to 2 p.m. on July 13th and August 15th in 2011, and August 6th and 7th in 2012.

Vegetative cover

We assessed vegetative cover of under and mid-story utilizing the vertical cover board method of Nudds (1977). The cover board was 3.48 cm wide, 2.5 m high, with five alternating painted black and white 0.5 m bands on the vertical axis. We used the eight sampling points created by the two 5 x 5 m sampling grids in each plot (Figure 5). Each corner (hereafter referred as “sampling point”) was numbered and permanently marked with ½” steel conduit placed into the ground. We estimated cover on two separate dates each year, one early (late May-mid June) and one late (mid July-early August) each season. On each sampling date we held the cover board vertically at a randomly selected sampling point, while a consistent observer (M.L.) would take a random compass bearing and walk 15 m away. Facing the cover board we visually assessed cover by estimating the percentage of each of the five alternating bands obscured by vegetation. This was repeated for another random compass direction for the same sampling point, and two sampling points per experimental unit were used, resulting in a total of 20 individual measurements per unit (four points x five height bands). If tree trunks completely obscured three or more bands of the coverboard, we shifted 15° counter clockwise before estimating cover in order to prevent inflating cover estimates by a vegetative component (mature trees) assumed to be equal among treatments and unaffected at that point in the management process.

Floral resources

We made visual assessments of the flowering of forb communities among treatments. Although the term “forb” refers to only herbaceous herbs, two species of woody angiosperms (i.e. *Ceanothus americanus* L. and *Elaeagnus umbellata* Thunb.) were also documented flowering in our plots, and are herafter included in our forb category. In each experimental unit, two “tally circles” with 10 m radii were established adjacent to sampling grids (Figure 5) where once every two weeks (six dates/season) a consistent observer (M.L.) would walk the perimeter of the circle and identify each forb species actively flowering within the circle, and tally the number of floral units for each flowering plant. A floral unit was defined as a discrete inflorescence separated in space from an adjacent inflorescence such that a medium-sized bee (e.g. honeybee) could not walk from one to another (Dicks et al. 2002). Species richness is defined here as the number of actively flowering forb species in each tally circle. The first date of floral sampling was standardized utilizing a base 10° C degree-day model (Baskerville and Emin 1969) using temperatures from a weather station ~40 km away (42°47’14” N, 84°45’75” W).

Data analysis

We performed two-way (on height and treatment) repeated measures ANOVA procedures on percent cover, utilizing arcsin square root transformations as suggested for proportional data (Crawley 2009) to rectify non-normal error distributions and heterogeneous variances (PROC MIXED; SAS 9.3). We analyzed light availability and floral abundance data using generalized linear mixed models that utilized Poisson distributions to reflect the non-normal error distribution of our data. We then applied a repeated measures ANOVA to analyze light availability and floral abundance data sets (PROC GLIMMIX; SAS 9.3).

We analyzed the diversity of forbs in flower in several ways to draw more comprehensive conclusions regarding the composition and response of this community to restoration. We conducted one-way (on treatment) ANOVA on ranked richness (PROC GLIMMIX; SAS 9.3), rarefied richness, Shannon's H, and mean Coefficient of Conservatism (CoC) (SigmaPlot version 11.0.0.75 for Windows, Systat Software Inc.). We also generated rarefied floral sampling curves to visually assess the completeness of our assessment of the richness of the floral community. These sampling curves display how newly encountered species accumulate with an increasing number of successful observations. When the sampling curve reaches an asymptote (i.e. relatively few new species are being documented per sampling effort) a community can be considered adequately characterized (Buddle et al. 2005).

Due to the difficulty in meeting assumptions of the error distribution in floral richness data, a non-parametric test was used to compare floral richness between treatments and years. The average number of species of forbs in flower for each treatment across each season was ranked (PROC RANK; SAS 9.3), giving the plot with the highest average species richness the highest rank, and so forth. A one-way ANOVA was then applied to ranked data using a general linear mixed model (PROC GLIMMIX; SAS 9.3). Model comparisons determined which random factors would be retained in all mixed models using Akaike's Information Criterion. Rarefied species richness means and variances were calculated for floral richness (EcoSim professional, version 1.2d, Acquired Intelligence Inc.) to account for unequal efficiency (sampling success) in encountering flowering forbs among treatments. This produces an appropriate diversity metric to reflect an inconsistent number of observations where flowering forbs were actually found among treatments and years. Richness analyses were rarefied to 18 observations, because the lowest common number of “successful” observations (i.e. where at least one species was detected flowering in a tally circle) was 19. Rarefaction analyses used 1,000 permutations were used to generate a mean number of species encountered at that given sampling success. Shannon’s H, rarefied to 18 observations was used to characterize diversity within flowering forb communities.

Patterns of individual species abundances and species’ conservatism among treatments were also examined. Increasing Coefficient of Conservatism (CoC) values (0-10) roughly correspond to the tendency of individual plant species to grow in high quality habitats. We calculated proportion of total and treatment floral tally plot occupation and applied pre-designated CoC values (Herman et al. 2001). Given that each treatment had five replications and each plot had two floral tally circles, we considered that each flowering forb species had 30 opportunities to be detected in a plot, and occupation was defined as presence of a forb in bloom in one tally circle in either year. Mean CoC estimates were generated by averaging all CoC values for all flowering forb species observed in a successful observation, then averaging plot means to generate one mean and standard deviation for each treatment by year combination. Exotic species were given a CoC value of 0. Pairwise differences for all analyses were analyzed using Tukey’s HSD.

Results

Restoration treatments frequently displayed incremental increases in mean values as management intensity increased (i.e. UN<BO<TB) in light availability and floral diversity, and incremental decreases in mean values with vegetative cover. In general, treatment differences became greater in 2012 than 2011. A modest diversity of flowering forb species was documented, with a range of abundances, responses to management, and conservatism values represented.

Light

There was no effect of treatment on light availability in 2011 ($F_{2, 27}$= 1.54, p= 0.233), but there was a significant difference in light availability among treatments in 2012 ($F_{2, 27}$= 9.56, p= 0.001) (Figure 6). Pairwise differences in mean light availability in 2012 were statistically significant between TB and both BO and UN (t_{27}= -3.14, p= 0.011 and t_{27}= 4.20, p= 0.001), while BO and UN treatments were statistically equivalent (t_{27}= 0.30, p= 0.549). Overall, mean light availability was lowest in UN (63.3 μmol/m^2), moderate in BO (100.1 μmol/m^2), and highest in TB (210.3 μmol/m^2).

Vegetative cover

The lowest tier of vegetative cover, 0.5 m, was never different among treatments in either year, while the upper four tiers of vegetative cover (1.0-2.5 m) were more statistically variable among treatments (Figures 7 & 8). In the upper four tiers in 2011, UN and BO treatments were always statistically equivalent, while TB always had significantly less vegetative cover than the other two treatments (Figure 7). In 2012 the upper four tiers of vegetation displayed a descending stepwise pattern of decreasing mean cover with increasing management intensity (Figure 8). However the only significant treatment differences in cover were between TB and UN at the three upper tiers of vegetation (1.5 m: t_{572}=-3.77, p= 0.015, 2.0 m: t_{572}=-5.34, p= <0.001, 2.5 m: t_{572}=-5.48, p=<0.001).

Floral resources

In 2011 floral abundance was not significantly affected by treatment ($F_{2, 60}$= 2.15, p= 0.126), despite a greater mean number of floral units in TB than either BO or UN (Figure 9). In 2012, however, floral abundance varied significantly by treatment ($F_{2, 72}$=12.16, p=<0.001), with a stepwise increase in mean floral abundance from UN to BO to TB. While the mean floral abundance was essentially the same in the UN treatment between years (2.26 to 2.76 mean floral units/circle), we observed large increases in the mean of floral abundance from 2011 to 2012 in BO and TB treatments. Mean floral abundance increased by more than five times in BO (mean 8.3 to 44.3 mean floral units/circle), and increased by more than seven times in TB (mean of 16.4 to 115.9 mean floral units/circle). Neither of these increases between years was significant within treatment at an alpha level of 0.05 (t_{24}=-3.06, p=0.054 and t_{24}=-2.89, p=0.077 respectively), but both BO and TB were significantly greater than UN treatments in 2012 (t_{72}=3.55, p=0.002 and t_{72}=4.78, p=<0.001 respectively).

In 2011 and 2012 floral richness was significantly affected by treatment ($F_{2, 48}$=3.88, p=0.027, $F_{2, 60}$=9.90, p=<.001 respectively) (Figure 10). Due to increases in the mean richness of BO and TB treatments in 2012, floral richness was significantly affected by year ($F_{1, 159}$=31.07, p=<.001), with significant interactive effects ($F_{2, 159}$=4.99, p=0.008). Pairwise comparisons for 2011 of treatment ranks reflecting floral richness show that BO treatments are statistically equivalent to both UN and TB treatments (t_{48}=1.85, p=0.164, t_{48}=-0.88, p=0.658), while TB treatments are significantly greater in richness than UN treatments (t_{48}=2.73, p=0.024). In 2012 all treatments are significantly different from one another, displaying the same stepwise increase in mean richness from UN to BO to TB from 2011 but more exaggerated and statistically distinct.

Flowering forb diversity showed a pattern of increasing richness of species with increasing management intensity and time (Figure 10, Table 2). Rarefication of observed richness and observed Shannon’s H changed the relative distance between treatment means of diversity, but the overall rank of diversity means among treatments is conserved between observed and rarefied estimates (Table 2). Rarefied richness analysis proved to be marginally more conservative than our analysis using mean ranks. Rarefied analyses showed that all treatments were statistically equivalent in 2011, while only TB treatments had greater species richness than both UN and B treatments. However, both observed and rarefied richness estimates still follow the stepwise pattern of mean richness increasing with management intensity (i.e. UN<BO<TB). Mean rarefied richness increased significantly in 2012 from 2011 in TB treatments, while UN and BO treatments were statistically equivalent between years (Table 2).

Results of Shannon's H analysis revealed that within year, all treatments were statistically equivalent. The only significant difference from comparison of Shannon's H between treatments and years was an increase in TB treatments from 2011 to 2012. Mean CoC of all treatments were equivalent in 2011. In 2012 the only treatment difference was a greater mean CoC in TB as compared to UN treatments. Mean CoC decreased significantly from 2011 to 2012 within all treatments (Table 2).

Floral rarefaction sampling curves in general approached asymptotes, with modest variation among treatments and years (Figure 11). Moderate differences in the slope of accumulation curves between 2011 and 2012 are evident for the UN curve, where 2011 appears to show a lesser slope than 2012 (Figure 11A). BO and TB treatments show the reverse trend (2012 showing a lesser slope than 2011), but with a more minor difference in slope between years (Figures 11B & 11C respectively). Overall, lines from all treatments and years appear to be approaching asymptotes, with the UN treatment being less asymptotic.

Forb species

A total of 60 total species of forbs in flower representing 27 taxonomic families were documented in this study (Table 3), including 49 forb species native to Michigan, and 11 exotic species. CoC values ranged from zero to eight (ten being the maximum possible value), total tally circle occupation (i.e. all possible floral plots) ranged from 3%-97%, and occupation of individual treatment tally circles (i.e. all possible floral plots within treatment) ranged from 0-100%. The ten forb species with the highest total plot occupation starting at the greatest occupation were as follows: *Galium circaezans* (97%, rank 1), *Hylodesmum nudiflorum, Potentilla simplex, Rubus sp.* (70%, rank 2), *Circaea canadensis, Hylodesmum glutinosum* (67%, rank 5), *Geum canadense*, *Hackelia virginiana* (60%, rank 7), *Phryma leptostachya* (50%, rank 9), and *Galium aparine* (43%, rank 10). With the exception of *Taenidia integerrima*, all of the most conservative species (CoC ≥ 8) were found in managed (i.e. BO & TB) plots.

Discussion

Goals for restoration of fire-suppressed oak savanna typically include decreased woody cover, increased light availability, and an increased density of the native understory plant community. The oak savanna restoration techniques we tested here positively influence each of those metrics, with intense management through thinning and burning generally leading to the greatest overall change. Many of these effects of management were only realized in the second year of the study, and highlight the gradual nature of restorative land management and the need for multi-year studies.

Light

When light availability was measured during 2011, both BO and TB plots had received one burn the spring prior, and additionally, TB plots had their non-oak woody shrub layer (≤4” DBH) removed. Although the mean light availability was numerically greater in TB in 2011, all treatments were statistically equivalent (Figure 6). This suggests that simply burning once, or burning and conducting thinning of the shrub layer may not be sufficient to increase light availability to the understory in general. Given that 2012 (when stage two of thinning had been conducted) revealed a statistically significant increase in mean light availability in the TB treatment, a greater degree of thinning (e.g. 4”≤7” DBH) seems necessary to increase light availability. In contrast, BO treatments did not have greater light availability than unmanaged treatments in 2012. Given the significantly greater richness of flowering forbs, and greater mean floral abundance of TB as compared to BO (Figures 9 & 10, Table 2), increased light availability in TB may be a driver of increased floral diversity. Leach and Givnish (1999) presented light availability as one of two principal ecological gradients affecting plant community composition in a comprehensive study of oak savanna groundlayers in Wisconsin (the other being soil texture). Light was also found to be the strongest predictor of understory vegetation growth in a study of variable sizes of canopy gaps in longleaf pine savannas (McGuire et al. 2001), and declines in canopy cover from management were associated with 100% increases in understory species richness of research plots in a remnant Eastern sand savanna (Bowles et al. 2011). Although we saw no significant increase in light availability in the ground layer of our BO treatment, this does not necessarily mean that using a burn only management method is ineffective at achieving increased light availability in the long term. We measured light availability at the initiation of savanna remnant management, and more than one burn may be necessary to achieve a significant level of increase in light penetration. This observation underscores the importance of sustained management (e.g. a long-term burning regime) once restoration of a remnant community is committed to.

Vegetative cover

Much of the change that we observed in vegetative cover in 2011 and 2012 was to be expected based on the anticipated change in woody vegetation from our management methods. In 2011, the significant differences between TB, BO, and UN at the four heights between 1-2.5 m reflect our first step of woody thinning in TB treatments, as the height of the shrub layer could be expected to span this height (Figure 7). The development of a native, dense, and herbaceous understory is a goal of our oak savanna management, and if this goal is being met, it should be reflected in treatment differences of cover from 0 and 1 m. However, all treatments were statistically equivalent in mean vegetative cover at 0.5 m in 2011, and 0.5 and 1.0 m in 2012 (Figure 7 & 8). From this, one could conclude that our management does not affect understory development, yet this is not reflective of our floral data or our general observations. A more likely explanation is the fact that our assessment of vegetative cover did not separate woody cover from herbaceous cover, and of particular importance may be the re-sprouting shoots of small top-killed trees and shrubs present in BO treatments.

The relationship between BO and TB treatments changed in vegetative cover from 2011 to 2012 (Figures 7 and 8). Pairwise comparisons show that our BO treatment was in a different statistical grouping from TB at four heights 1-2.5 m in 2011, but in the same statistical grouping at all five heights in 2012. An additional level of thinning that took place in TB treatments in the fall of 2011 that would be expected to lower mean cover in TB, and further separate its mean from the BO treatments, yet they were more statistically similar in 2012. The reductions in mean vegetative cover in 2012 at the upper four heights (1-2.5 m) from both TB and BO treatments related to this change are visually evident (Figure 8). An increase in standard error of the mean of the upper four vegetation heights for one or both the TB and BO treatments would reflect an increase in variability and could cause this change in the statistical relationship from 2011 to 2012. However, we did not observe an increase in error (Figures 7 & 8). As such, we suspect that this observation results from an authentic biological process. One hypothesis is that there is a delayed pattern of mortality or reduced vigor in fire-sensitive woody species that contributes to a lower mean cover in 2012 but not 2011 in BO treatments. In 2011 we observed substantial woody vegetative cover in burn only treatments resulting from resprouting of fire-intolerant woody species (e.g. *Prunus serotina*) as a physiological stress response to the spring burn (M.L. personal observation). A study of the effects of fire in an oak forest in Kentucky, USA, found a similar response with a rapid flush of stump sprouts that was responsible for a short term decline in understory openness or "gap fraction" (Chiang et al. 2005) following initial prescribed burns. In some cases, a reduction in the canopy and/or shrub layer may not occur with repeated burnings if the recovery of woody species outpaces the setbacks induced by fire (Alexander et al. 2008, Haney et al. 2008). This same vigorous regrowth at MacCready Reserve could have maintained adequate vegetative cover in 2011 to create similar mean vegetative cover between unmanaged and burn only treatments. In 2012 the MacCready Reserve region received approximately half its normal accumulation of rainfall from January 1st to August 30th (41.86 cm), compared with the same period in 2011 (75.41 cm) (www.enviroweather.msu.edu, Leslie, Michigan station). This atypical reduction in precipitation combined with a decrease of the moisture retaining capacity of the litter layer (burned off the spring prior) could have created droughty soil conditions and exerted additional stress on mesic-adapted woody species already stressed from burning. The overall effect could be a delayed reduction in cover of fire-sensitive mesic forest species resulting from direct (e.g. heat damage) and indirect (e.g. reduction of moisture retaining capacity of the soil) physiological stresses from our prescribed burn and low precipitation, although we do not have data to directly support this hypothesis. The conceptual intent of the restoration methods presented here are to reverse the degradative effects rendered by the successional process of mesophication. Our hypothesis of this reduction in fire-sensitive woody plants through the effects from fire on litter, soil moisture, and direct stress supports this concept, and these species-specific mortality effects are documented in similar studies (Peterson and Reich 2001, Alexander et al. 2008).

Floral resources

Flowering forb communities were significantly affected by management method over time. We observed an increase in floral abundance, ranked richness, and rarefied richness with increasing management intensity, but not in rarefied Shannon's H (Figure 6, Figure 7, Table 2). These patterns were mixed in significance in 2011 but with more consistency in 2012. Mean abundance of floral units in TB treatments was greater than both UN, and BO treatments in 2011, yet there were no statistically significant treatment differences until 2012 (Figure 6). Similarly, modest treatment differences in floral richness in 2011 became more exaggerated in 2012 (Figure 6, Table 2). In a similar system, Thomas et al. (1999) found that silvicultural thinning increased richness of understory plants, as well as understory vegetative cover relative to non-manipulated forest stands. It appears that a more intense management method (i.e. TB) in our study similarly leads to greater mean floral abundance than a less intense (i.e. BO) approach, although this trend was not significant. In 2011, comparisons of Shannon's H between treatments displayed the reoccurring stepwise pattern we observed in the other diversity metrics we calculated (Table 2). In 2012 however, BO treatments had a significantly lower Shannon's H value than both UN and TB treatments. Given that other estimates of diversity show BO treatments with a greater mean number of species than UN, but fewer than TB (Table 2), the lower mean value of Shannon's H suggests that evenness (which only Shannon's H accounts for) could be responsible for this discrepancy. In contrast to BO treatments, the TB restoration method mechanically and uniformly reduces non-oak woody cover, while BO treatments rely on the less consistent nature of fire alone to reduce woody cover. The patchy effects of fire have been documented and discussed in the context of oak ecosystem restoration, and have been cited as a mechanism to create habitat heterogeneity and resultant high levels of biodiversity (Leach and Givnish 1999, Alexander et al. 2008). Fire alone in this study could result in patchy reductions in cover and subsequent patchy increases in light penetration in BO plots, which could lead to patchy understory flowering and a low evenness (lowering Shannon's H) of flowering forbs in BO treatments in 2012.

The delayed differences in floral abundance and richness, and the similar patterns they display over time suggest several things. First, the fact that the sharp increase in floral abundance in 2012 was paralleled by increased floral richness (Figures 9 & 10) suggests that, at least in part, a greater number of species actively flowering (as opposed to just an increase in flowering from 2011 species) in 2012 is responsible for this overall increase in floral abundance. The consistently low floral abundance and richness in UN treatments shows that restoration is responsible for these increases in floral abundance and richness. In managed treatments, we observed a delayed flowering response for many species following prescribed burning as management progresses and/or more time is allowed for physiological recovery of the understory vegetation.

This delayed flowering response could be explained in several ways. Dormant seed of a seed banking species could be stimulated into germination with removal of leaf litter, scarification, and/or smoke (Keeley and Fotheringham 1998, Glasgow and Matlock 2006) associated with burning, and simply require two seasons (biennial flowering species or perennial) to build up the energy required to come into flower, or simply flower more during the second season than the first. *Hackelia virginiana* for example, is a native forb species of biennial habit. *H. virginiana* was one of the most abundant flowering species in the study, occupying 60% of total floral tally plots, and just 10% of UN plots (Table 2), yet was never observed blooming until 2012 (Lettow unpublished data). *Verbascum thapsus*, an exotic biennial forb, followed a similar trend. It occupied only 10% of total plots, all of which were TB plots, but also was only observed in 2012. It is reasonable to suggest that these species were stimulated by the disturbance of our restoration activities (mechanical thinning fall 2010, spring 2011 burn) and subsequently bloomed in their second year of growth. A species that is light-deprived and therefore suppressed from flowering, could also be present in a vegetative state prior to burning, could be set back from the physiological damage attributed to fire, and require a greater amount of time (e.g. two growing seasons) to recover and build up sufficient energy reserves to come into flower, or flower more heavily in the second year following the burn. This concept highlights the inherent short-term damage that using prescribed fire as a management tool can cause on desirable biota. Yet burning will be required in long-term oak savanna management to stimulate understory growth through maintenance of high light levels, litter removal, and reduce competition from fast growing fire-sensitive woody species.

Occupancy of treatment floral tally plots by forbs in flower revealed species with a combination of habitat associations, conservatism, and abundances. The combination of understory species adapted to forest, savanna, and prairie-like conditions documented in our study could support the concept that oak savannas retain their high diversity through niche heterogeneity across physical gradients (e.g. light). Forest-adapted species such as *Podophyllum peltatum*, *Persicaria virginiana*, and *Boehmeria cylindrica* might be expected to decrease in frequency over time due to increased fire mortality, light intensity, competition, and a reduction of forest-microsites as restoration progresses. On the other hand, species associated with prairies and open areas like *Monarda fistulosa* and *Triodanis perfoliata* might be expected to increase in abundance as conditions rendered by restoration reflect more prairie-microsites. Each of these open-site adapted species was only present in one tally plot (Table 3), a likely reflection of the smaller number of prairie-microsites, given the early stage of our closed canopy oak savanna restoration. Putative oak savanna specialist species such as *Apocynum androsaemifolium*, *Asclepias exaltata*, *Ceanothus americanus*, *Krigia biflora*, *Lysimachia quadrifolia*, and *Taenidia integerrima* that have been discussed in recent oak savanna restoration studies (e.g. Bader 2001) and classic savanna studies (Curtis 1959) were observed in floral plots of our study in low abundances (Table 3). We anticipate increases of abundance in these somewhat conservative species over time. Sources of this increase of oak savanna specialists and open-adapted species could come from continued seedbank emergence, increased vigor in light-suppressed vegetative forms, and migration from light gaps, trailsides, and forest edges where light levels may retain historical intensity. Several understory species documented in our study (e.g. *Boechera canadensis*, *Erigeron philadelphicus*, *Galium aparine*) displayed a gradual increase in their presence in floral tally plots along a gradient of management intensity. This trend may reflect a direct response of understory plant vigor (i.e. flowering) to the gradual increase in light availability across our restoration treatments (Figure 6).

In addition to conservative plant species (e.g. *Paronychia canadensis*, CoC=8), we documented a number of species with low conservatism values that are either "weedy," mostly annual natives (e.g. *Conyza canadensis*, CoC=0), or exotics (e.g. *Meililotus albus*). A large proportion of the lowest CoC species either show increased abundance or exclusive presence in TB treatments as compared to BO and UN (Table 3). This suggests that high light levels and/or physical disturbance associated with mechanical removal of woody vegetation may be related to an abundance of weedy species. The weedy native species include *Chenopodium simplex*, *Conyza canadensis*, *Erigeron philadelphicus*, *Lobelia inflata*, *Oxalis stricta*, *Potentilla* *norvegica*, while exotics are *Cirsium vulgare*, *Leonurus cardiaca*, *Melilotus albus*, *Silene latifolia*, *Torilis japonica*, and *Verbascum urticifolia*. We do not consider the aforementioned weedy natives to be a management concern. On the contrary, these annual disturbance-adapted species may play an important role of early colonization of exposed soil following a disturbance. Given the mixed response of the understory in this study, these weedy natives may help compete for resources with exotics, and will likely decrease in abundance in time as more conservative, perennial species increasingly dominate at the site. Hutchinson et al. (2005) for example, found that *Erechtites hieraciifolius* (fireweed), a seedbanking annual species also documented in our study, displayed sharp increases in abundance during the season immediately following a spring fire, but returned to pre-burn levels during years when fire was absent. Although the exotic species we documented weren't widespread in our floral tally plots (tally circle occupancy ranges from 3-23%), their early detection at the site is important and points out key considerations regarding savanna restoration. There is a grazing history of variable intensity and location at MacCready Reserve, a common land use history associated with many oak savanna remnants (Curtis 1959, Considine et al. 2013). The presence of grazing by livestock might have maintained openness after regular burning ceased and potentially delayed the effects of mesophication, and has even been investigated as an oak savanna restoration tool (Harrington and Kathol 2009). However, this land use may have inadvertently introduced and maintained many of the exotic species found in this study into the understory plant community.

We have demonstrated here that a thin and burn restoration approach can provide greater short term restoration success in terms of abiotic conditions (i.e. light and vegetative cover) and understory plant response (i.e. richness of forbs in flower), yet this method may produce negative effects of stimulation of exotic plants through physical disturbance and increased light. Although the exotics we found vary in their degree of invasiveness and abundance in our plots, restoration involving stimulation of the seed bank and/or understory plants with fire or other physical disturbance should be followed by monitoring and subsequent management of targeted exotic species.

We realize a limitation of our floral diversity study in that we only recorded understory plant species that were actively flowering and thus potentially underrepresented or missed those species present but not flowering, or flowering outside of the sampling window of our study. Further work could investigate flowering suppression in the context of restoration by looking into the proportion of plants actively flowering in the understory relative to all species that are present, even if only in a vegetative state. We also did not conduct analyses here that might inform us of what specific habitat covariates (e.g. light) might be directly responsible for changes in the flowering forb community, and as such our inference on mechanisms for floral diversity patterns is limited to associative comparisons. Although we were not able to find research on factors affecting understory flowering in oak ecosystems, Kudo et al. (2008) suggested that flowering and fruit set of early summer bloomers (the period when most of our sampling took place) in a deciduous forest understory was most limited by light. The critical role of light availability in driving dynamics of oak savanna understory communities demonstrated in other research (Leach and Givnish 1999) in combination with our results (Figures 6, 9, 10, Table 2), suggests that even modest increases in light availability could produce dramatic effects on flowering of forb species in the understory of oak savannas.

This study demonstrates that in the short term (e.g. 2-3 yrs, and the length of most grant supported restoration efforts), a more intensive restoration method could achieve a higher degree of success of restoration objectives related to increases in light availability, reduction of woody cover, and rehabilitation of the flowering of the understory plant community. However, we observed delayed effects from burn only restoration in cover reduction, increases in light availability, and floral diversity. This suggests that perhaps burn only treatments may be on a trajectory to approach the degree of success that thin and burn treatments have attained, but require longer term monitoring to detect. However, many researchers have pointed out that due to the great periods of fire suppression of many oak savanna remnants, large increases in girth of fire-sensitive trees are realized and actually increase fire resistance in overstory trees. Therefore, in some cases burning alone may not be sufficient to reduce canopy cover to the presettlement levels often identified in restoration objectives. In some cases then, and a more intensive method may be necessary to achieve restoration objectives (White 1983, Abella et al. 2004, Wolf 2004, Karnitz and Asbjornsen 2006, Considine et al. 2013).

Conclusions

Different restoration methods such as those presented here may be utilized under different temporal, financial, and ecological scenarios or used simultaneously. For example, if goals or financial support are limited to the short term (e.g. 2 yrs), an intensive management method (e.g. thinning) may be necessary. Conversely, if funds for restoration are limited, but the time frame to achieve restoration objectives is long, a lower intensity, burn only method may be sufficient. It has been suggested that in order to maintain high biodiversity in oak savanna restorations, a range of disturbance regimes (and by extension multiple restoration methods) should be utilized (Leach and Givnish 1999). Given the differential yet generally positive results on abiotic conditions and floral diversity from the two restoration methods presented here, both could be utilized at the same site to create greater within-site heterogeneity. This utilization of multiple restoration methods and their resultant heterogeneity could serve to further promote the notably high biodiversity of oak savanna ecosystems.

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CHAPTER 3

A GRADIENT OF RESTORATION INTENSITY DIFFERENTIALLY AFFECTS POLLINATOR COMMUNITIES IN OAK SAVANNA

Abstract

Oak savannas of the North American Midwest are a rare fire-dependent natural community, characterized by a high proportion of understory forbs. Oak savanna restoration therefore, should be considerate of pollinator communities, which are relevant to savanna understories containing many forbs that require insect pollination. For this reason, we conducted an experiment sampling bee and butterfly communities in the context of the restoration of a fire-suppressed oak savanna in Southern Michigan. We used unmanaged references along with two different restoration methods (burning only and burning + thinning) to examine the effects of restoration intensity on the abundance, diversity, and habitat relationships of pollinators. Butterfly distributions across treatments were mixed depending on taxonomic family, possibly due to affects of restoration on host plant abundance. We found that our thinning and burning rapidly and significantly increased bee abundance, richness, and Shannon's H relative to unmanaged references, where burn only restoration largely failed to do so. Thinning and burning also resulted in a distinctly different bee community after two seasons, while bee communities in burn only restoration plots were similar to those from unmanaged references. Differences in bee diversity and community structure between treatments may be due to the influence of restoration on nesting resources, which is reflected in the differential captures of various nesting guilds. Association between bee communities, floral communities, light, and vegetative cover were variable, likely due to progressing effects of restoration on habitat, and annual variation in environmental variables. Overall, thinning and burning oak savanna restoration has positive effects on bee diversity, while burn only restoration only increased bee abundance. We hypothesize that a burn only restoration method may require more time to shift bee communities, yet both methods are viable and the restoration community may employ both complimentarily.

Introduction

A frequent goal of ecological restoration is to recover and retain high levels of biodiversity in degraded ecosystems, thus, biodiversity metrics are often used to assess restoration success (Ruiz-Jaen and Aide 2005, Brudvig 2011). Since the concept of biodiversity encompasses a range of organisms, restoration success should be assessed across a range of taxa to test whether biodiversity as a whole is being increased. Yet habitat restoration studies most often assess metrics related to ecosystem structure or the plant community alone, neglecting to monitor other taxa (Brudvig 2011, Montoya et al. 2012). While monitoring plant diversity and structure is useful, it is not well understood whether changes in diversity of other taxa parallel those of plant taxa or vegetative structure following restoration.

Pollinators are a ubiquitous and speciose group that can be used to monitor changes in biodiversity during ecological restoration. In addition to species-level metrics, pollinators can also be partitioned into functional groups, as is commonly done for plants (Leach and Givnish 1999, Peterson et al. 2007). Analyses of functional groups provide a method for assessing diversity beyond just those of taxonomic means. Bees, which are generally recognized for their high degree of adaptation to pollination/floral visitation (Kevan and Baker 1983), can be partitioned into functional groups such as nesting (soil, stem, wood) and feeding guilds (oligolectic, polylectic), or by life history strategies (cleptoparasites, self-provisioners) (Wolf and Ascher 2008, Grundel et al. 2010, Williams et al. 2010, Sheffield et al. 2013).

Pollinators provide valuable supporting ecosystem services for humans in agricultural landscapes, but also carry out critical ecosystem functions in natural areas. This latter utility of pollinators has been studied far less than the former (Dixon 2009), due to the economic interest related to increased yield of insect-pollinated crops. However, plant communities are of primary importance in natural ecosystem function, and pollinators have the ability to regulate the forbs in these natural communities (Benadi et al. 2012). Pollinators therefore influence forb communities directly, through changes in pollination and seed set, and indirectly via resulting changes in plant community demographics, species composition, and trophic interactions. Given that restoring functions such as pollination is one of the primary tenets of restoration ecology, investigation of pollinator communities in response to ecological restoration is an important yet understudied phenomenon (Montoya et al. 2012).

Recently, there has been acknowledgement of the need to monitor biodiversity in restoration through functional means, not just through species richness (Brudvig 2011, Montoya et al. 2012). Given the difficulty and impracticality of directly measuring ecosystem function for most restoration projects, monitoring groups of species with a direct link to critical ecosystem function (e.g. pollinators), could provide greater insight towards this function (Petchey and Gaston 2006).

Oak savannas are fire-dependent natural communities that were formerly abundant in the North American Midwest, where they were widespread over the broad ecotonal area between mid-continental grasslands and Eastern forests (Curtis 1959, Nuzzo 1986). The fires that characterized oak savannas were frequent low-intensity surface fires that led to or maintained scattered distributions of overstory oak trees and a continuous understory. These fires acted to suppress woody plant encroachment in a region that could otherwise support forest vegetation. However, with suppression of fire, fire sensitive woody species were released from suppression, and encroachment often followed (Nowacki and Abrams 2008). This woody encroachment, along with conversion for agricultural use and degradation by residential and urban development, led to a >99% loss of high quality Midwestern oak savannas (Nuzzo 1986). Many species of conservation concern are associated with oak savannas, and the declines of Midwestern savannas and associated species are broadly paralleled (Davis et al. 2000, O'Connor 2006). The potential benefits available to the conservation of biodiversity through restoration of Midwestern oak savannas have been recognized for some time (Leach and Ross 1995). For example, in studies examining biodiversity patterns in a gradient of canopy covers ranging from tallgrass prairie to oak forest, plant and bird species richness were found to peak in restored oak savannas (Leach and Givnish 1999, Au et al. 2008). This suggests that oak savanna-focused restoration may yield substantial increases in biodiversity across multiple taxa.

The vast majority of the plant species richness associated with oak savannas lies in the understory community, which is noted for its high proportion of flowering plants (Leach and Givnish 1999), 78% of which require animal (typically insect) pollination in temperate regions (Ollerton et al. 2011). These rich understory communities are frequently studied and monitored as the focus of oak savanna restoration (Leach and Givnish 1999, Peterson et al. 2007, Brudvig and Mabry 2008, Pavlovic et al. 2011). Given the importance attributed to savanna understories, pollinator communities may be of critical importance to the recovery and persistence of the forb species found in oak savannas.

While several studies have examined insects in the context of oak savanna restoration (Nicolai 1991, Siemann et al. 1997, Grundel et al. 1998, Ritchie et al 1998, Summerville et al. 2005, Kay et al. 2007 Panzer et al. 2010, Houdeshell et al. 2011, Ryndock et al. 2012), far fewer have studied pollinator taxa in the context of oak savanna restoration (Swengel and Swengel 2001, Pickens and Root 2008, Grundel et al. 2010), and as such, pollinator responses to these restoration practices are still largely unknown. Furthermore, a series of approaches to oak savanna restoration exist, such as the use of prescribed surface fires, mechanical reduction of fire-sensitive woody vegetation, or a combination of both (Nielsen et al. 2003, Peterson et al. 2007, Brudvig et al. 2011). Uncertainty exists regarding the overall benefits and drawbacks between these two restoration methods. A burn only approach to savanna restoration is less costly and less labor intensive but some have suggested that low-intensity surface fires alone may not induce the necessary level of tree mortality in order to significantly reduce canopy cover and/or basal area to historical levels (Tester 1989, Considine et al. 2013). Mechanical thinning however, is costly, and may thereby limit the overall area to which restoration can then be applied. Thinning could also potentially increase mortality of desirable overstory oaks due to increased wind stress, and may promote invasion from exotic understory species (Nelsen et al. 2008). Gauging the effect of restoration approaches on pollinator communities, as well as their ability to meet goals of oak savanna restoration, is critical to the recovery of savannas in the future. Implementing identical restoration methodology on the same degraded ecosystem type has been noted for its variable outcome and minimally predictable endpoints, perhaps following alternative restoration trajectories (Hughes et al. 2005, Choi 2007, Mathews et al. 2009). Variable restoration methods in the same ecosystem then, which may be justified through their ability to meet restoration goals or operate within financial and logistical constraint, can be expected to result in restoration trajectories with even greater variability. Furthermore, following different restorative approaches to the same system over time may create distinctly different biological communities. If so, the ability of each method to meet its restoration goals (e.g. biodiversity targets) may also differ.

In order to assess the effect of variable approaches to restoration on biological diversity, we characterized pollinator communities along a gradient of experimentally applied restoration intensity (i.e. no management, burning only, and thinning and burning) applied to a fire-suppressed Midwestern oak savanna. We focused on bee and butterfly communities, using both passive and active sampling techniques to capture pollinators within our experiment. We also measured biotic and abiotic variables potentially related to pollinator communities in order to understand which components of this changing habitat best predicted variation in pollinator diversity. Our hypothesis was that pollinator diversity would increase along the gradient of management intensity, responding to changes in the floral community, canopy openness, and nesting resources affected by the restoration methods.

Methods

Study site

Our study site was a set of fire-suppressed closed-canopy oak savanna remnants at the Michigan State University MacCready Reserve, located in Jackson County, Michigan (42°07’36” N, 84°23’38”). The savanna remnants are surrounded by a matrix of other post-agricultural wetland and upland remnant communities in the context of the 408 acre reserve, some of which have been the focus of experimental restoration (see Fiedler et al. 2012). Aerial photography from 1938, presettlement vegetation maps, and the abundance of open grown oaks at MacCready Reserve reflect historical savanna vegetative structure and support the designation of this area as a remnant oak savanna community. Aerial imagery from 2005 and the closed-canopy state of formerly open areas at the initiation of restoration (2010), indicate that canopy closure took place over the several intervening decades. We attribute this canopy closure largely to a natural succession of fire-sensitive mesic tree species released from suppression following the removal of disturbances. This process of “mesophication” is reflective of a widespread trend occurring in fire-dependent ecosystems across much of the Eastern United States (Nowacki and Abrams 2008).

Experimental Design

In 2010, we identified 10 comparable plots of remnant oak savanna. These plots ranged in size from one-half to two acres. We then randomly assigned each plot to one of two treatments. “Burn only” treatments received a spring prescribed fire every other year, while “thin and burn” treatments received this same burning plus a three-step mechanical thinning treatment. Each step of the thinning process targeted non-oak woody species, first those ≤ 4” diameter at breast height (DBH), followed by ≤ 7” DBH, and ≥ 7” DBH, which all then receive glyphosate-based herbicide applications to cut stumps to ensure mortality and prevent resprouting. We conducted thinning steps one and two in the fall of 2010 and 2011 respectively, while step three is anticipated to take place in fall 2013. One prescribed burn was applied to both treatments in the spring of 2011. These two treatments represent variable approaches to oak savanna restoration, both of which are actively practiced by restoration practitioners. In order to further establish a gradient of management intensity, an additional five “unmanaged” reference patches of remnant savanna were identified on site in the spring of 2011. Treatments thin and burn, burn only, and unmanaged will be referred to as TB, BO, and UN, respectively, hereafter.

Pollinator communities

We sampled the bee community using a combination of bee bowls and active collecting. Bee bowls were 3.75 oz plastic cups (Solo Cup Company, Chicago, IL) presented in arrays of three, each of which was a different color to account for pollinator preferences and capture a broad representation of bee taxa (Figure 12A). Bowl colors were white (no paint), yellow and blue (Guerra Paint and Pigment, New York, NY after Droege 2012). Bowls within arrays were held apart equidistantly on a 25.4 cm green play tray (Fiskars Brands, Madison, WI) on which three empty cups were permanently attached with brads (The Paper Studio, Oklahoma City, OK). Colored bowls could then easily be set into and removed from the attached bowls for sampling purposes. A 1.5 cm hole in the center of each tray allowed it to be mounted on 1.5 cm diameter steel conduit 1.52 m long, and pounded into the ground 0.61 m. A 11 x 11 cm square of plywood with a comparable 1.5 cm hole in the center, was attached to the underside of the tray with carpet tacks for added stability (Figure 12 C). A 2.54 cm spring clamp attached to the steel conduit underneath the plant tray allowed it to be adjusted to the understory vegetation canopy height (Figure 12B). Eight sampling stations were positioned in two 2 x 2 grids 10 m apart in the center of each experimental unit (Figure 5). Adjacent stations within grids were placed 5 m apart, with grids oriented perpendicular to the slope of each plot. We randomly designated four of the eight positions for bee bowl sampling, with the other four positions used for other experimental purposes. Trays were placed upside-down at the bottom of poles when not in use.

We sampled pollinators every other week, from May through August in 2011 and 2012, for a total of six sampling periods per season. To control for advanced floral phenology in 2012, sampling was initiated when degree day accumulations matched those of the first sampling date in 2011 (Baskerville and Emin 1969). We used a threshold of 10° C to calculate the accumulation of degree days because this threshold largely coincides with developmental thresholds for stem-nesting hymenopteran species occurring in central North America (Forrest and Thomson 2011). A weather station ~40 km away (42°47’14” N, 84°45’75” W) maintained by Michigan State University’s Enviroweather online service (www.enviroweather.msu.edu) provided degree day information. Within a sampling week, we chose a sampling period based on the predicted temperature (highest), wind speed (lowest), and cloud cover (least) to ensure high pollinator activity. In each sampling period we deployed colored cups at all 60 pollinator stations (three treatments x five replications x four subsamples), filled all cups with soapy water of a dilution of ~ 15 ml scentless soap per 3.8 l of water. We randomly selected the initial plot for each sampling period before following a predetermined sequence of bowl deployment along plots. After 24 hrs we collected bowl contents in the same order. Contents were strained and placed in containers filled with a 70% ethanol solution. Bees (Hymenoptera: Apoidea: Anthophila) were later removed, dried (according to Droege 2012), pinned and identified to species where possible. J.G., R.J., and M.L. identified bees using Discover Life online identification matrix (www.discoverlife.org) and the metallic *Lasioglossum* dichotomous key (Gibbs 2011). Butterflies were identified according to Nielsen (1999) and Michigan State University's A. J. Cook Arthropod Collection.

To account for sampling bias of pollinator sampling with bee bowls, namely a failure to capture relatively large taxa, observational sampling of butterflies was also used. During each sampling period following bee bowl deployment, from 10 a.m.-4:30 p.m., we made observations from the center of a predetermined observation circle of 10 m in radius. Two circles were established in each experimental unit immediately adjacent to, but not overlapping with pollinator stations. For four minutes, two observers stood back to back in the center of each circle, noting each species, or otherwise notable characters, of butterflies that entered the circle, and attempted to capture these individuals. When captured, individuals were transferred to sealed jars containing hardened plaster-of-Paris and ethyl acetate, and were later pinned and identified as above. Bee taxa *Andrena roberstsonii*/*brevipalpus*, *Ceratina calcarata/dupla/mikmaqi,* *Hylaeus modestus*, *Osmia taurus/cornifrons*, and *Sphecodes sp.* 1-3, were held at St. Mary of the Woods College in St. Mary of the Woods, IN, for continued identification, while all other voucher specimens of all captured pollinator species were deposited at the Michigan State University A. J. Cook Arthropod Collection.

Pollinator predictive variables

In addition to floral resources, we predicted that vegetative cover and light would affect bee communities between treatments. As such, we measured light and cover each season to quantify these habitat variables according to the preceding methods (Chapter 2).

Statistical analysis

Pollinator communities

To test whether use of restoration treatments differed by butterfly families and bee nesting guilds, we used multiple likelihood ratio analyses. Due to the low resolution of our butterfly species observations, we performed analyses by taxonomic family, which then served as the individual taxonomic units used in analyses. For the family *Hesperiidae*, total observations were inadequate for analysis (n=13, n=10 respectively, across all treatments in 2011 and 2012), and thus were not tested. Bee species were grouped by nesting guild (i.e. soil, wood, cavity, pithy stem, hive, parasitic) according to Wolf and Ascher (2008) and where species information was not found, by Dr. Jason Gibbs (pers. comm.) (Table 6). Bee species belonging to cavity, hive, and parasitic nesting guilds were too few for likelihood ratio tests and were not tested. Stem nesting bee captures were large enough for analyses, but due to the absence of individuals in UN treatments in 2011, only frequencies between BO and TB were tested in that year. Frequencies of individual species belonging to the same guild were pooled by plot, so that every trapping effort would have the six potential aforementioned guilds to capture. We assessed overall differences in the frequency distributions of butterfly families and bee nesting guilds between treatments using G tests, and assessed the frequencies of individual families and nesting guilds among treatments relative to expected frequencies by random chance using chi square goodness of fit analyses. For the former, we totaled butterfly observations, generated proportions of family by treatment from this total, and compared proportions of families between treatments (PROC FREQ; SAS 9.3), which we repeated for bee nesting guilds. For the latter, we tested the null hypothesis that observations or samples of individuals from a family or guild between treatments were simply due to random chance (i.e. 33% observations within a family or guild in each of the three treatments).

Additional analyses compared bee captures between treatments with multiple metrics and statistical methods to draw more comprehensive inferences about the effect of restoration intensity on bee diversity. We calculated bee abundance, richness, and Shannon's H for each treatment by year combination. We calculated observed bee diversity metrics over the course of a season within treatment, but also calculated rarefied bee diversity metrics for statistical comparisons, as is recommended for comparative arthropod biodiversity studies (Buddle et al. 2005). Our calculation of rarefied bee diversity metrics used a relatively high number of "successful" trapping efforts (i.e. samples where at least one specimen was captured) common to all treatments during both years (in this case, 20). Rarefaction analyses using 1,000 permutations were used to generate a mean number of species encountered at that given sampling success (EcoSim professional, version 1.2d, Acquired Intelligence Inc.). We then conducted ANOVA on means and standard deviations of rarefied abundance, richness, and Shannon's H, using Tukey's

HSD for pairwise comparisons (SigmaPlot version 11.0.0.75 for Windows, Systat Software Inc.). We also generated bee sampling rarefaction curves displaying species accumulation against an increasing number of successful sampling efforts.

In addition to multiple diversity metrics, a complimentary analysis using individual species identities was used to compare bee communities. We used community similarities in a matrix generated by the Bray-Curtis index. Here, each replicate comparison across treatments is assigned a value that corresponds to the level of similarity (ranging from 0 to 1) between communities of the two. We then utilized non-metric multidimensional scaling (NMDS) to display all community comparisons visually (Primer 6, Version 6.1.13, Primer-E ltd.). This technique displays each community from treatment replicates as a point in two-dimensional space where the distance between points is proportional to their dissimilarity. When NMDS is visualized in three-dimensional space, many individual comparisons can be made with relatively high quantitative precision. When it is visualized in two-dimensions, the precision of each comparison is sacrificed to varying degrees. This deviation, or stress value, increases as the precision of multiple spatial comparisons are sacrificed. To perform statistical comparisons of significance on treatment communities, we used analysis of similarity (ANOSIM). This tests whether between treatment dissimilarities, which are converted to ranks, are greater than within treatment dissimilarities. Where global test statistics (R values) indicated significant differences, pairwise comparisons were conducted between treatments.

Pollinator predictive variables

We used Spearman rank correlations to understand relationships between treatments, time, biotic variables (i.e. bee and floral diversity), and abiotic variables (i.e. light and cover).

Plot averages of measured variables were sequentially ranked with increasing value, and simple linear regressions between all possible variable and treatment combinations were conducted on ranks rather than averages. Analyses were performed in R (R version 2.15.1 (Roasted Marshmallows)). Spearman’s rho values vary between -1 and 1, and higher absolute values of rho correspond to dependency between variables (which can be both negative and positive associations), while low absolute values of rho, indicate little or no dependency between variables. A significance level of alpha=0.05 was used for all analyses. Lines connecting variables and/or treatments in diagrams therefore represent significant dependencies, where line thickness corresponds to increasing Spearman’s rho values, and solid or dotted lines represent positive and negative relationships respectively (Figures 22-25). We categorized statistically significant Spearman’s rho values as weak, moderate, or strong by dividing the range of Spearman’s rho values generated in our analyses within resolution by three, and assigning strengths based on the value within this range. Due to the fact that biotic variables were measured biweekly, and abiotic variables were measured twice per season, analyses were performed at two different temporal resolutions. One analysis was performed at the biweekly resolution, using variables of bee richness, bee abundance, floral abundance, floral richness, Julian day, and all three treatments. The other analysis was performed at the seasonal resolution using the variables of light and vegetative cover (heights 0.5-2.5 m) in addition to the aforementioned variables, but excluding Julian day. Data for each year were analyzed separately.

Results

Pollinator communities

We observed a total number of 328 adult butterflies across two years and 11 sampling dates, representing 16 species and four taxonomic families (Table 4). We made relatively few observations of Hesperiidae (7.3%), while Papilionidae (32.3%), Nymphalidae (24.3%), and Satyridae (36.1%) made up the majority of the observations. G tests revealed that the distributions of these butterfly families were significantly different among treatments in both 2011 ($G=9.7$, $p=0.046$) and 2012 ($G=27.8$, $p=<0.001$). Chi square goodness of fit tests showed that distributions of individual butterfly families also varied among treatments. In both years, Papilionids showed a trend among treatments of increasing frequency of observations from BO to TB to UN (Figure 13), and were significantly different from random in both years (2011: $\chi^2=22.7$, $p=<0.001$, 2012: $\chi^2=13.8$, $p=0.001$ respectively). Nymphalid distributions among treatments were not different in 2011 ($\chi^2=0.5$, $p=0.788$) but differed in 2012 ($\chi^2=16.1$, $p=<0.001$) with proportionately more observations made in TB plots (Figure 14). Satyrid distributions among treatments were also not different in 2011 ($\chi^2=0.7$, $p=0.713$) but differed significantly in 2012 ($\chi^2=6.2$, $p=0.046$), with increasing frequency in UN plots (Figure 15).

We trapped a total of 532 adult bees across two years and 12 sampling dates, documented 57 species from five taxonomic families (Table 6). Halictidae dominated the bee bowl captures (84.9%), followed by Apidae (11.5%), Megachilidae (2.2%), Andrenidae (1.0%), and Colletidae (0.4%).

Bee rarefied sampling curves generally approached asymptotes, with slight variation in slope between treatments and years (Figure 16). Sampling curves from UN treatments are slightly less steep in 2011 than 2012, while BO and TB treatments show the opposite trend between years. Species accumulation per successful sampling effort appears to be greater in 2012 for all treatments, although these differences were slight. Overall, bee rarefaction sampling curves suggest that the intensity of our sampling effort was sufficient to characterize bee richness in our study.

Analysis of variance tests of bee abundance, richness, and Shannon's H among treatment by year combinations showed significance between years ($F_{5, 114}$=44.22, p=<0.001, $F_{5, 114}$=78.65, p=<0.001, $F_{5, 114}$=70.87, p=<.001, respectively). Bee diversity displayed fairly consistent patterns across treatments and years, where UN and BO treatments were generally statistically equivalent, and TB always had significantly greater bee diversity (Table 5). Treatments UN and BO were statistically equivalent in 2011 and 2012 in mean richness (q_5=0.595, p=0.998, q_5=1.069, p=0.974) and Shannon's H (q_5=3.873, p=0.076, q_5=3.149, p=0.159), while statistically equivalent abundances in 2011 (q_5=3.552, p=0.129), became significant in 2012 (q_5=5.607, p=0.002) due to an increase in bee abundance in BO. The TB treatments displayed greater bee abundance than both UN and BO in 2011 (q_5=8.948, p=<0.001, q_5=05.396, p=0.003) and 2012 (q_5=18.462, p=<0.001, q_5=12.855, p=<0.001), greater richness than both UN and BO in 2011 (q_5=12.468, p=<0.001, q_5=13.064, p=<0.001) and 2012 (q_5=20.022, p=<0.001, q_5=18.953, p=0.001), and greater Shannon's H than UN and BO in 2011 (q_5=11.192, p=<0.001, q_5=15.065, p=<0.001) and 2012 (q_5=15.116, p=<0.001, q_5=11.698, p=<0.001).

Although the NMDS configurations presented here (Figures 20 & 21) have relatively low stress values (0.12 in 2011, and 0.15 in 2012 respectively), it should be noted that our figures may lack fine-scale precision between individual points due to it's presentation in two, rather than three, dimensions. ANOSIM analyses on similarities showed that overall bee community comparisons among treatments were not statistically significant in 2011 at an alpha level of 0.05 (Global R=-0.029, p=0.646), but were significant in 2012 (Global R=0.272, p=0.020). This is visually evident (Figures 20 & 21) as over time, dissimilarities become greater between TB and both UN and BO. This was reflected in pairwise comparisons in 2012 where TB was significantly different from UN and BO (R=0.526, p=0.024, R=0.312, p=0.048), yet UN and BO were statistically equivalent (R=0.036, p=0.373).

G tests of the distribution of bee nesting guilds among treatments resulted in statistically significant differences in 2011 (G=17.6, p=0.002) and 2012 (G=13.0, p=0.011). There were generally increasing proportions of total bee abundance within nesting guilds from UN to BO to TB, although the magnitude of this trend was variable. The proportions of wood-nesters showed significantly different proportional representation across treatments in 2011 (χ^2=10.1, p=0.007) and 2012 (χ^2=15.8, p=<0.001), with an increasing proportion of individuals from UN to BO to TB (Figure 17). Soil nesters were also different among treatments in 2011 (χ^2=10.0, p=0.007) and 2012 (χ^2=38.5, p=<0.001), with an increase in proportion of bees from UN to BO to TB was observed (Figure 18). In 2012, TB treatments had a ~ 25% increase in the proportion of total soil nesting bees found there, BO treatments essentially remained constant, while UN treatments decreased by ~ 50%. Finally, stem-nesters showed a differential distribution across treatments in 2011 (χ^2=9.9, p=0.002) and 2012 (χ^2=32.1, p=<0.001). Although the general trend of increasing proportion of bees from UN to BO to TB was again seen, the magnitude of the difference was much more dramatic. In 2011, no stem-nesting bees were trapped in UN treatments, while TB treatments trapped nearly 90% of stem-nesters, with the remainder represented in BO treatments (Figure 19). In 2012, one stem-nesting bee was captured in UN treatments, but again, dramatically more stem-nesters were captured in TB treatments than either BO or UN. Although overall numbers were low, and too few to perform statistical tests, parasitic, cavity, and hive bee nesting guilds showed similar trends to soil, wood, and stem nesters. Parasitic nesters were absent from UN treatments, were highest in TB treatments (n=7), with fewer in B treatments (n=2). Cavity nesters were represented in UN and BO treatments by singletons, with the greatest number in TB treatments (n=6). Hive nesters (i.e. *Bombus spp.*) were represented by a singleton in UN treatments, a doubleton in BO treatments, with again, the greatest number in TB treatments (n=4).

Pollinator predictive variables

Spearman rank correlations showed that dependencies of variables and treatments vary in significance, magnitude, and sign between years and between different resolutions of sampling. Biweekly resolution of bee and floral variables in 2011 show that bee richness had a significant positive correlation of strong association with bee abundance (ρ=0.90), weak positive association with TB treatments (ρ=0.40), floral abundance (ρ=0.28), and floral richness (ρ=0.23), and weak negative association with UN treatments (ρ=-0.25) (Figure 22). Similarly, bee abundance has significant positive correlations of weak association with TB treatments (ρ=0.33), floral abundance (ρ=0.32), and Julian day (ρ=0.31), weak association with floral richness (ρ=0.28), and significant negative correlations with UN treatments of weak association (ρ=-0.25) (Figure 22).

In 2012 biweekly resolution, bee richness lacked significant floral relationships, and developed a weak negative association with Julian day (ρ=0.32) (Figure 23). Strong positive correlations with bee abundance (ρ=0.97), weak association with TB treatments (ρ=0.46), and weak negative association with UN treatments (ρ=0.45) were retained. Similarly, 2012 bee abundance displayed significant positive correlations of weak association with TB treatments (ρ=0.47), floral richness (ρ=0.22), and significant negative correlations of weak association with UN treatments (ρ=-0.44), and Julian day (ρ=-0.32) (Figure 23).

Rank correlations of yearlong average resolutions displayed somewhat different patterns than biweekly ones. In 2011, bee richness had significantly positive correlations of strong association with bee abundance (ρ=0.94), weak association with TB treatments (ρ=0.57), and significant negative correlations of weak association with vegetative cover at 0.5 m (ρ=-0.59), and 1.5 m (ρ=-0.53) (Figure 24). Bee abundance only had a significant relationship with bee richness. In 2012 the number of significant correlations between bee diversity and both treatments and abiotic variables increased fourfold (Figure 25). Bee richness had significant positive correlations of strong association with bee abundance (ρ=0.96), moderate association with floral abundance (ρ=0.79), floral richness (ρ=0.70), and TB treatments (ρ=0.77), weak association with light (ρ=0.63), and significant negative correlations of strong association with cover at levels 1.5-2.5 m (ρ=-0.85, ρ=-0.88, ρ=-0.88 respectively), moderate association with UN treatments (ρ=-0.75), and weak association with cover at 1.0 m (ρ=-0.67). Bee abundance had significant positive correlations of moderate association with TB treatments (ρ=0.80), floral abundance (ρ=0.77), floral richness (ρ=0.66), weak association with light (ρ=0.64), and significant negative correlations of moderate association with cover at levels 1.5-2.5 (ρ=-0.80, ρ=-0.81, ρ=-0.79 respectively), and weak associations with cover at 1.0 m (ρ=-0.60), and UN treatments (ρ=-0.75) (Figure 25).

Discussion

In our examination of pollinator communities during oak savanna restoration, we found that butterfly abundance varied across treatments depending on taxonomic family (Figures 13, 14, and 15). We also generally observed increases in bee diversity in response to restoration, which were consistently significant in TB treatments (Table 5). We saw a distinct bee community develop in TB treatments over time, while BO treatments remained similar to UN treatments (Figures 20 and 21). The functional groups set by bee nesting guilds were consistently affected by treatment over time, with particular guilds displaying individual treatment patterns (Figures 17, 18, and 19). Bee diversity co-varied with different habitat variables depending on resolution of sampling (i.e. yearlong averages or biweekly), and year (Figures 22, 23, 24, and 25). Furthermore, BO treatments did not produce similar shifts in bee diversity or community composition, reflected in the lack of significant correlations with biotic variables of multiple temporal resolutions.

Pollinator communities

We found that butterfly families responded variably to restoration activities. Nymphalids showed no response to treatment in 2011, yet were more abundant in 2012 in TB treatments than UN and BO (Figure 14). In contrast, Satyrids showed no response to treatment in 2011, but displayed greater mean abundances in UN treatments than either BO or TB in 2012 (Figure 15). Similarly, Papilionids were more abundant in UN treatments than either BO or TB in during both

2011 and 2012 (Figure 13). This differential response to restoration treatments could be due the effects of management on key host plant groups of each taxa (Table 4), rather than just the floral resources sampled in this study. For example, all Papilionid species documented in this study have host plant associations with woody mesophytic species, which are not only sensitive to fire, but also targeted for removal in our restoration treatments. Decreased host plant vigor or abundance in restoration plots could cause Papilionidae species to preferentially utilize unmanaged areas where preferred host plants are still abundant. Alternatively, negatively affected butterfly taxa could have fire-sensitive life stages near the understory vegetation during early spring, when burns are conducted at MacCready and therefore favor unburned UN treatments.

Nymphalidae, however, showed increased use of restoration treatments, particularly TB treatments, relative to UN treatments. Although species in this family use both woody and herbaceous host plants (Table 4), the increased development of an herbaceous understory in TB treatments could attract these individuals to oviposit and/or utilize increased floral resources, which have been shown to alter distributions of butterflies (Steffan-Dewenter & Tscharntke 1997). For example, *Speyeria cybele cybele* was our most commonly observed Nymphalid (unpublished data), and females prefer to oviposit on *Viola spp.* (Table 4), an herbaceous plant taxa found in the understory. Alternatively, this group may be responding to increasing light in TB treatments (Chapter 2), suggested as a mechanism of response of the butterfly community in ponderosa pine (*Pinus ponderosa*) restoration (Waltz and Covington 2004). The authors observed an increase in abundance and richness of butterflies in restoration plots that were thinned and burned, which differed from control plots in light intensity, but not the understory floral community. This hypothesis is partially supported by our observations of positive associations of floral resources and light associated with TB treatments (Figure 25), where Nymphalidae were most often observed. Understory host plant abundance and light availability likely covary as well, and Nymphalid butterflies could be responding to either or both of these factors. In any case, the differential responses among butterfly families highlights the inherent tradeoff in using restoration to shift an ecosystem from one type toward another. Where overstory trees and woody vegetation not historically associated with oak savannas are targeted during restoration, obligate fauna of that vegetation may be expected to respond negatively. Although we believe the benefits to conservation and biodiversity through oak savanna restoration outweigh reductions in these common and widespread species, butterfly diversity could be maximized on site by maintaining unburned areas where sensitive species may find refugia, and Papilionids may find mesophytic woody species for oviposition.

In general, the composition of the bee community that we documented in remnant oak savanna plots at MacCready Reserve shares many commonalities with bee surveys of forested areas (Giles and Ascher 2006) and of other Midwestern locales (Wolf and Ascher 2008, Grundel et al. 2011). We documented only five species of wood-nesting bees (8.8% total species), yet these species made up 51.5% of the total abundance of our sampled bee community (Table 6). This dominance of wood nesters reflects the abundance of rotting wood on the site (Giles and Ascher 2006), which includes large cut stumps and logs from past silvicultural activities. Although wood nesting resources were fairly equally distributed among treatments at the time of sampling, we found significantly different proportions of total wood nesting bees among treatments (Figure 17), possibly due to an increasingly favorable combination of nesting, light, and floral resources in BO and TB treatments. Our future and final stage of thinning of mesophytic trees (≥7” DBH) in TB treatments is likely to continue to provide future nesting sites in the form of cut stumps and downed wood, while BO treatments may continue to provide wood nesting sites through standing fire-killed mesophytic trees.

In contrast to the low species richness of wood nesters, we documented 27 species of soil nesters (47.4% total species), comprising 34.6% of total bee abundance. We believe this high richness and abundance of soil nesters represents a marked response to the initiation of our burning regimes, whereby soil is exposed in BO and TB treatments. However, a thick litter layer remains in UN treatments, which may be prohibitive to the nesting activities of small soil nesting bee species. This was reflected by our significant chi-square goodness of fit tests, particularly in 2012. Although both treatments were burned, the proportion of soil nesters was greater in TB than BO treatments (Figure 18), suggesting a more favorable combination of resources contributing to soil nesting bee populations. Continual burning should ensure this nesting resource is maintained, although the abundance of bare ground may be reduced as perennial understory vegetation continues to establish.

Four species of stem nesting bees were represented in our samples, comprising 9.4% of the total bee catch. We expect that this group is nesting in herbaceous and pithy-woody plant stems (e.g. *Rubus* canes) found in the understory. The low numbers of stem nesting bees in UN treatments, in contrast to a large proportion of total stem nesting bee captures in TB treatments, and minor representation in BO treatments (Figure 19), are a reflection of understory vegetation development. Understory vegetation in our study strongly paralleled changes in light (Figure 6, 9, and 10), and a gradient of understory development is reflected in 2012 by the negative association, lack of association, and positive association with light of UN, BO, and TB treatments, respectively (Figure 25). Continued understory development resulting from our restoration treatments should further facilitate the nesting and foraging requirements of this group as well.

Hive nesters (e.g. *Bombus spp.*) and cavity nesters (e.g. *Megachile spp.*) were scarcely represented in our sampling (1.32% and 1.5% of total bee catch respectively, see Table 6). This is likely due the sampling bias of bee bowl trapping, as these species are strong fliers and not easily trapped using this technique (Giles and Ascher 2006). Although parasitic-nesting bees were too few to draw statistical inferences from, it is interesting that they were most abundant in TB, least abundant in BO, and absent in UN treatments, reflecting the general trend of bee diversity across treatments. However, given their dependency on sufficient host populations to support their own, cleptoparasitic bees may be thought of as a higher trophic level, and have been proposed as an indicator group for bee communities (Sheffield et al. 2013). Furthermore, this diverse group is sensitive to environmental change, and its presence in restoration plots further suggests that robust bee communities are establishing there. Overall, we predict that wood, soil, and stem nesting groups will also benefit from our developing oak savanna restorations as more nesting sites become available through overstory thinning, continued burning, and the continued development of the herbaceous understory plant community.

The bee community we documented at MacCready Reserve was dominated by generalists (polylectic), and only three species were considered floral specialists (Table 6). Generalist plant-pollinator relationships dominate in natural pollinator communities as compared to specialist relationships (Memmott 1999). The presence of generalists in a plant-pollinator network increases connectance, which can increase robustness of a community to future species losses (Hegland et al. 2010), and thus maintain function. Thus, pollination in general may not be affected by this relative lack of specialists. The specialists from our study were *Andrena distans*, a floral specialist on *Geranium maculatum*, *Lasioglossum nelumbonis*, a specialist on Nympheales (water lilies/lotuses), and *Melissodes desponsa*, a specialist on *Cirsium spp*. These plant groups are all common and widespread in the area of MacCready Reserve, and thus the specialist plant-pollinator relationships suggested by our three bee species could be expected to be fairly common in the surrounding landscape. If floral diversity of the oak savanna understory continues to increase as we anticipate with progressing restoration, the subsequent development of specialist relationships with these new forb species will depend on the dispersal ability of specialist bees and the abundance of the specialist floral resource in the surrounding landscape. *Lasioglossum nelumbonis* is a specialist on Nympheales pollen, which actively grow in aquatic habitats surrounding upland oak savanna areas on the property. The presence of this floral specialist, albeit in fairly low quantities (0.6% total) in traps in our savanna plots suggests that these individuals are either using upland savanna areas to disperse from one patch of floral resources to another, or for nesting.

Although we do not have pretreatment bee community data, if we assume that prior to restoration, bee communities resembled those of UN treatments, we could conclude that our TB restoration treatment has successfully and rapidly increased bee diversity in oak savanna remnants at MacCready Reserve (Table 5). This result was consistent across all three of the diversity metrics we calculated in both years. This finding is partially consistent with the findings of Grundel et al. (2011) where bee abundance was positively associated with fire frequency, and negatively associated with overstory tree basal area. They found that both bee richness and abundance were significantly higher in oak savannas than oak forests along the same gradient of canopy cover. Only in one measured metric of the bee community during one year of our study, bee abundance in 2012 (Table 5), did BO treatments significantly shift the bee community. Using increased biodiversity as a restoration goal (Ruiz-Jaen and Aide 2005), we suggest that in the short-term, TB restoration treatments have achieved restoration success, while BO restoration treatments have achieved only partial success. A greater perturbation of habitat through restoration may then be necessary to result in significant shifts in bee communities, which we failed to see in BO treatments.

A failure to shift biological communities from low intensity restoration has been observed by multiple researchers monitoring arthropod communities in the context of a gradient of restoration intensity. Ryndock et al. (2012) examined spider communities in the context of oak woodland restoration in Mississippi across multiple restoration intensities (thinning + one burn, thinning + three burns), in addition to old field and fire-suppressed forest controls. The high intensity restoration method achieved significantly higher spider richness, while the lower intensity restoration method failed to reach this metric. The authors suggest that low-intensity restoration methods failed to reduce canopy cover enough to increase light levels, trigger understory plant growth, and lead to the increased habitat structure that is important to spider diversity. Similarly, Campbell et al. (2007) sampled flower-visiting insects in North Carolina oak-hickory forests where fuel reductions were being conducted. Two years after initiation of management, these researchers examined two low intensity methods (thinning, burning), and one high intensity method (thinning + burning) relative to unmanaged controls. While the high intensity fuel-reduction method led to significantly higher flower-visiting insect diversity, neither low intensity method achieved this difference. Furthermore, the authors found that increased understory plant cover was associated with increasing number of floral visitors, while woody basal area was negatively associated with number of visitors. These studies suggest that specific restoration methodology is less important than achieving the goal of woody vegetation reduction and increasing light availability. This then should result in a robust herbaceous understory that promotes pollinator diversity. However, most of these studies, including our own, are short term and thus inferences regarding restoration method on long-term effects on arthropod diversity are limited. We anticipate that BO treatments will display increased effects on floral resources, cover, and light availability as time and restoration activities progress, and in this way, perhaps BO treatments will approach the bee diversity we observed in TB treatments in the long-term.

We did not directly measure pollination in our three restoration treatments, but rather used pollinator diversity metrics as proxies, and thus we cannot say that the function of pollination was enhanced through our restoration activities (however, see Appendix B). There is substantial evidence from the literature however, that increased pollinator functional and species richness leads to enhanced pollination (Albrecht et al 2007, Winfree and Kremen 2009, Albrecht et al. 2012). This enhanced function could be achieved through species redundancy, where multiple pollinator species perform the same pollination function, so that in the case of species extinction or reduction, function is maintained by another species of pollinator. At MacCready Reserve, the establishment and maintenance of a diverse understory of flowering plants is desired, and restoration methodologies that most effectively enhance bee diversity could help achieve this functional goal. Proctor et al. (2012) studied pollinator and plant communities under canopy gaps in Ontario forests created by silvicultural methods that are somewhat similar to those employed in our study. The creation of canopy gaps in this case not only resulted in increased pollinator abundance, but also led to an increased proportion of fertilized ovules of an understory forb, *Claytonia caroliniana*, relative to forest tracts with no canopy gaps. Enhanced pollination in one of many understory forbs may not be representative of the entire community of flowering plants, but its occurrence represents an important example of a direct measure of increased pollination function following management activities that increase pollinator diversity.

Although we have demonstrated that multiple metrics of the bee community are different in TB restoration treatments relative to BO and UN (Table 5), these metrics do not take species identity into account. However, our ANOSIM analyses (Figures 20 and 21), do take species identity into account, and show that our diversity findings are robust. Thin and burn treatments not only increase bee diversity, but also show a distinct bee community not shared with BO and UN treatments, which have statistically equivalent bee communities (Figures 21). This finding may be due to the fact that we sampled bee communities in early stages of the restoration, when BO treatments still share many attributes with UN treatments. Only one low intensity surface fire had been conducted in BO treatments prior to sampling of bee communities, and it is likely that the time or ecosystem perturbation that has taken place was not yet sufficient to shift community composition. Although not statistically significant, we did demonstrate increases in the mean of almost all bee community metrics and years in BO relative to UN treatments (Table 5), and gradual segregation of bee communities between the two treatments in 2012 (Figures 20 & 21). We therefore anticipate that with time and continued restoration activities, BO treatments could display increased diversity and a distinct bee community. We do not know, however, if differences between BO and TB bee communities will be conserved over time, potentially signaling different restoration trajectories resulting from different restoration methods, or if they will converge.

Pollinator predictive variables

We interpret the different trends between Spearman rank correlations of biweekly sampling and yearlong averages in part as the differences between short and long-term predictors of bee diversity respectively. We also acknowledge that correlations between variables are not causative, and as such only allow us make associations, and subsequently propose mechanisms of change. Both biweekly and yearlong analyses demonstrated different variable associations over time, as well as differing magnitudes of these associations (Figures 22, 23, 24, and 25). These differences could be the result of both the ecological changes caused by restoration, and/or annual variation caused either by stochasticity and environmental conditions. We suggest both factors are influencing bee diversity in our study. Our 2011 biweekly sampling shows that floral resources (richness and abundance), linked TB restoration treatments (Figure 22), could be important determinants of bee diversity in the short term. Bee abundance also increased throughout our 2011 sampling period, as suggested by the significant positive association with Julian day. We suspect that this change in association over time is due to variation in environmental conditions between years. In 2011 the MacCready Reserve region received 48.99 cm of rainfall between June 1st-August 17th, a period which precedes our entire sampling period by a week, through the end of sampling. In 2012 however, there was a dearth of rainfall, where only 10.84 cm of rainfall fell between May 16th-August 1st during the same length of time (www.enviroweather.msu.edu, Leslie, Michigan station). We speculate then, that this change in relationship between Julian day and bee diversity is due to the droughty sampling period, and may have also contributed to the significant and non-significant decreases in mean bee abundance between years in UN and BO treatments respectively (Table 5).

Interestingly, our Spearman rank correlations using yearlong averages and including abiotic variables show that floral richness and floral abundance are not associated with bee richness in abundance in 2011 (Figure 24), but are associated in 2012 (Figure 25), the opposite trend of the biweekly analysis. This analysis also shows that bee diversity is negatively associated with vegetative cover at 0.5 m and 1.5 m, and positively associated with TB treatments. Perhaps then, in 2011, bees near our research plots were strongly attracted to open areas with little cover (TB treatments), where their week-to-week fluctuations are dictated by relatively low but temporally variable floral resources. In 2012 we observed significant and dramatic increases in floral resources, particularly across TB treatments (Figure 9, 10, Table 2). We speculate that in 2012, bee catch was greater in plots where floral resources were most abundant, but floral abundance was consistent enough across the overall sampling period that it did not predict short-term variance in bee abundance or richness. We continued woody plant removal in the fall of 2011, thereby reducing cover measured in 2012, as suggested by the development of significant negative correlations between cover and TB treatments from 2011 to 2012 (Figure 7 and 8). It appears that this reduction in cover covaries with light, which bees may have responded to, and which is not significantly correlated with floral resources (Figure 25). Furthermore, in 2011 both types of analyses show significant positive associations between bee diversity and TB treatments, and significant negative associations with UN treatments. The strength of each of these significant positive and negative relationships increased in 2012. This increase in correlation between bee diversity and treatment in both UN and TB treatments over time reflects the increasing distinction in conditions between these two treatments, reflected by the bee community. Consistently significant and positive associations between bee diversity and

TB, non-significant associations with BO, significant negative associations with UN treatments, further support the trend of increasing bee diversity along a gradient of restoration intensity.

Conclusion

Restoration of degraded ecosystems is often driven by goals to develop structure, conditions, and biological communities found in the high quality reference ecosystem emulated by restoration activities. Given that high quality oak savannas were not available, we do not know if pollinator communities developing in the context of our restoration treatments have achieved or are approaching a restored state. We provide strong evidence however, that we have increased bee diversity, and developed distinct bee communities, utilizing our high-intensity TB restoration method. Low-intensity BO restoration treatments consistently failed to achieve significant shifts in their pollinator community in the short-term, but given more time, these shifts may still be observed. Great importance is placed on native understory forb species in oak savanna restoration. The obligate connection between forb and pollinator communities, and the benefit to pollination function from pollinator diversity, suggests that TB treatments may achieve a short-term enhanced pollination function and benefit this plant group relative to BO treatments. Future research could investigate realized seed set of native understory forbs as it pertains to pollinator diversity in the context of savanna restoration. We also saw strong effects of year in our examination of bee communities and habitat covariates, likely due to a combination of progressing effects of restoration, and annual variation in environmental conditions. Our results also suggest that oak savanna restoration in the form of thin and burn methodology, is generally beneficial to bee communities through enhanced floral and nesting resources. With the exception of decreased use by cosmopolitan butterfly species, we failed to observe adverse affects from an intense restoration method on pollinator communities. Therefore, we recommend for use of this restoration method where financial, logistical, and ecological constraints allow the restoration community to do so.

Implications for practice

- Currently used “thin and burn” oak savanna restoration techniques can rapidly increase bee diversity, although affects on butterfly communities are mixed, depending on taxonomic family and potentially, host plant association
- Mechanical thinning, burning, and development of understory vegetation in oak savanna restoration may directly affect nesting resources of wood nesting, soil nesting, and stem nesting bees
- “Burn only” oak savanna restoration practices provide minimal benefit for pollinator diversity and may require repeated burning to meet this goal
- In order to maximize heterogeneity of structure, plant and pollinator communities, land managers should use a combination of compatible oak savanna restoration methods within the same site

Acknowledgements

We would like to thank I. Lane and other members of the Landis Lab for invaluable field assistance. G. Kowalewski, Mickey Trimmer, Brett Kuipers, Cody Johnson, James Curtis, Robert Kipp, and John Cumbers with MSU Forestry, conducted woody vegetation reductions, conducted, and provide burn assistance. R. Zuniga-Villegas and D. Tison from the Nature Conservancy, D. Mindell, M. Demmon, L. Root, C. Tinney, and S. Zellers from PlantWise, LLC, and J. McGowan-Stinski for also leading and assisting with burns. B. Carson provided valuable input on the review of this manuscript. Research funding was provided by the American Recovery and Reinvestment Act through the Great Lakes Bioenergy Research Center, and by the MSU MacCready Endowment.

APPENDICES

APPENDIX A

CHAPTER 1 TABLES AND FIGURES

Table 1. Savanna communities defined by their moisture conditions. Adapted from O'Connor (2006).

	Wetlands		*Uplands*	
Moisture	**Wet-mesic**	**Mesic**	**Dry-mesic**	**Dry**
Savanna type	Lakeplain oak openings	Bur oak plains	Oak openings Lakeplain oak openings	Oak barrens Oak-pine barrens Pine barrens

Figure 1A. Distribution of prairie and savanna communities in Michigan interpreted from the General Land Office Survey, conducted from 1816-1856. Map provided with permission from Michigan Natural Features Inventory. For interpretation of the references to color in this and all other figures, the reader is referred to the electronic version of this thesis.

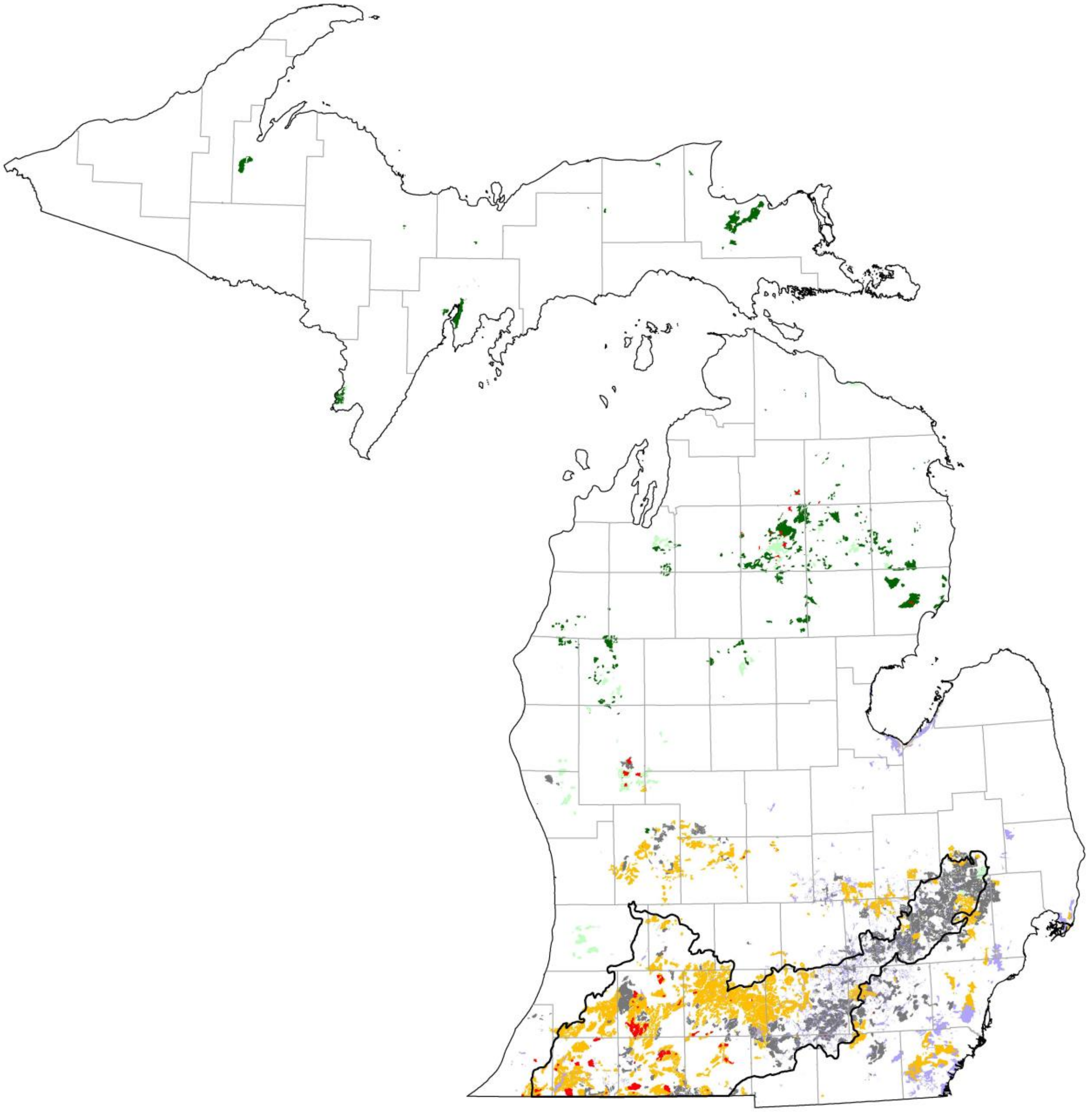
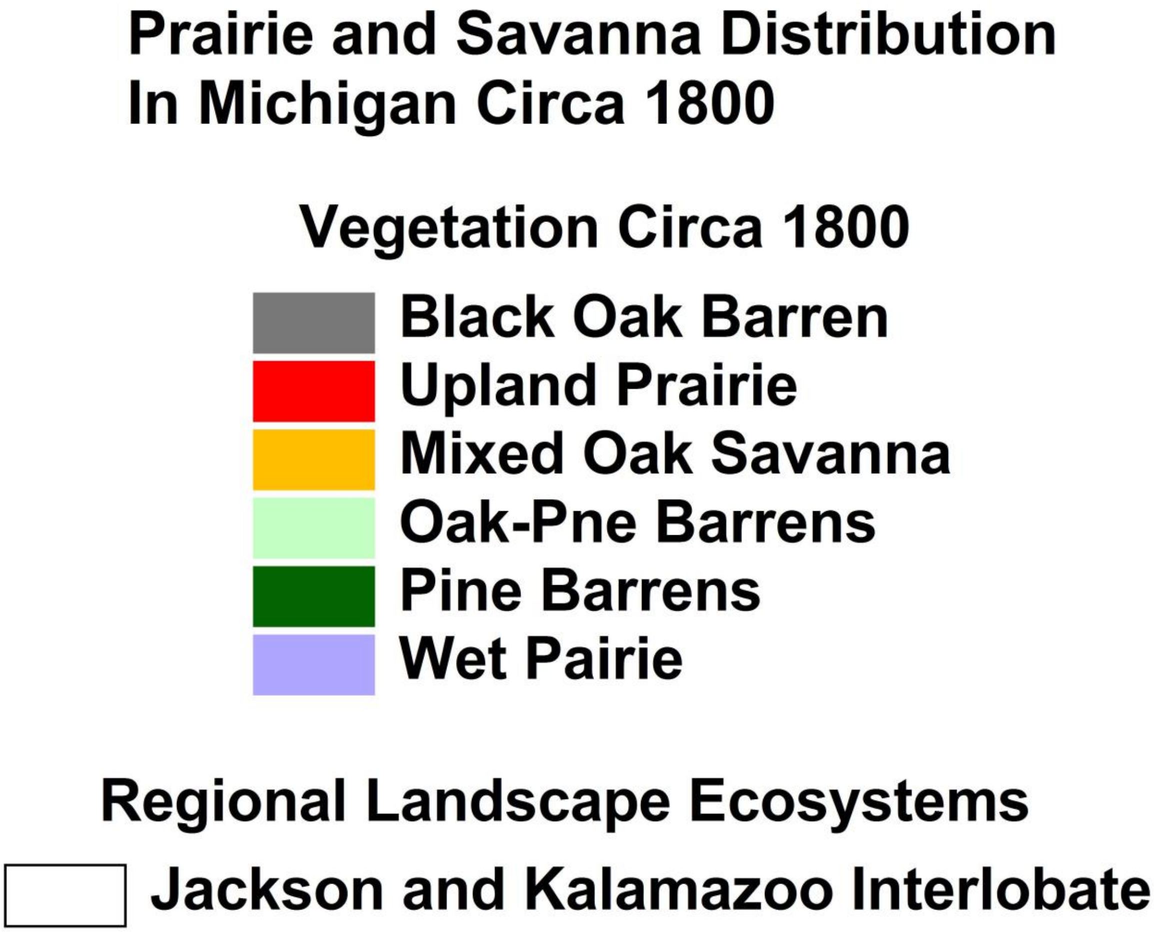


Figure 1B. Legend of Michigan prairie and savanna community types circa 1816-1856. Legend provided with permission from Michigan Natural Features Inventory.



Prairie and Savanna Distribution
In Michigan Circa 1800

Vegetation Circa 1800

- ◼ Black Oak Barren
- 🟥 Upland Prairie
- 🟧 Mixed Oak Savanna
- 🟩 Oak-Pne Barrens
- 🟩 Pine Barrens
- 🟪 Wet Pairie

Regional Landscape Ecosystems

- ☐ Jackson and Kalamazoo Interlobate

Figure 2. Illustration of white oak (*Quercus alba*) grub. After repeated burnings the central taproot has rotted away and sprouting continues to occur at the margins of the calloused woody plate (Beal 2008).

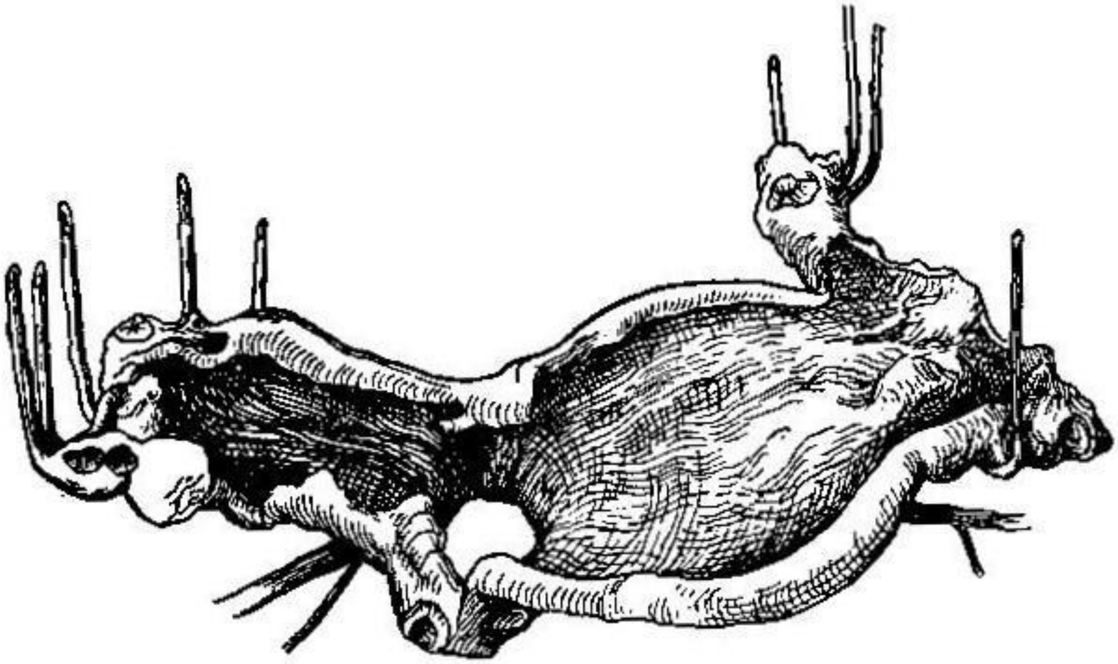


Figure 3A. Presettlement vegetation map of Kalamazoo County, Michigan interpreted from General Land Office surveyor data (1816-1856). Note the presence of several savanna types (Mixed-Oak and Oak Barrens) as well as the Prairie-Forest gradient (Grassland, Mixed-Oak Savanna, Oak-Hickory Forest) present as a community mosaic. Map provided with permission from Michigan Natural Features Inventory.

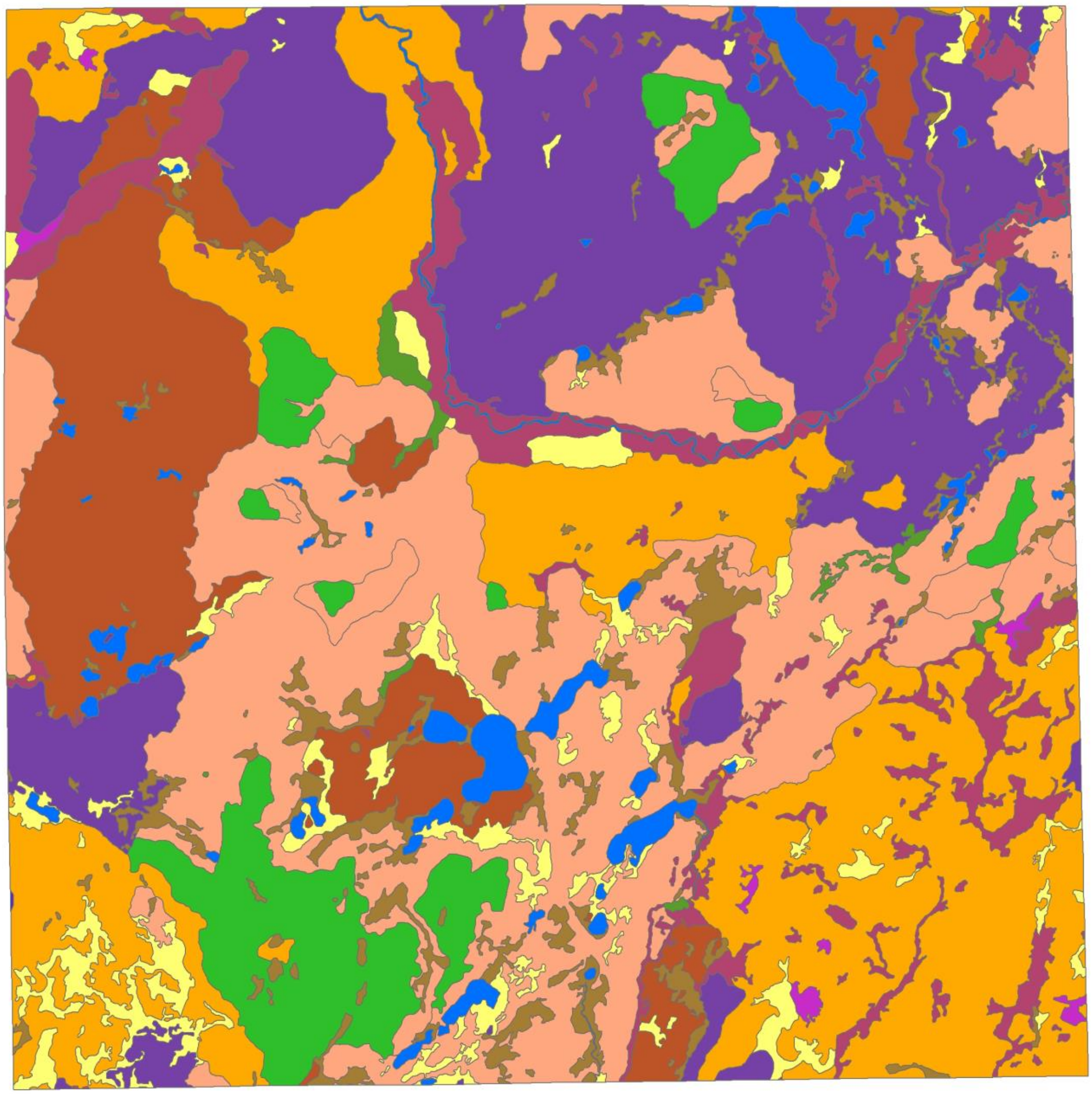


Figure 3B. Legend of Kalamazoo County vegetation types circa 1816-1856. Legend provided with permission from Michigan Natural Features Inventory.

Kalamazoo County
Circa 1800 Vegetation

- 🟧 BEECH-SUGAR MAPLE FOREST
- 🟪 BLACK ASH SWAMP
- 🟫 BLACK OAK BARREN
- 🟩 GRASSLAND
- 🟨 MIXED CONIFER SWAMP
- 🟥 MIXED HARDWOOD SWAMP
- 🟪 MIXED OAK FOREST
- 🟧 MIXED OAK SAVANNA
- 🟦 MUSKEG/BOG
- 🟪 OAK-HICKORY FOREST
- 🟫 SHRUB SWAMP/EMERGENT MARSH
- 🟩 WET PRAIRIE
- 🟦 LAKE/RIVER

APPENDIX B

CHAPTER 2 TABLES AND FIGURES

Table 2. Observed and rarefied flowering forb diversity metrics and conservatism rankings for all treatment by year combinations. Samples yielding flowering forb observations were subjected to rarefaction analysis with the rarefaction index set to 18 samples. Observed means are the non-rarefied diversity metrics based on the total number of flowering forbs of each species observed in a sampling year in each treatment. One-way ANOVA was conducted on all rarefied metrics of diversity and conservatism, using Tukey’s HSD for mean separation at α=0.05.

		Richness				Shannon's H				CoC		
	Sample total	Obs.	Rar.	SD		Obs.	Rar.	SD		Obs.	SD	
Unmanaged 2011	19	13	12.80	0.40	B	1.71	1.69	0.06	B	3.89	1.62	A
Burn only 2011	36	20	14.00	2.47	B	2.07	1.92	0.20	B	3.80	1.73	A
Thin and burn 2011	40	32	21.16	3.05	AB	2.22	1.99	0.19	AB	3.45	1.50	AB
Unmanaged 2012	28	20	16.07	1.70	B	2.33	2.20	0.12	AB	1.97	1.01	BC
Burn only 2012	59	25	16.96	1.87	B	2.15	1.96	0.23	AB	2.87	1.22	CD
Thin and burn 2012	57	41	28.54	2.95	A	2.85	2.61	0.13	A	2.56	1.10	D

Table 3. Flowering forb species and percent occupation of floral tally circles at MacCready Reserve, 62 total. CoC=Coefficient of Conservatism, *=exotic species. ** *Rubus sp.* refers to both *R. flagellaris* Willd. and *R. pubescens* Raf. which were not separated in the field and were combined in analysis.

				% Occupation			
Family	**Genus species**	**Common Name**	**CoC**	**Total**	**UN**	**B**	**TB**
Rosaceae	*Agrimonia gryposepala* Wallr.	Tall agrimony	2	0.23	0.00	0.30	0.40
Brassicaceae	*Alliaria petiolata* (M. Bieb.) Cavara & Grande	Garlic mustard	*	0.10	0.10	0.00	0.20
Apocynaceae	*Apocynum androsaemifolium* L.	Spreading dogbane	3	0.03	0.00	0.00	0.10
Apocynaceae	*Apocynum cannabinum* L.	Indian-hemp	3	0.03	0.00	0.00	0.10
Apocynaceae	*Asclepias exaltata* L.	Poke milkweed	6	0.03	0.00	0.10	0.00
Brassicaceae	*Boechera canadensis* (L.) Al-Shehbaz	Sickle-pod	7	0.23	0.10	0.20	0.40
Urticaceae	*Boehmeria cylindrica* (L.) Sw.	False nettle	5	0.03	0.00	0.10	0.00
Rhamnaceae	*Ceanothus americanus* L.	New Jersey tea	8	0.03	0.00	0.10	0.00
Amaranthaceae	*Chenopodium simplex* Raf.	Maple-leaved goosefoot	1	0.03	0.00	0.00	0.10
Onagraceae	*Circaea canadensis* (L.) Hill	Enchanter's-nightshade	2	0.67	0.40	0.70	0.80
Asteraceae	*Cirsium vulgare* (Savi) Ten.	Bull thistle	*	0.03	0.00	0.00	0.10
Lamiaceae	*Collinsonia canadensis* L.	Stoneroot	8	0.07	0.00	0.20	0.00
Asteraceae	*Conyza canadensis* (L.) Cronq.	Horseweed	0	0.23	0.00	0.10	0.60
Elaeagnaceae	*Elaeagnus umbellata* Thunb.	Autumn-olive	*	0.03	0.10	0.00	0.00
Asteraceae	*Erechtites hieraciifolius* (L.) Raf.	Fireweed	2	0.10	0.00	0.10	0.20
Asteraceae	*Erigeron philadelphicus* L.	Common fleabane	2	0.20	0.00	0.10	0.50
Asteraceae	*Eurybia macrophylla* (L.) Cass.	Large-leaved aster	4	0.17	0.00	0.20	0.30
Asteraceae	*Eupatorium perfoliatum* L.	Boneset	4	0.03	0.00	0.00	0.10
Rubiaceae	*Galium aparine* L.	Cleavers	0	0.43	0.10	0.50	0.70
Rubiaceae	*Galium boreale* L.	Northern bedstraw	3	0.10	0.00	0.10	0.20
Rubiaceae	*Galium circaezans* Michx.	White wild licorice	4	0.97	0.90	1.00	1.00
Rubiaceae	*Galium concinnum* Torr. & A. Gray	Shining bedstraw	5	0.03	0.10	0.00	0.00
Geraniaceae	*Geranium maculatum* L.	Wild geranium	4	0.20	0.10	0.10	0.40

Table 3 (cont'd).

Family	Genus species	Common Name	CoC	% Occupation Total	UN	B	TB
Rosaceae	*Geum canadense* Jacq.	White avens	1	0.60	0.30	0.70	0.80
Boraginaceae	*Hackelia virginiana* (L.) I. M. Johnst.	Beggar's lice	1	0.60	0.10	0.80	0.90
Asteraceae	*Hieracium caespitosum* Dumort.	King devil	*	0.03	0.00	0.10	0.00
Fabaceae	*Hylodesmum glutinosum* (Willd.) H. Ohashi & R. R. Mill	Clustered-leaved tick-trefoil	5	0.67	0.40	0.80	0.80
Fabaceae	*Hylodesmum nudiflorum* (L.) H. Ohashi & R. R. Mill	Naked tick-trefoil	7	0.70	0.20	0.90	1.00
Asteraceae	*Krigia biflora* (Walter) S. F. Blake	False dandelion	5	0.30	0.10	0.00	0.20
Asteraceae	*Lactuca canadensis* L.	Wild lettuce	2	0.03	0.00	0.10	0.00
Lamiaceae	*Leonurus cardiaca* L.	Motherwort	*	0.20	0.10	0.20	0.30
Campanulaceae	*Lobelia inflata* L.	Indian tobacco	0	0.07	0.00	0.00	0.20
Campanulaceae	*Lobelia spicata Lam.*	Pale spiked lobelia	4	0.03	0.00	0.00	0.10
Myrsinaceae	*Lysimachia quadrifolia* L.	Whorled loosestrife	8	0.07	0.00	0.10	0.10
Convallariaceae	*Maianthemum racemosum* (L.) Link	False spikenard	5	0.03	0.00	0.00	0.10
Fabaceae	*Melilotus albus* Medik.	White sweet-clover	*	0.03	0.00	0.00	0.10
Fabaceae	*Monarda fistulosa* L.	Wild-bergamot	2	0.03	0.00	0.00	0.10
Apiaceae	*Osmorhiza claytonii* (Michx.) C. B. Clarke	Hairy sweet-cicely	4	0.03	0.10	0.00	0.00
Oxalidaceae	*Oxalis stricta* L.	Yellow wood-sorrel	0	0.10	0.00	0.00	0.30
Asteraceae	*Packera aurea* (L.) À. Löve & D. Löve	Golden ragwort	5	0.03	0.00	0.00	0.10
Caryophyllaceae	*Paronychia canadensis* (L.) Alph. Wood	Tall forked chickweed	8	0.10	0.00	0.10	0.20
Polygonaceae	*Persicaria virginiana* (L.) Gaertn.	Jumpseed	4	0.37	0.40	0.30	0.40
Phrymaceae	*Phryma leptostachya* L.	Lopseed	4	0.50	0.10	0.90	0.50
Phytolaccaceae	*Phytolacca americana* L.	Pokeweed	2	0.30	0.20	0.30	0.40

Table 3 (cont'd).

Family	Genus species	Common Name	CoC	% Occupation Total	UN	B	TB
Berberidaceae	*Podophyllum peltatum* L.	May-apple	3	0.03	0.00	0.00	0.10
Rosaceae	*Potentilla norvegica* L.	Rough cinquefoil	0	0.03	0.00	0.00	0.10
Rosaceae	*Potentilla simplex* Michx.	Common cinquefoil	2	0.70	0.50	0.90	0.70
Lamiaceae	*Prunella vulgaris* L.	Self-heal	0	0.10	0.10	0.10	0.10
Rosaceae	*Rubus allegheniensis* Porter	Common Blackberry	1	0.10	0.10	0.00	0.20
Rosaceae	****** *Rubus sp.*	Raspberry	2.5	0.70	0.30	1.00	0.80
Asteraceae	*Rudbeckia hirta* L.	Black-eyed Susan	1	0.03	0.10	0.00	0.00
Caryophyllaceae	*Silene latifolia* Poir.	White campion	*	0.03	0.00	0.00	0.10
Solanaceae	*Solanum ptychanthum* Dunal	Black nightshade	1	0.20	0.00	0.20	0.40
Brassicaceae	*Berteroa incana (L.) DC.*	Hoary alyssum	*	0.03	0.00	0.00	0.10
Apiaceae	*Taenidia integerrima* (L.) Drude	Yellow-pimpernel	8	0.03	0.10	0.00	0.00
Apiaceae	*Torilis japonica* (Houtt.) DC.	Japanese hedge-parsley	*	0.23	0.20	0.00	0.50
Commelinaceae	*Tradescantia ohiensis* Raf.	Ohio spiderwort	5	0.17	0.00	0.10	0.40
Campanulaceae	*Triodanis perfoliata* (L.) Nieuwl.	Venus's looking-glass	6	0.07	0.00	0.00	0.20
Scrophulariaceae	*Verbascum thapsus* L.	Common mullein	*	0.10	0.00	0.00	0.30
Verbenaceae	*Verbena urticifolia* L.	White vervain	4	0.20	0.00	0.20	0.40

Figure 4A. 1938 aerial photo of MacCready Reserve. Experimental plots outlined in yellow and labeled with treatment type UN (unmanaged), B (burn only), or TB (thin and burn) (pink lines show public trail system). Compare the relatively scattered canopy of 1938 to the closed canopy in 2005 (Figure 4B).

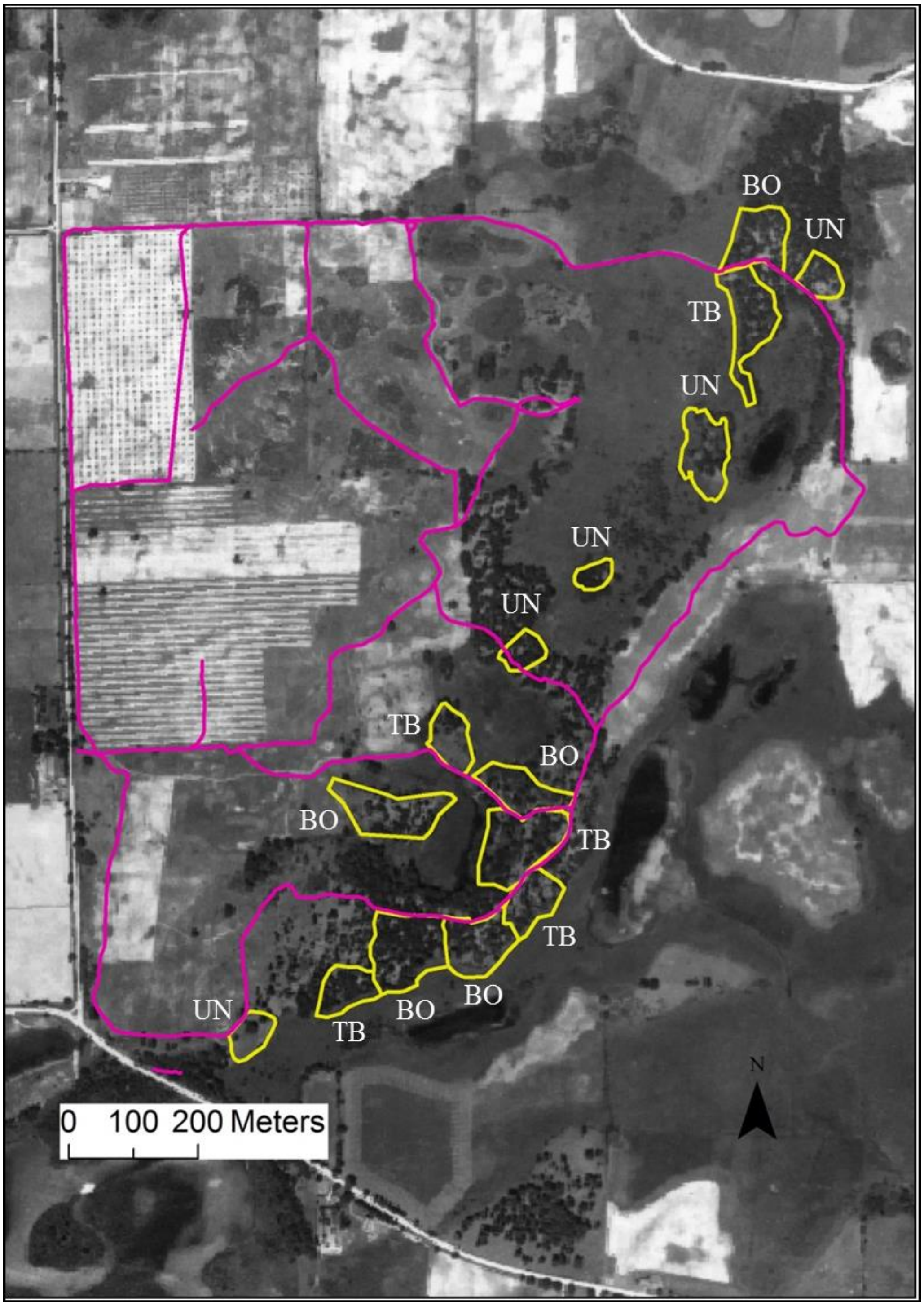


Figure 4B. Contemporary (2005) aerial photos of MacCready Reserve. Experimental plots outlined in yellow and labeled with treatment type UN (unmanaged), B (burn only), or TB (thin and burn) (pink lines show public trail system). Compare the relatively scattered canopy of 1938 (Figure 4A) to the closed canopy in 2005.

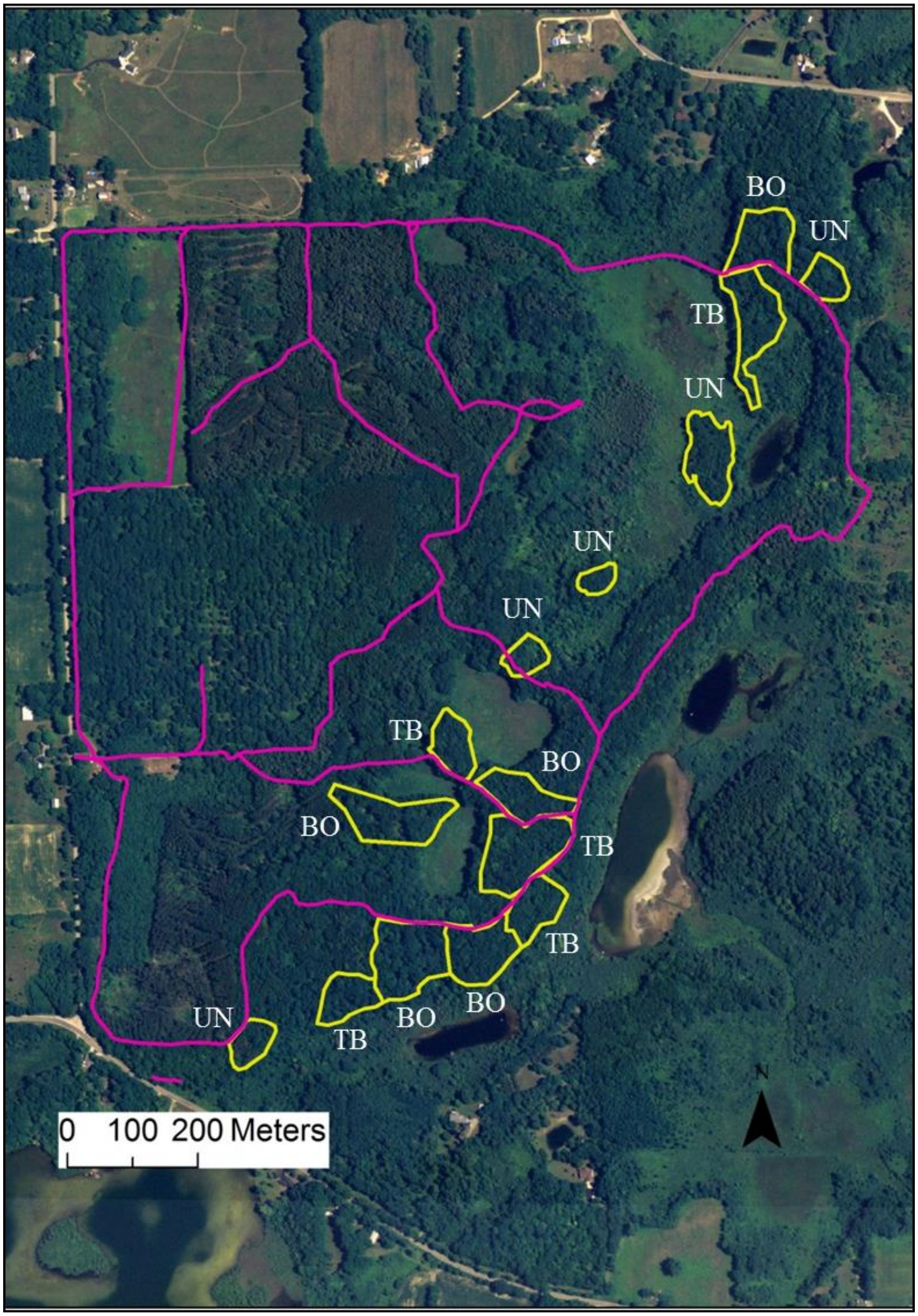


Figure 5. Schematic of sampling design in research plot. Sampling points were randomly chosen from the two 5m x 5m grids for light and cover measurements. Circular floral tally plots were repeatedly measured (5-6 times) over the season. *Alliaria petiolata* was removed by hand from all plots, with the exception of two 10m x 10m "no pull" areas established in all experimental units.

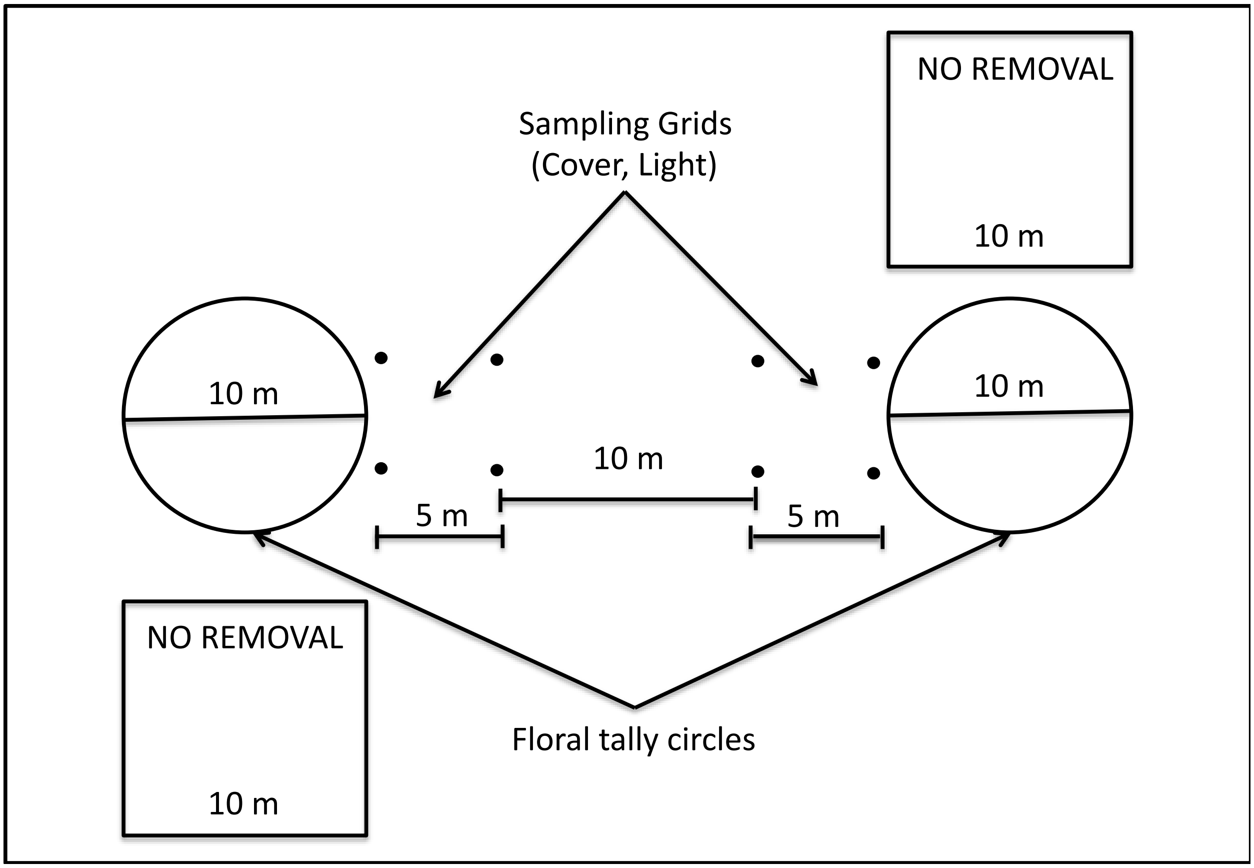


Figure 6. Means ±SEM for light availability at 1 m among the three management treatments. A one-way ANOVA was performed using Tukey's HSD for treatment comparisons within year. Different letters indicate statistically significant differences within years α =0.05.

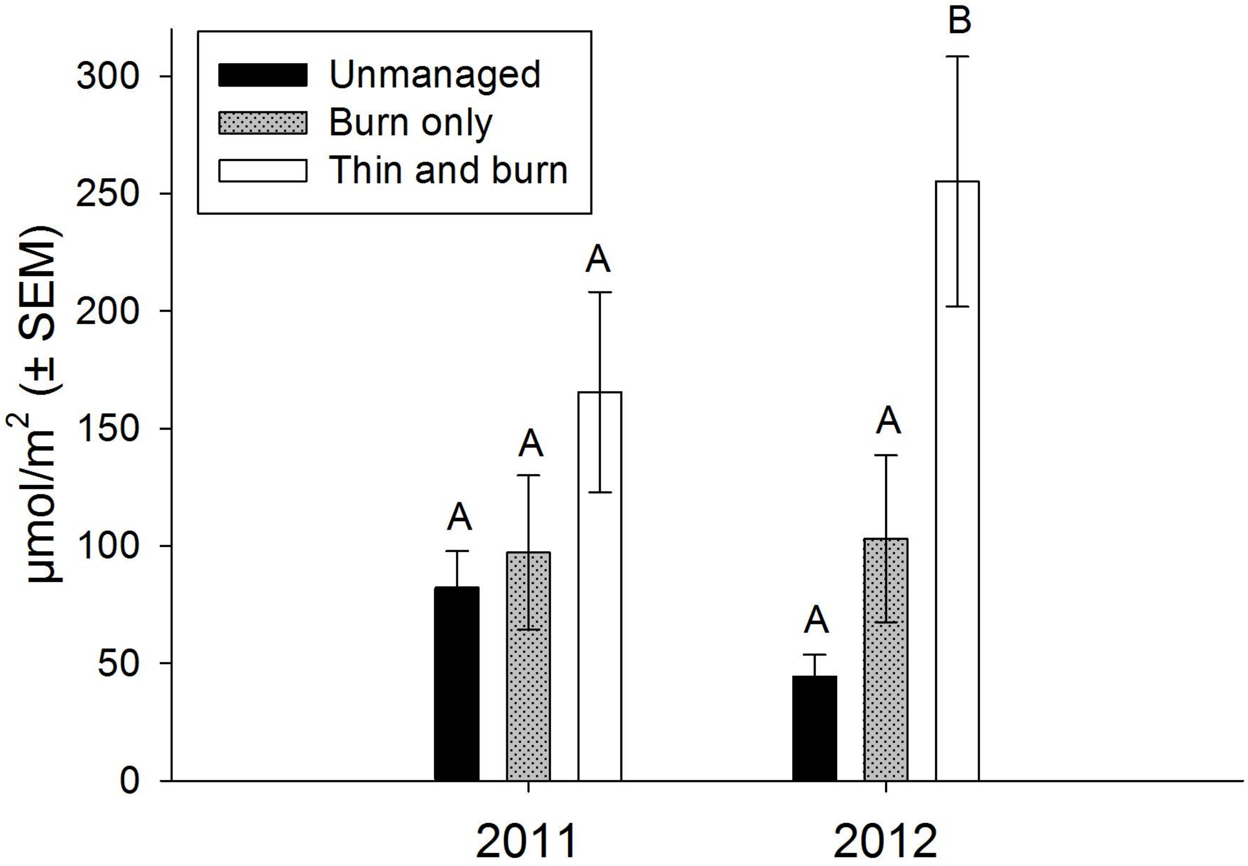


Figure 7A. Means ±SEM for 2011 under and mid-story cover among the three management treatments. A two-way ANOVA was performed using Tukey's HSD for treatment comparisons within height level. Different letters indicate statistically significant differences α =0.05.

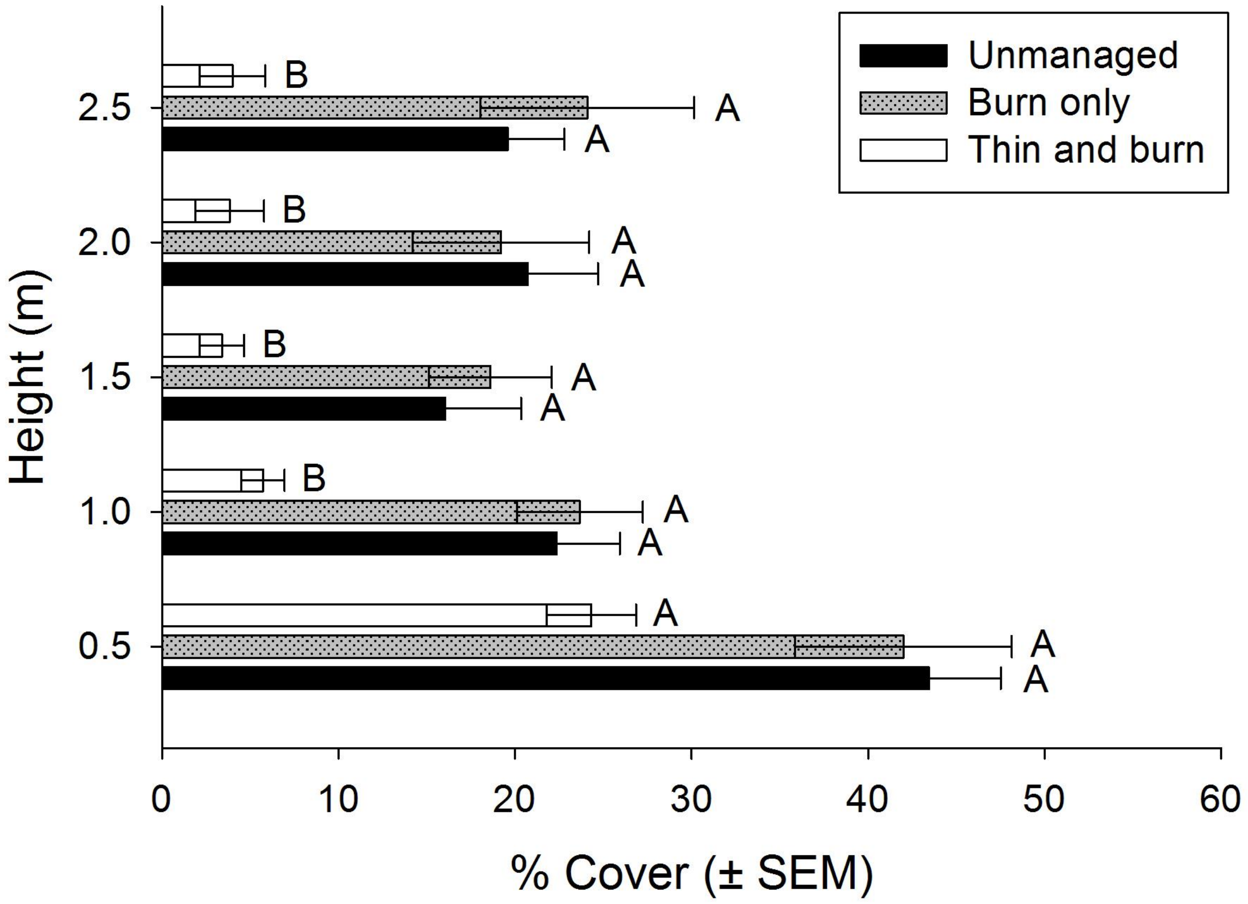


Figure 7B. Means ±SEM for 2012 under and mid-story cover among the three management treatments. A two-way ANOVA was performed using Tukey's HSD for treatment comparisons within height level. Different letters indicate statistically significant differences α =0.05.

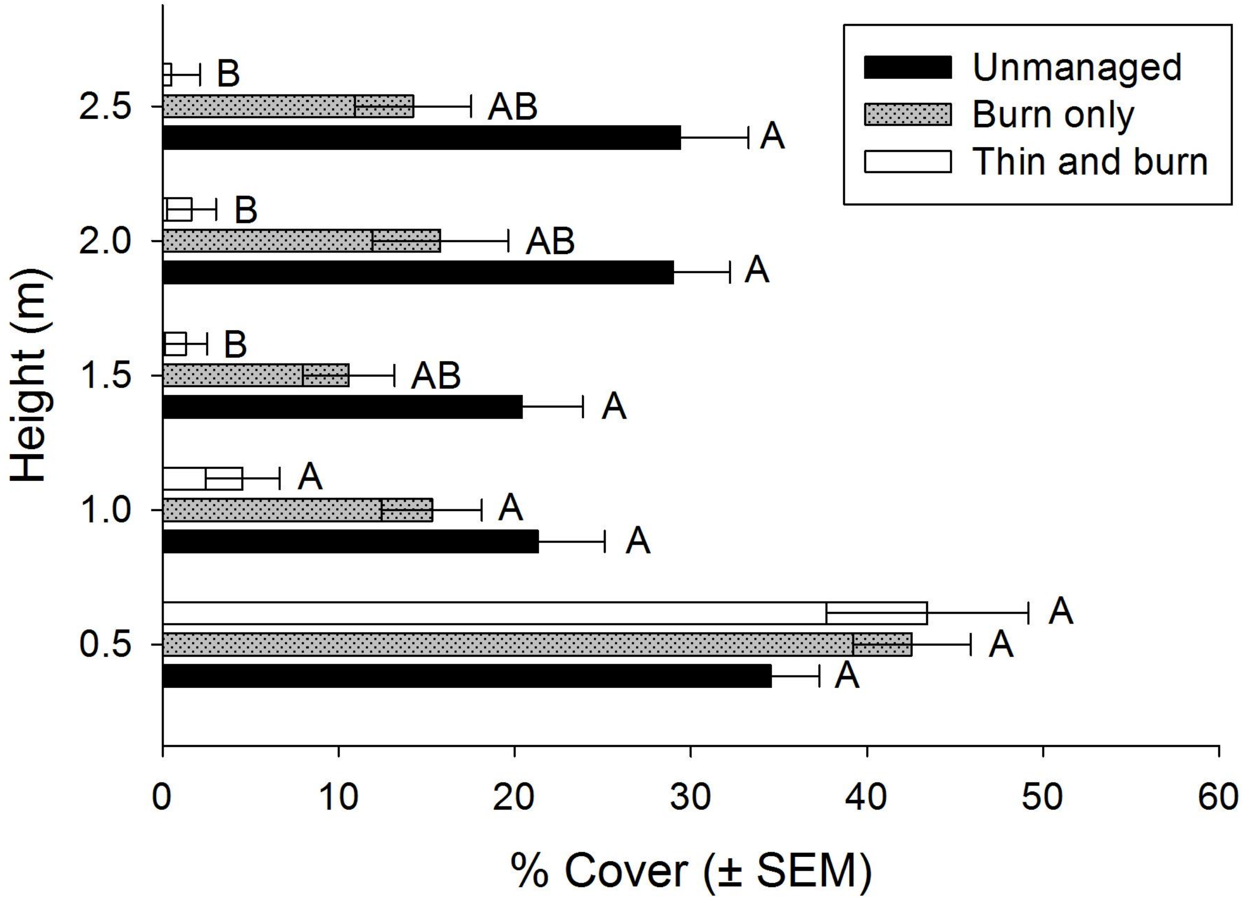


Figure 8. Means ±SEM for floral abundance among the three management treatments between years. A one-way ANOVA was performed using Tukey's HSD for treatment comparisons within year. Different letters indicate statistically significant differences α =0.05.

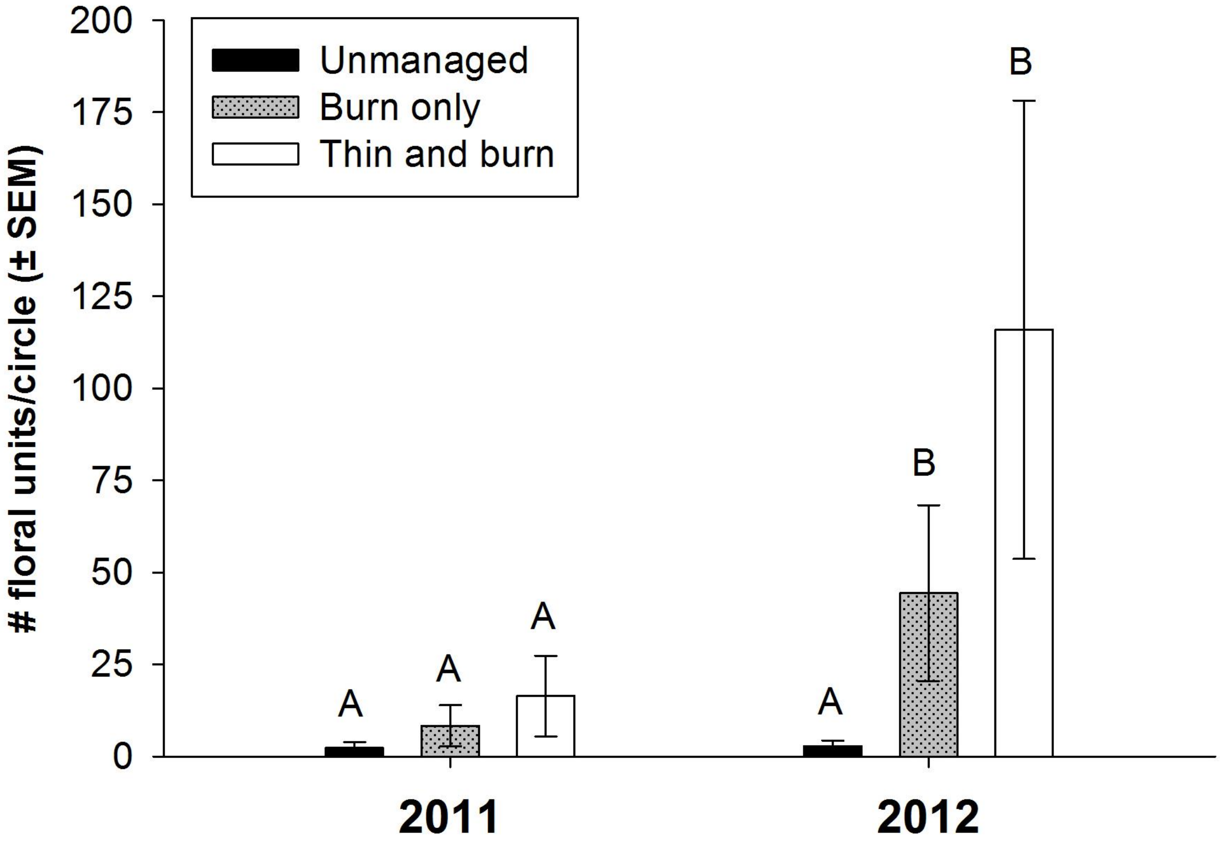


Figure 9. Mean ranks ±SEM for floral richness among the three management treatments between years. A one-way ANOVA was performed using ranked plot means. Tukey's Honestly Significant Difference for treatment comparisons within year. Different letters indicate statistically significant differences α =0.05.

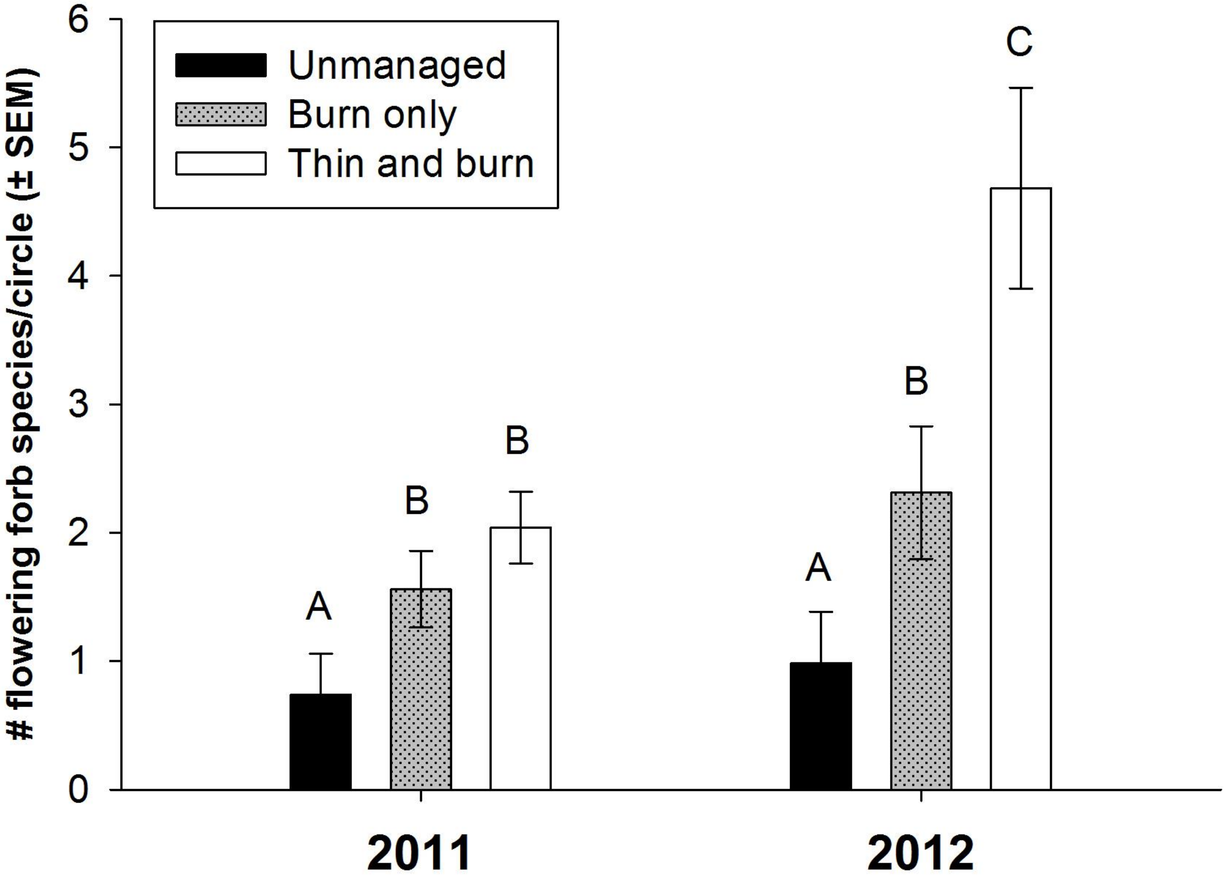


Figure 10. Rarefied floral sampling curves and 95% confidence intervals displaying flowering forb species accumulation against number of successful observations based on floral abundance data taken from the three restoration treatments. Depicted are restoration treatments unmanaged (A), burn only (B), and thin and burn (C) of both 2011 (dark circles) and 2012 (white circles).

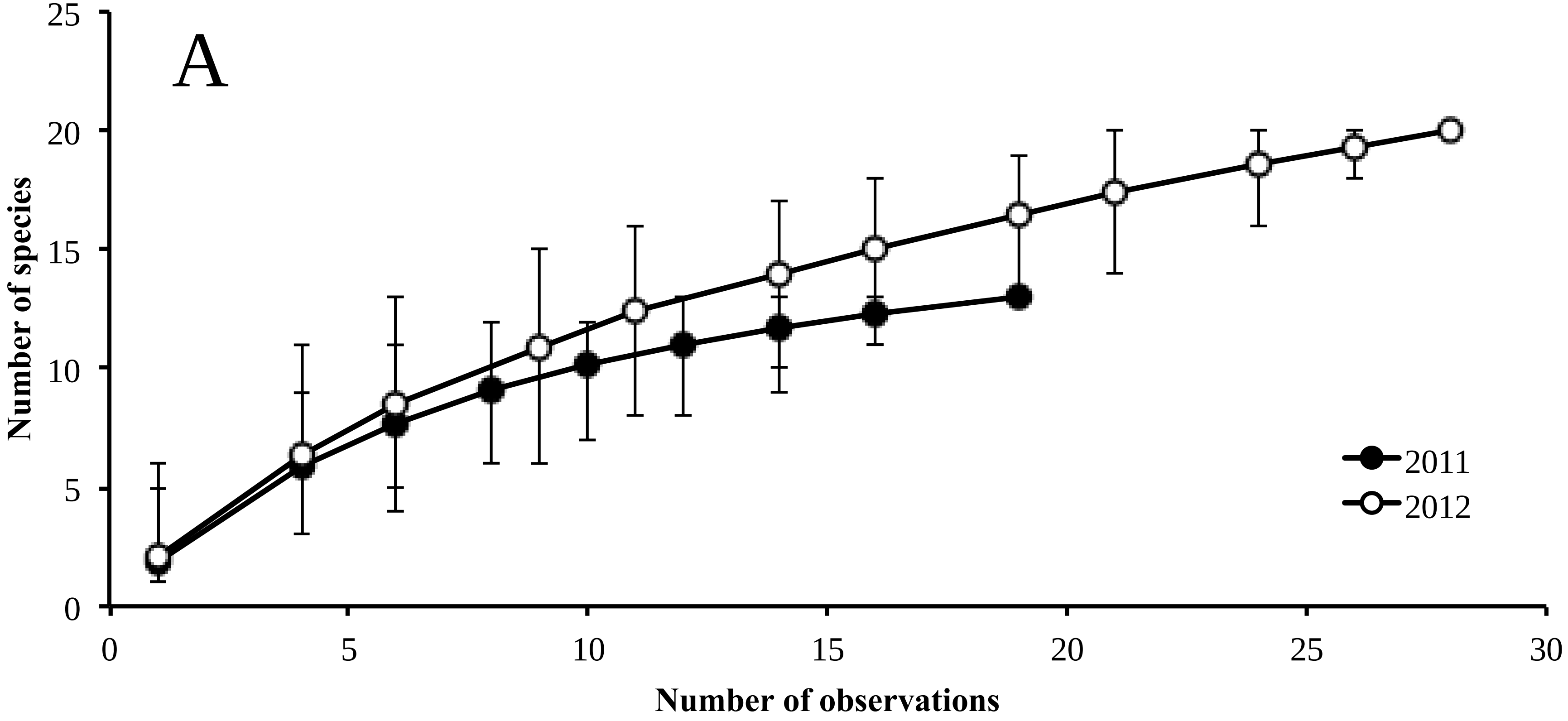


Figure 10 (cont'd).

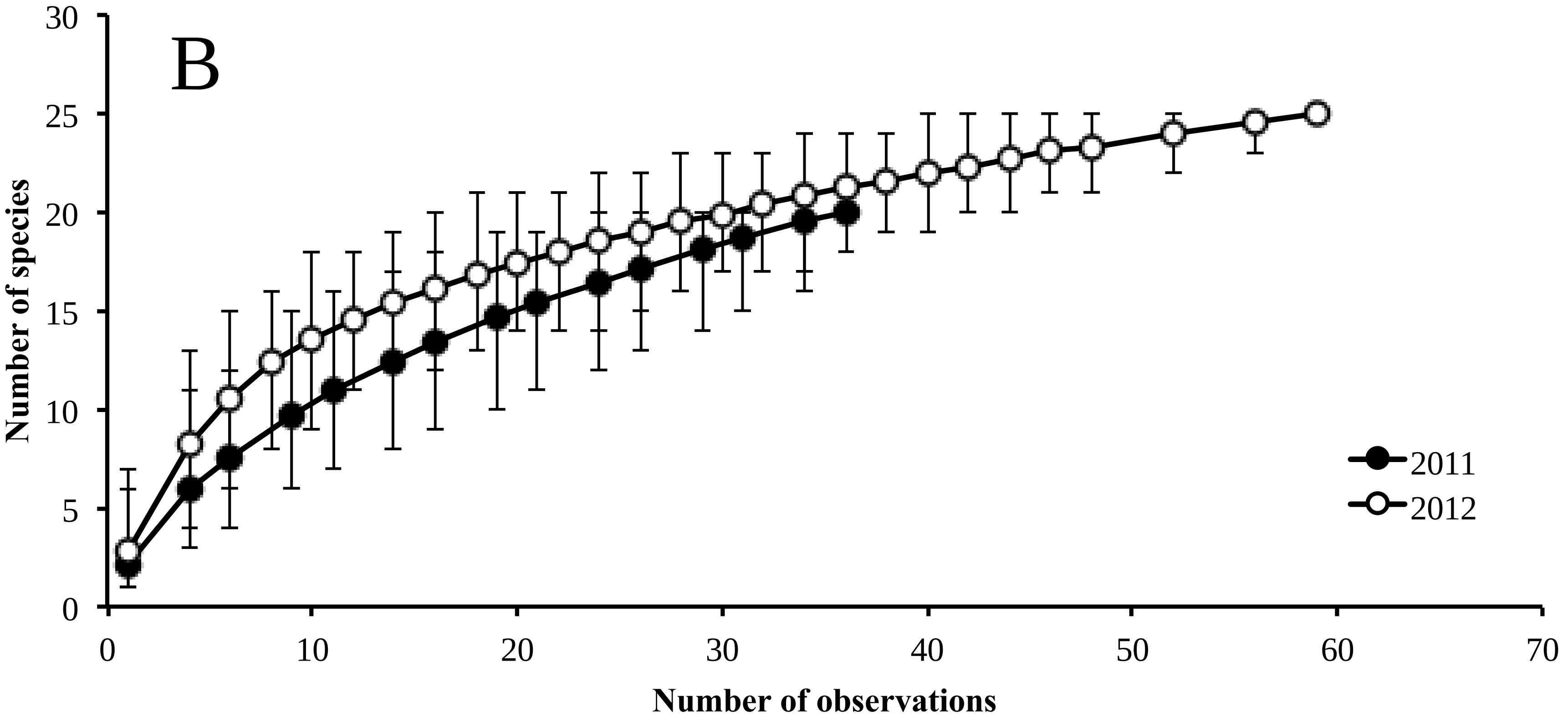
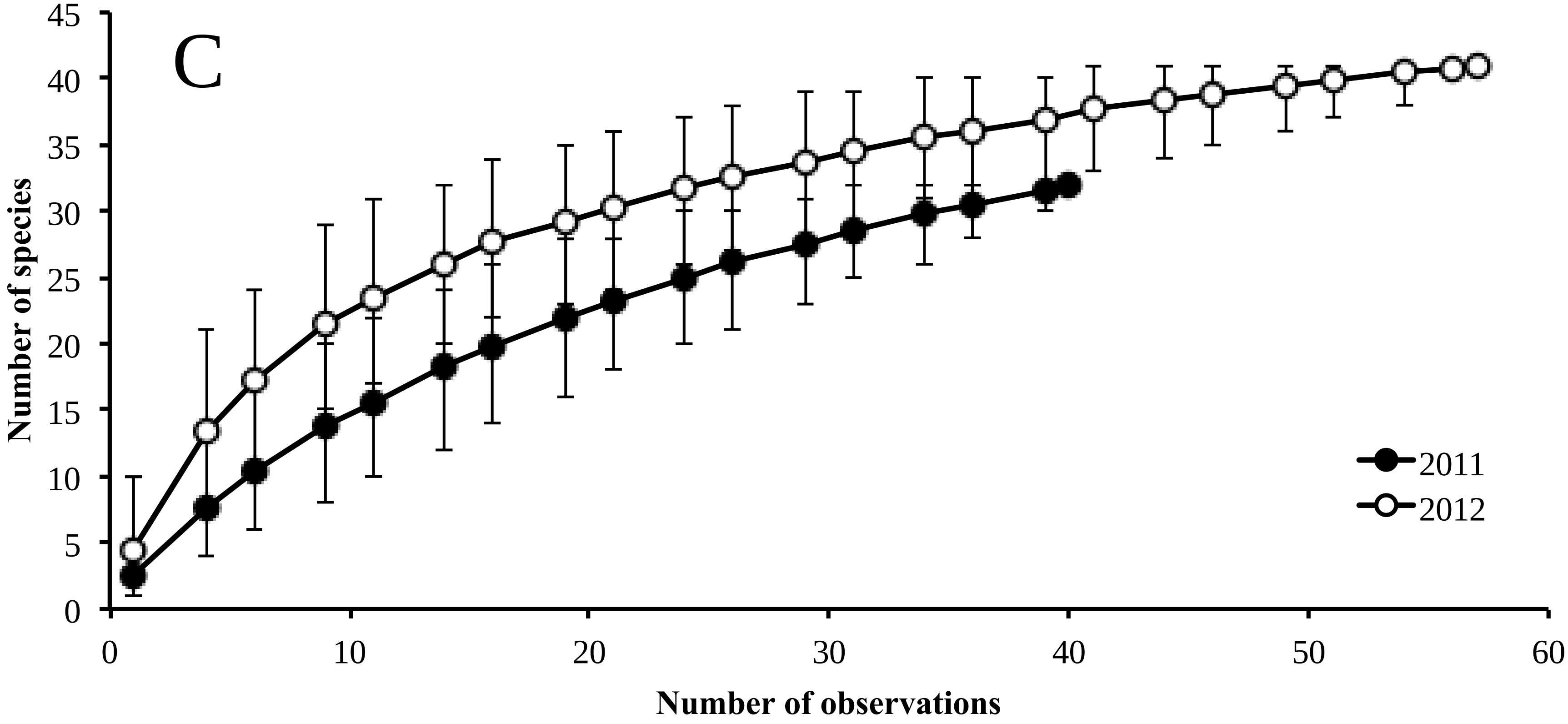


Figure 10 (cont'd).



APPENDIX C

CHAPTER 3 TABLES AND FIGURES

Table 4. List of 16 butterfly species, taxonomic families, and host plant associations documented from timed pollinator observations from the two year study at MacCready Reserve. Host plant taxa are the preferred host plant for egg oviposition according to Nielsen (1999).

Family	**Genus species**	**Common Name**	**Host plant group**	**Host plant taxa**
Hesperiidae	*Poanes hobomok* (Harris)	Hobomok skipper	Grass	*Poa spp., Dicanthelium spp., . Panicum spp*
Hesperiidae	*Epargyreus clarus* (Cramer)	Silver-spotted skipper	Forb	Fabaceae
Hesperiidae	*Amblyscirtes vialis* (W.H. Edwards)	Roadside skipper	Grass	Poaceae
Nymphalidae	*Vanessa virginiensis* (Drury)	American painted lady	Forb	*Anaphalis spp., Antennaria spp.*
Nymphalidae	*Vanessa atalanta rubria* (Fruhstorfer)	Red admiral	Forb	Urticaceae
Nymphalidae	*Speyeria cybele cybele* (Fabricius)	Great spangled fritillary	Forb	*Viola spp.*
Nymphalidae	*Polygonia interrogationis* (Fabricius)	Question mark	Forb/Woody	*Ulmus spp., Celtis spp., Urticaceae, Humulus lupulus*
Nymphalidae	*Phyciodes tharos* (Drury)	Pearl crescent	Forb	*Aster spp.*
Nymphalidae	*Nymphalis antiopa* (Linnaeus)	Mourning cloak	Woody	*Salix spp.*
Nymphalidae	*Limenitis arthemis astyanax* (Fabricius)	Red-spotted purple	Woody	*Prunus serotina*
Nymphalidae	*Danaus plexippus* (Linnaeus)	Monarch	Forb	*Asclepias spp.*
Papilionidae	*Papilio troilus* (Linnaeus)	Spicebush swallowtail	Woody	*Sassafrass albidum*
Papilionidae	*Papilio glaucus* (Linnaeus)	Tiger swallowtail	Woody	*Prunus serotina*
Papilionidae	*Papilio cresphontes* (Cramer)	Giant swallowtails	Woody	*Zanthoxylum americanum, Ptelea trifoliata*
Satyridae	*Megisto cymela* (Cramer)	Little wood satyr	Grass	Poaceae
Satyridae	*Enodia anthedon* A.H. Clark	Northern pearly eye	Grass	Poaceae

Table 5. Observed and rarefied bee community metrics for all treatment by year combinations. Samples yielding one or more bees were subjected to rarefaction analysis with the rarefaction index set to 20 samples. Observed means are the non-rarefied metrics based on the total number of bee species captured in a sampling year in each treatment. One-way ANOVA was conducted on all rarefied metrics, using Tukey's HSD for mean separation at α=0.05.

	Abundance				Richness				Shannon's H			
	Obs.	Rar.	SD		Obs.	Rar.	SD		Obs.	Rar.	SD	
Unmanaged 2011	55.0	36.5	3.2	C	15.0	11.5	1.2	C	2.1	2.0	0.1	D
Burn only 2011	82.0	41.0	5.1	C	18.0	11.3	1.8	C	2.1	1.9	0.2	D
Thin and burn 2011	129.0	47.9	8.7	B	28.0	17.0	2.2	B	2.7	2.4	0.2	B
Unmanaged 2012	35.0	30.5	1.3	D	13.0	12.2	0.7	C	2.2	2.2	0.1	C
Burn only 2012	77.0	37.6	4.5	C	16.0	12.6	1.5	C	2.4	2.3	0.1	BC
Thin and burn 2012	154.0	53.9	7.7	A	36.0	20.9	3.2	A	3.0	2.7	0.2	A

Table 6. List of 57 bee species, taxonomic families, and life history traits captured at MacCready Reserve, 2011-2012. Most bees were captured in bee bowls. ***=** species captured in timed pollinator observations, and were not accounted for in percentage of total abundance calculations. **#=** exotic species. Life history traits were taken from Wolf and Ascher (2008) and from J. Gibbs (personal communication) where species were not found therein. Nesting guild: S=soil, H=hive, W=soft wood, P=pithy stem, C=cavity, (H)=usurped hives, (S)=existing soil nests. Sociality: S=solitary, E=eusocial, P=parasitic, S/Sub.=solitary/subsocial.

Bee Species	**Family**	**Nesting guild**	**Sociality**	**Floral guild**	**% total abundance**
Agapostemon sericeus (Forster)	Halictidae	S	S	Polylectic	0.4
Agapostemon texanus Cresson	Halictidae	S	S	Polylectic	0.6
Agapostemon virescens (Fabricius)	Halictidae	S	S	Polylectic	1.3
Andrena distans Provancher	Andrenidae	S	S	*Geranium*	0.2
Andrena nasonii Robertson	Andrenidae	S	S	Polylectic	0.2
Andrena nivalis Smith	Andrenidae	S	S	Polylectic	0.2
Andrena perplexa Smith	Andrenidae	S	S	Polylectic	0.2
Andrena robertsonii/brevipalpus	Andrenidae	S	S	Polylectic	0.2
Anthophora bomboides Kirby	Apidae	S	S	Polylectic	0.8
#*Apis mellifera* Linnaeus	Apidae	H	E	Polylectic	0.2
Augochlora pura (Say)	Halictidae	W	S	Polylectic	15.4
Augochlorella aurata (Smith)	Halictidae	S	E	Polylectic	7.3
Bombus bimaculatus Cresson	Apidae	H	E	Polylectic	0.4
Bombus impatiens Cresson	Apidae	H	E	Polylectic	0.9
Ceratina calcarata/dupla/mikmaqi	Apidae	P	S/Sub.	Polylectic	6.0
Ceratina strenua Smith	Apidae	P	S/Sub.	Polylectic	2.6
Halictus confusus Smith	Halictidae	S	E	Polylectic	0.4
Halictus ligatus Say	Halictidae	S	E	Polylectic	0.4
Halictus rubicundus (Christ)	Halictidae	S	E	Polylectic	0.8
Heriades variolosa (Cresson)	Megachilidae	C	S	Polylectic	0.2
Hoplitis producta (Cresson)	Megachilidae	P	S	Polylectic	0.4
Hoplitis truncata (Cresson)	Megachilidae	P	S	Polylectic	0.4
Hylaeus annulatus (Linnaeus)	Colletidae	C	S	Polylectic	0.2

Table 6 (cont'd).

Bee Species	**Family**	**Nesting guild**	**Sociality**	**Floral guild**	**% total abundance**
Hylaeus modestus Say	Colletidae	C	S	Polylectic	0.2
Lasioglossum bruneri (Crawford)	Halictidae	S	E	Polylectic	0.2
Lasioglossum cattellae (Ellis)	Halictidae	S	E	Polylectic	0.6
Lasioglossum coeruleum (Robertson)	Halictidae	W	E	Polylectic	14.1
Lasioglossum coriaceum (Smith)	Halictidae	S	S	Polylectic	8.1
Lasioglossum cressonii (Robertson)	Halictidae	W	E	Polylectic	7.0
Lasioglossum divergens (Lovell)	Halictidae	S	S	Polylectic	1.3
Lasioglossum foveolatum (Robertson)	Halictidae	S	E	Polylectic	0.2
#Lasioglossum leucozonium (Schrank)	Halictidae	S	S	Polylectic	0.8
Lasioglossum lineatulum (Crawford)	Halictidae	S	E	Polylectic	0.2
Lasioglossum macoupinense (Robertson)	Halictidae	S	S	Polylectic	0.4
Lasioglossum nelumbonis (Robertson)	Halictidae	S	S	Nymphaeales	0.6
Lasioglossum nigroviride (Graenicher)	Halictidae	S	E	Polylectic	0.2
Lasioglossum oblongum (Lovell)	Halictidae	W	E	Polylectic	0.2
Lasioglossum obscurum (Robertson)	Halictidae	S	E	Polylectic	0.2
Lasioglossum pectorale (Smith)	Halictidae	S	S	Polylectic	2.4
Lasioglossum pilosum (Smith)	Halictidae	S	E	Polylectic	0.8
Lasioglossum subviridatum (Cockerell)	Halictidae	W	E	Polylectic	14.8
Lasioglossum timothyi Gibbs	Halictidae	S	E	Polylectic	0.6
Lasioglossum versans (Lovell)	Halictidae	S	E	Polylectic	1.9
Lasioglossum versatum (Robertson)	Halictidae	S	E	Polylectic	3.0
Megachile campanulae (Robertson)	Megachilidae	C	S	Polylectic	0.2
Megachile montivaga Cresson	Megachilidae	C	S	Polylectic	0.2

Table 6 (cont'd).

Bee Species	**Family**	**Nesting guild**	**Sociality**	**Floral guild**	**% total abundance**
Melissodes coreopsis Robertson	Apidae	S	S	Polylectic	0.2
Melissodes desponsa Smith	Apidae	S	S	*Cirsium*	0.4
Nomada (toothed) *sp. 1*	Apidae	(S)	P	Apoidea	0.6
Nomada (toothed) *sp. 2*	Apidae	(S)	P	Apoidea	0.2
Nomada (toothed) *sp. 3*	Apidae	(S)	P	Apoidea	0.2
Osmia pumila Cresson	Megachilidae	C	S	Polylectic	0.4
#Osmia taurus/cornifrons	Megachilidae	C	S	Polylectic	0.2
Sphecodes sp. 1	Halictidae	(S)	P	Apoidea	0.2
Sphecodes sp. 2	Halictidae	(S)	P	Apoidea	0.2
Sphecodes sp. 3	Halictidae	(S)	P	Apoidea	0.2
Stelis lateralis Cresson	Megachilidae	(C)	P	Megachilidae	0.2

Figure 11. Photo of bee sampling setup. A) Colored cups were placed in an array of three, within cups attached to plant trays, where they were filled with soapy water prior to sampling. B) Trays were vertically adjustable through use of a spring clamp and C) stabilized with attached plywood, both fitting around steel conduit.

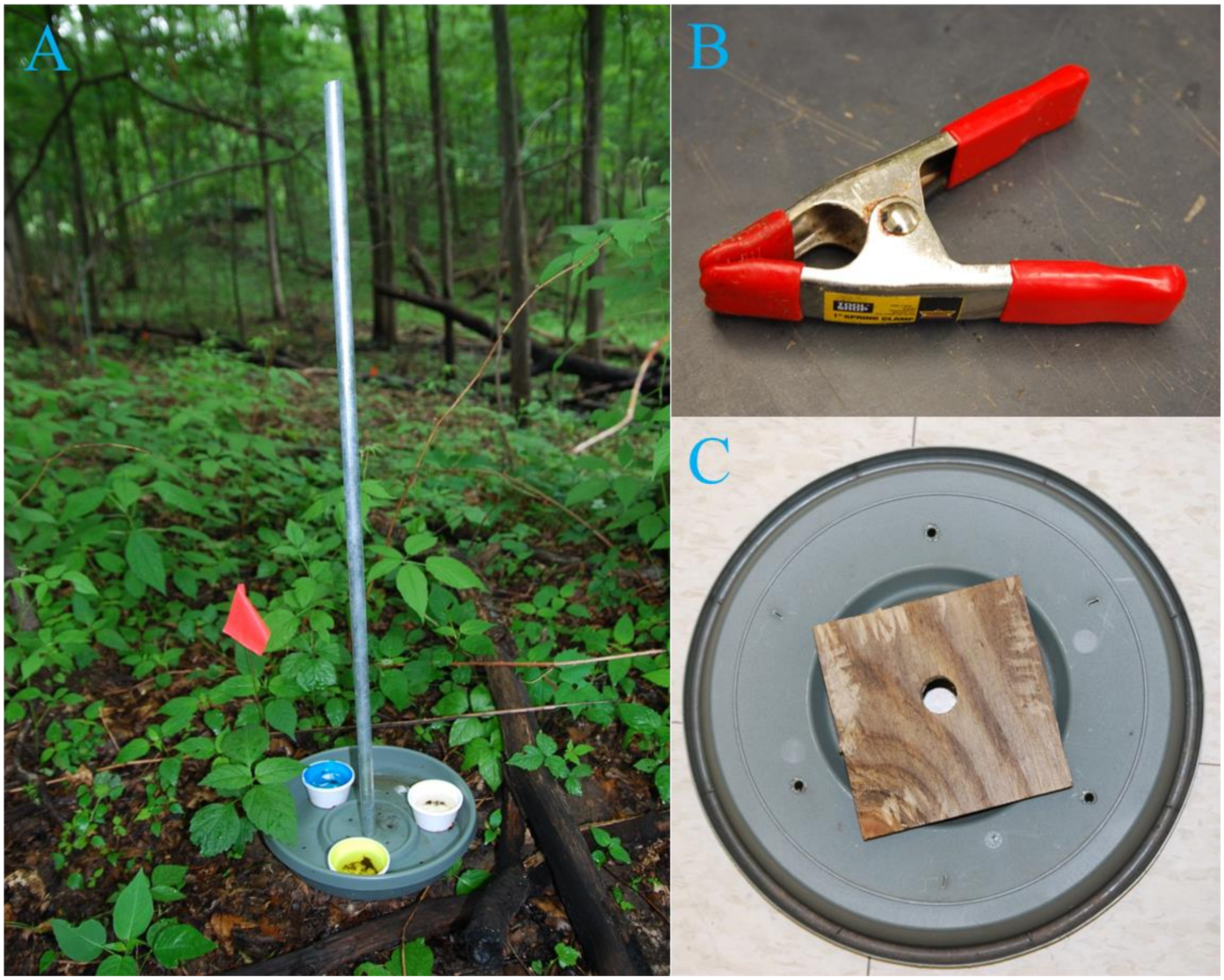


Figure 12A. Distribution of Papilionid butterflies between three restoration treatments in 2011 and 2012 (n=58, n=46, respectively) at MacCready Reserve.

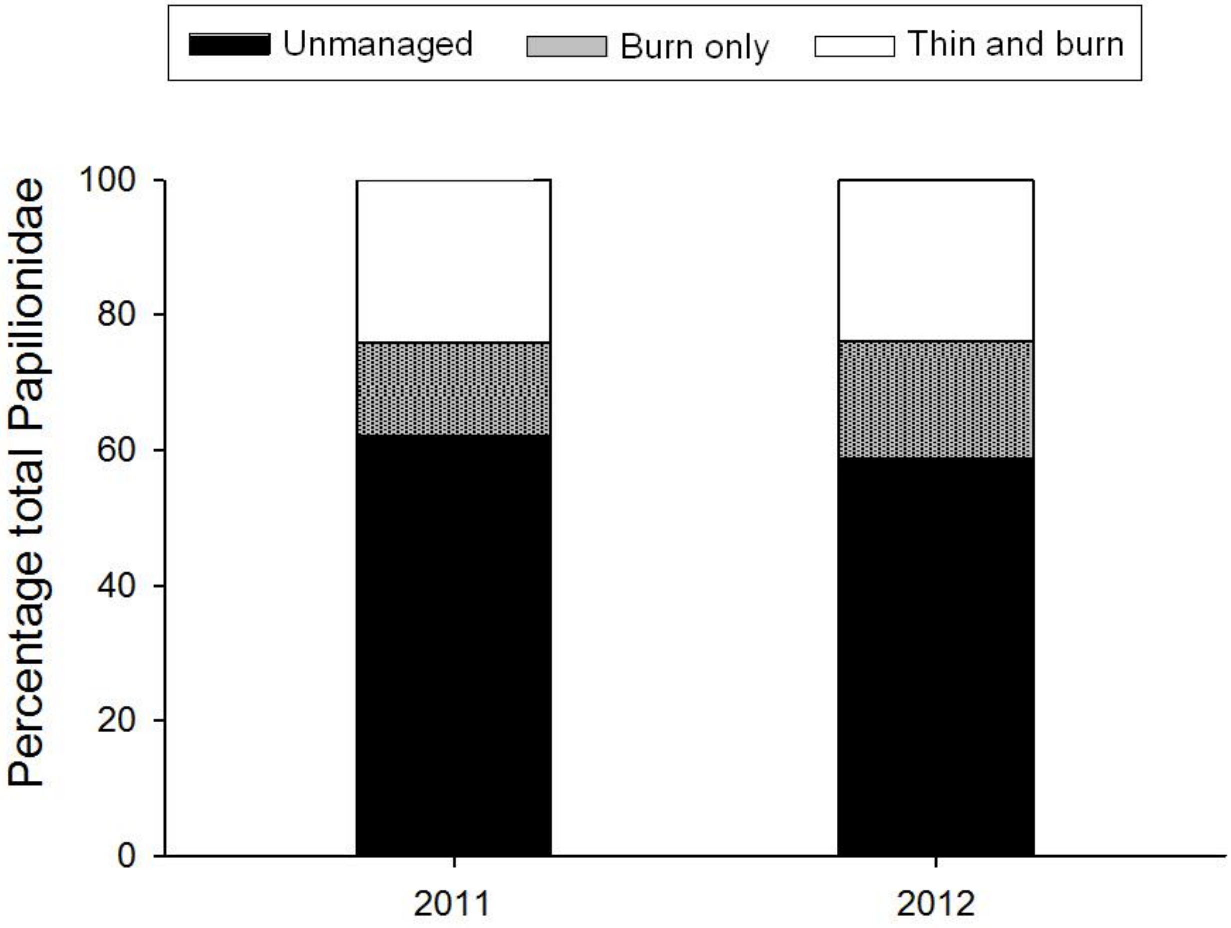


Figure 12B. Distribution of Nymphalid butterflies between three restoration treatments in 2011 and 2012 (n=17, n=61, respectively) at MacCready Reserve.

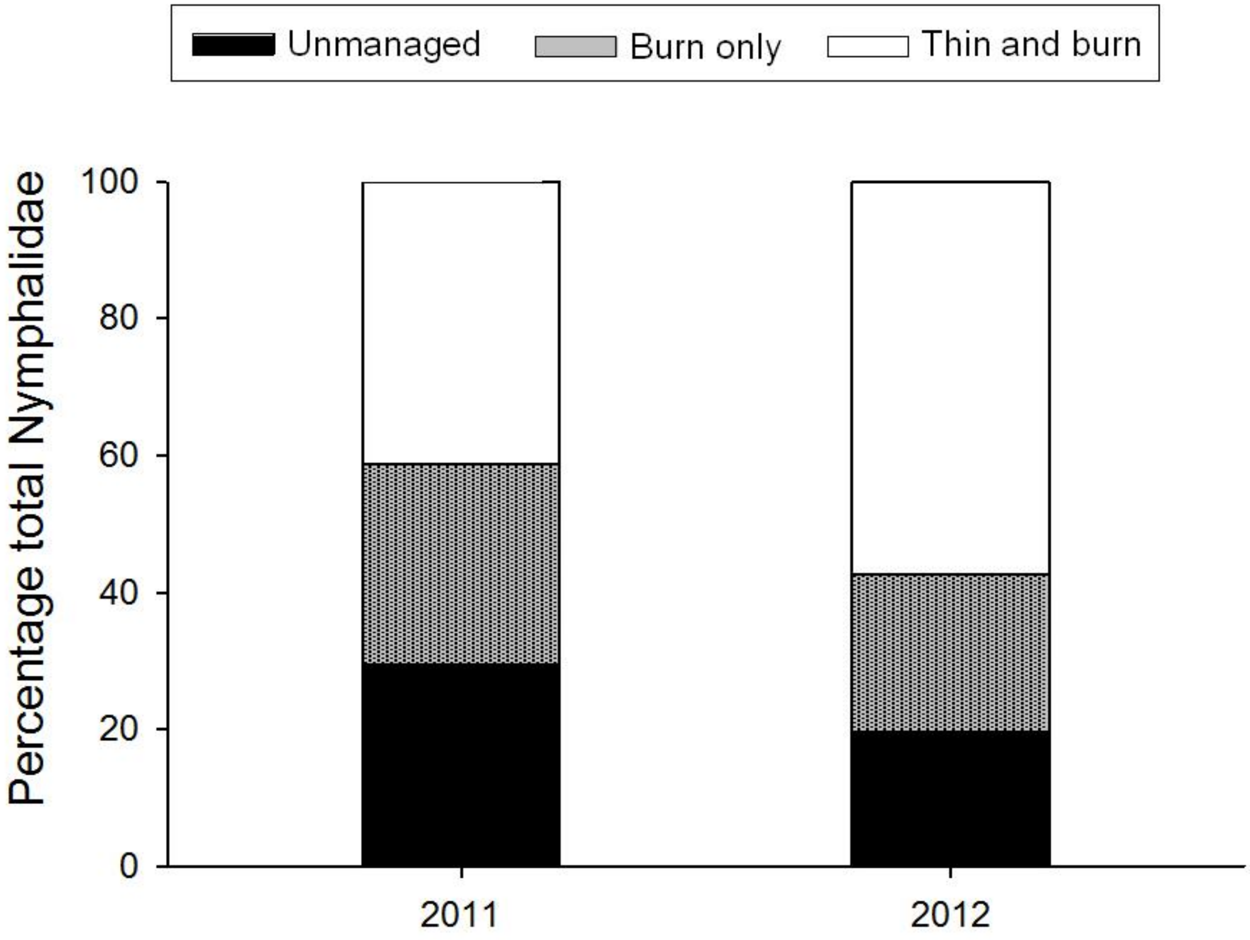


Figure 12C. Distribution of Satyrid butterflies between three restoration treatments in 2011 and 2012 (n=36, n=80, respectively) at MacCready Reserve.

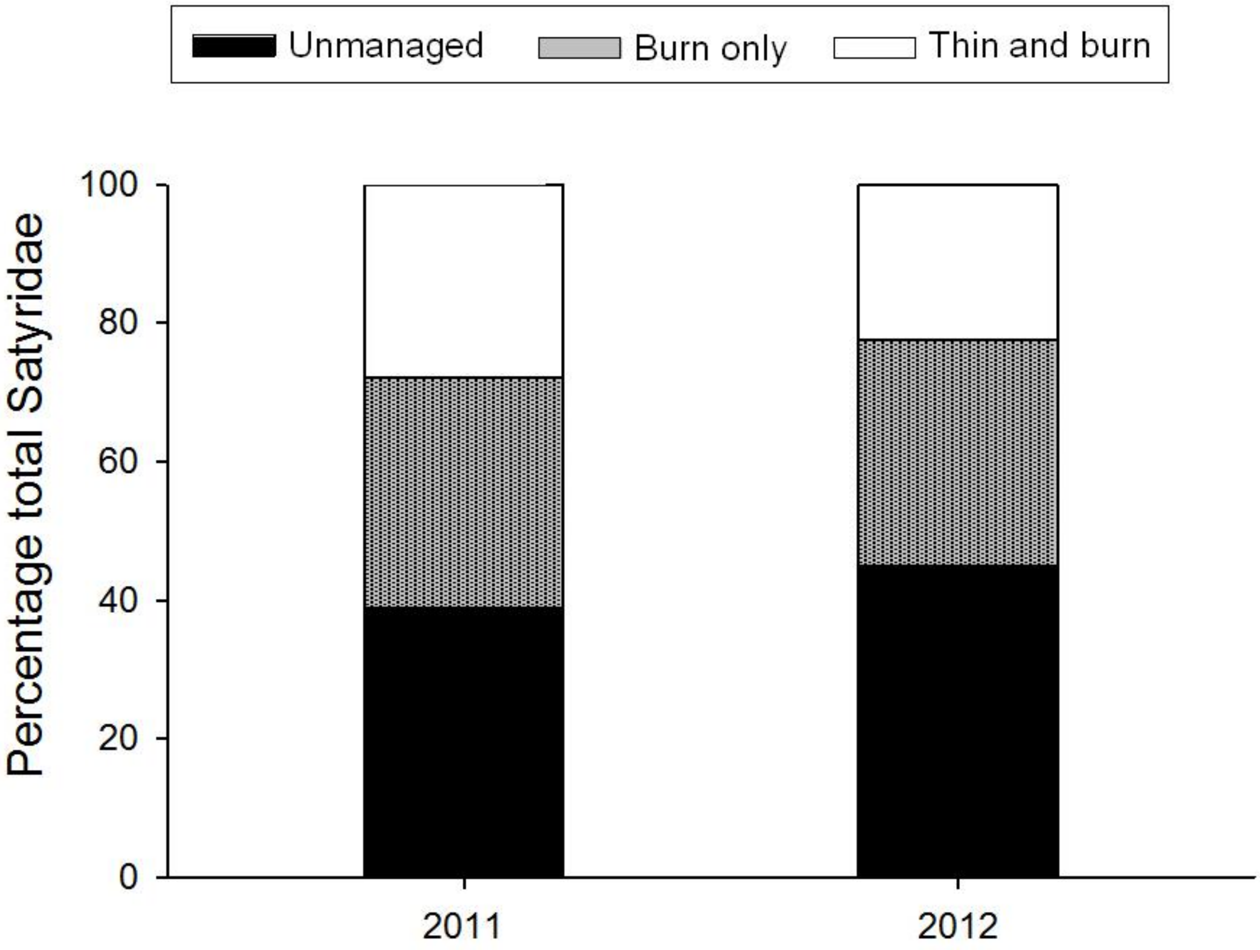


Figure 13. Rarefied bee sampling curves and 95% confidence intervals displaying bee species accumulation against number of successful samples based on bee abundance data taken from the three restoration treatments. Depicted are restoration treatments unmanaged (A), burn only (B), and thin and burn (C) of both 2011 (dark circles) and 2012 (white circles).

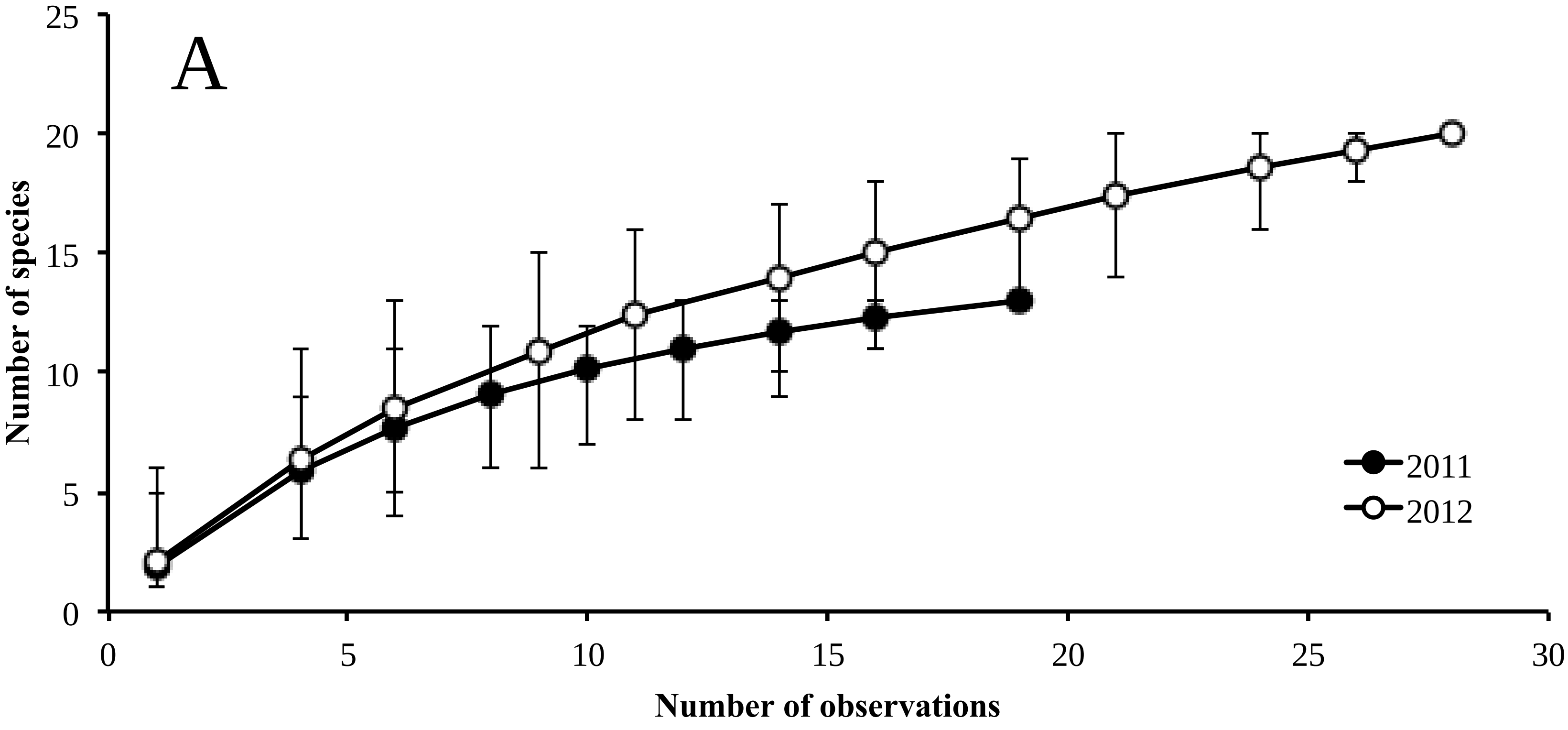
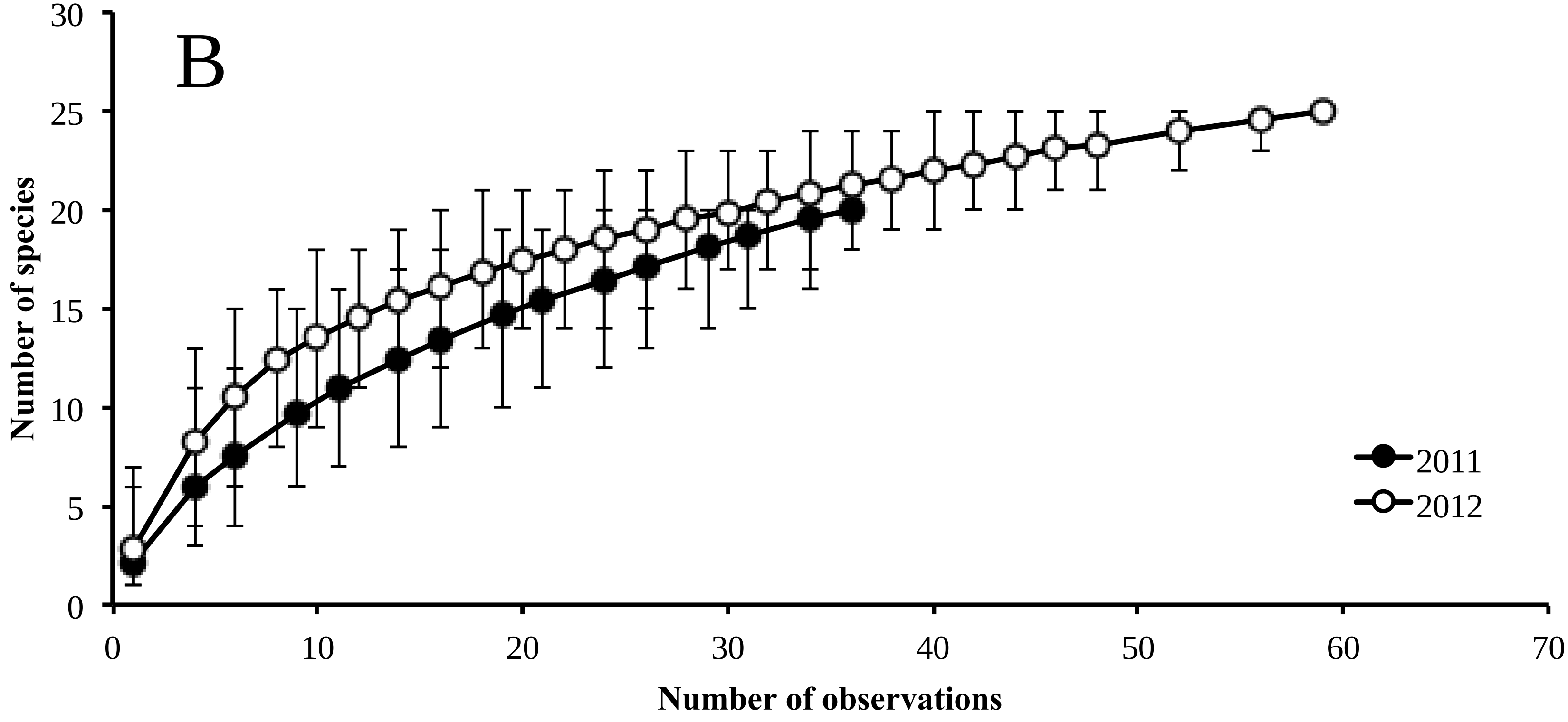


Figure 13 (cont'd).



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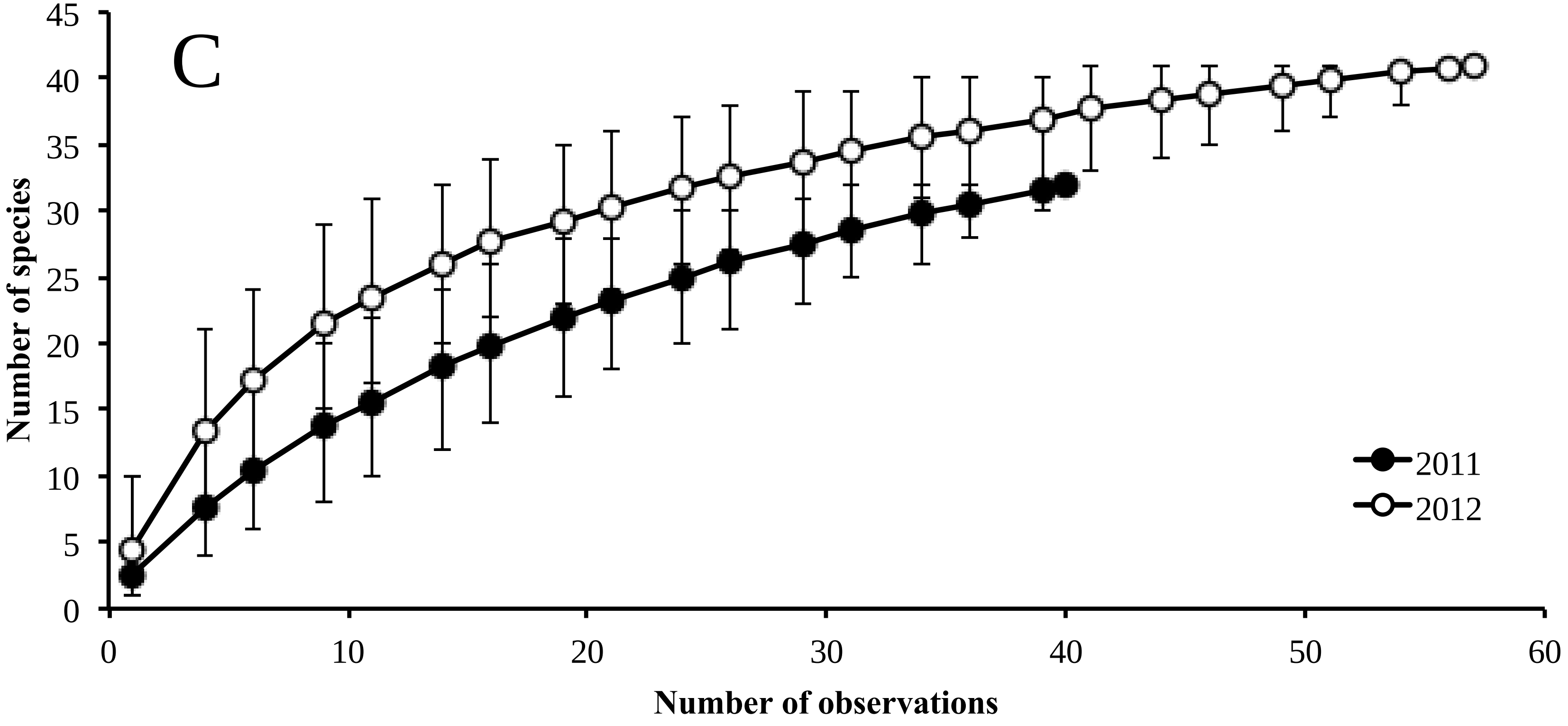


Figure 14A. Distribution of wood-nesting bees between three restoration treatments in 2011 and 2012 (n=156, n=118, respectively) at MacCready Reserve.

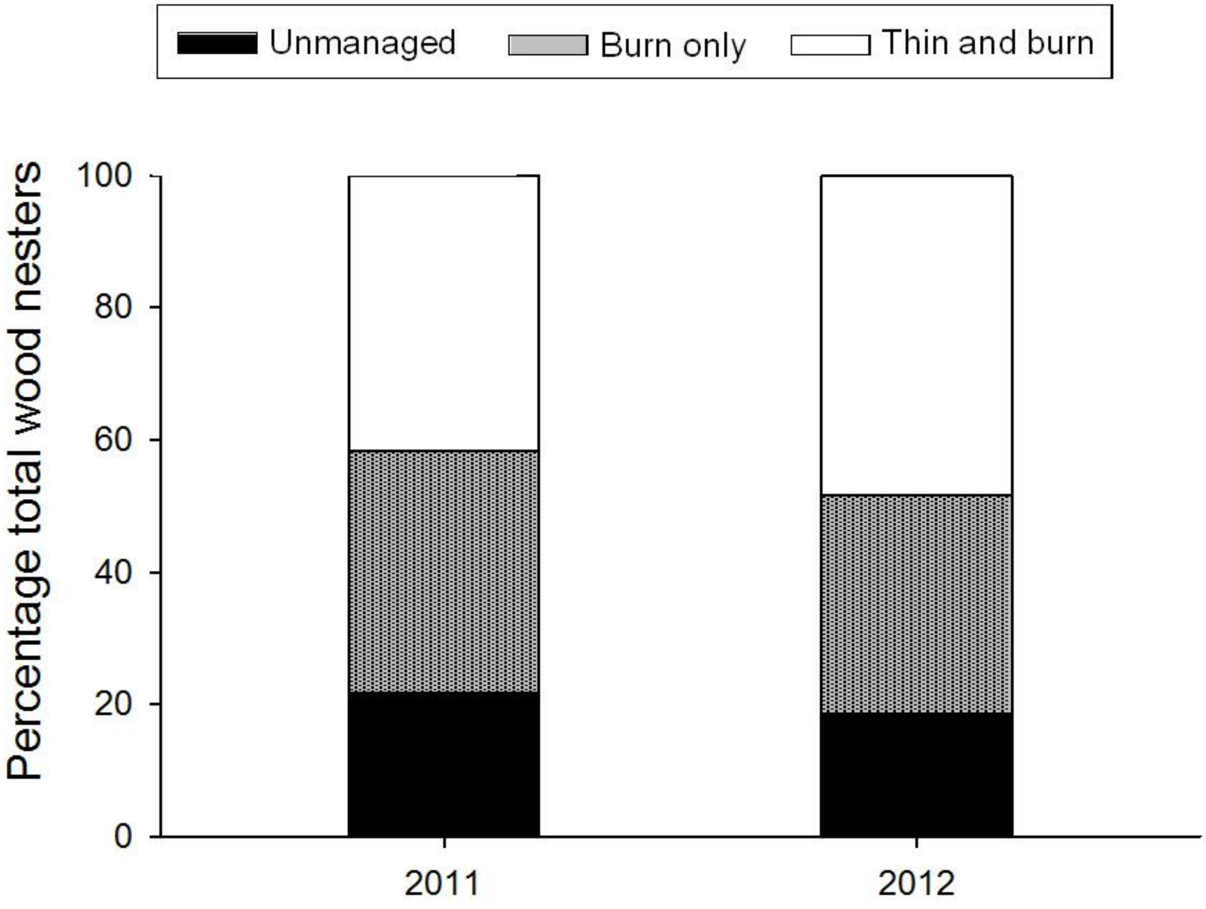


Figure 14B. Distribution of soil-nesting bees between three restoration treatments in 2011 and 2012 (n=83, n=101, respectively) at MacCready Reserve.

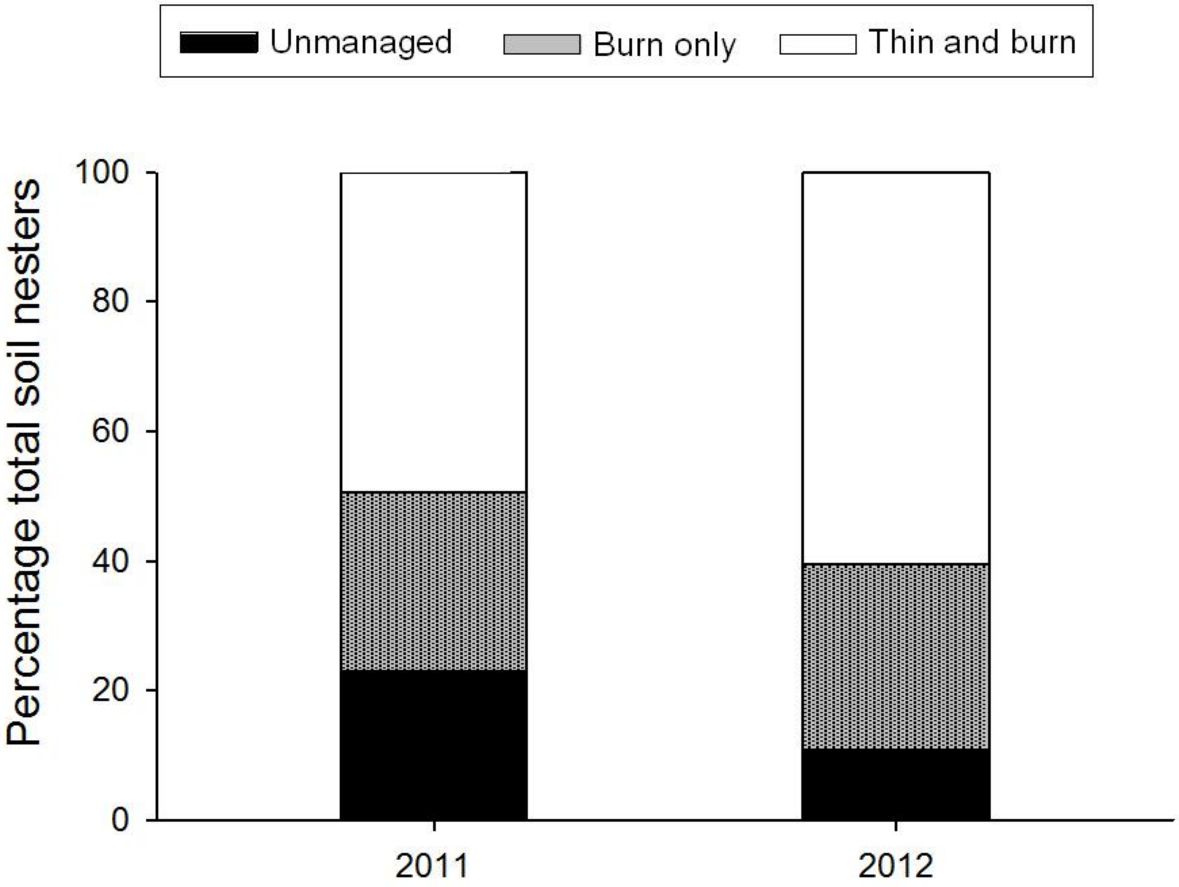


Figure 14C. Distribution of stem-nesting bees between restoration treatments in 2011 and 2012 (n=17, n=33, respectively) at MacCready Reserve.

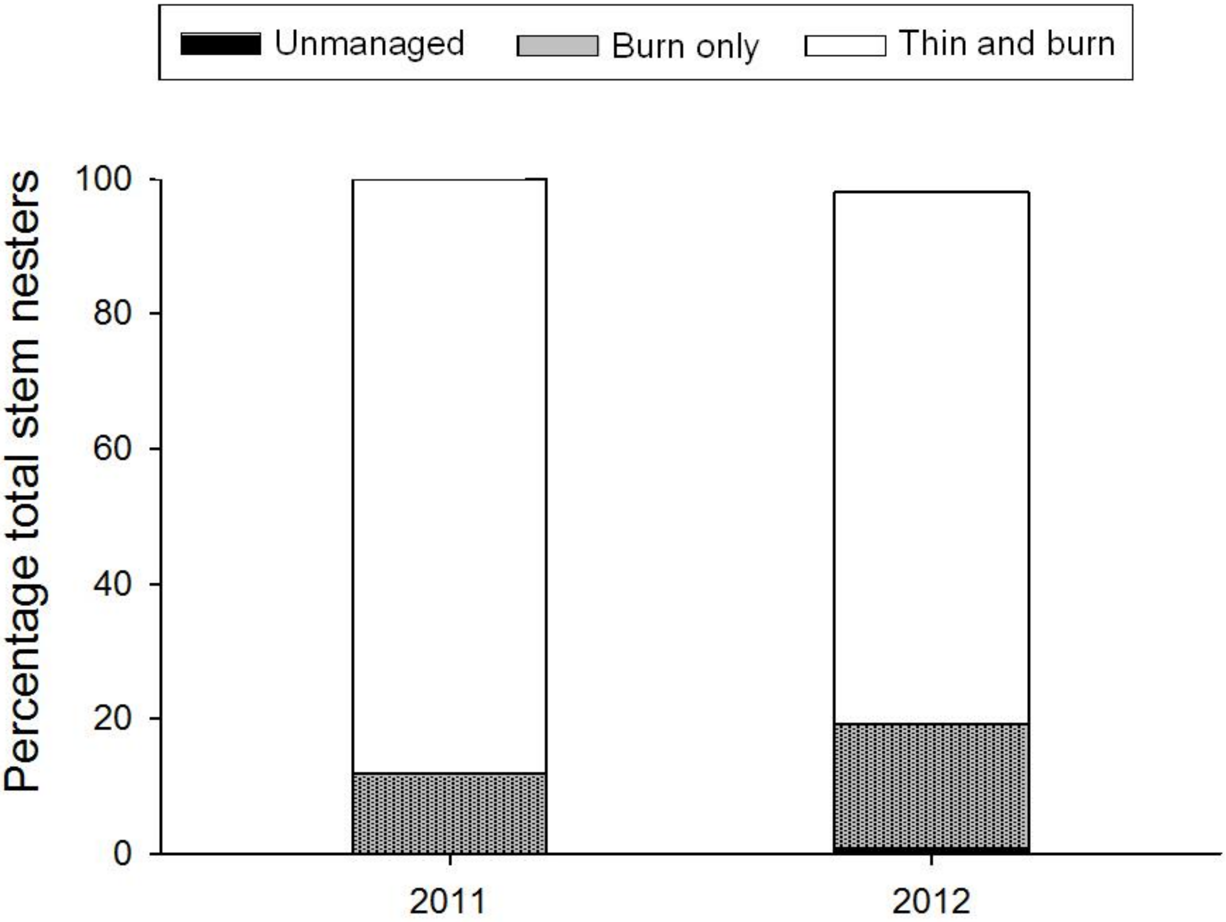


Figure 15A. Two-dimensional MDS ordinations of bee communities among restoration treatments in 2011. Increasing distance between points corresponds to decreasing similarity between bee communities of individual treatment replications, and vice versa. Community comparisons were made using Bray-Curtis similarity matrix values generated from replicate means across multiple dates within a season. Lines encircling points correspond to statistical groupings of treatments resulting from pairwise comparisons according to ANOSIM. Stress value of the two-dimensional ordination was 0.12.

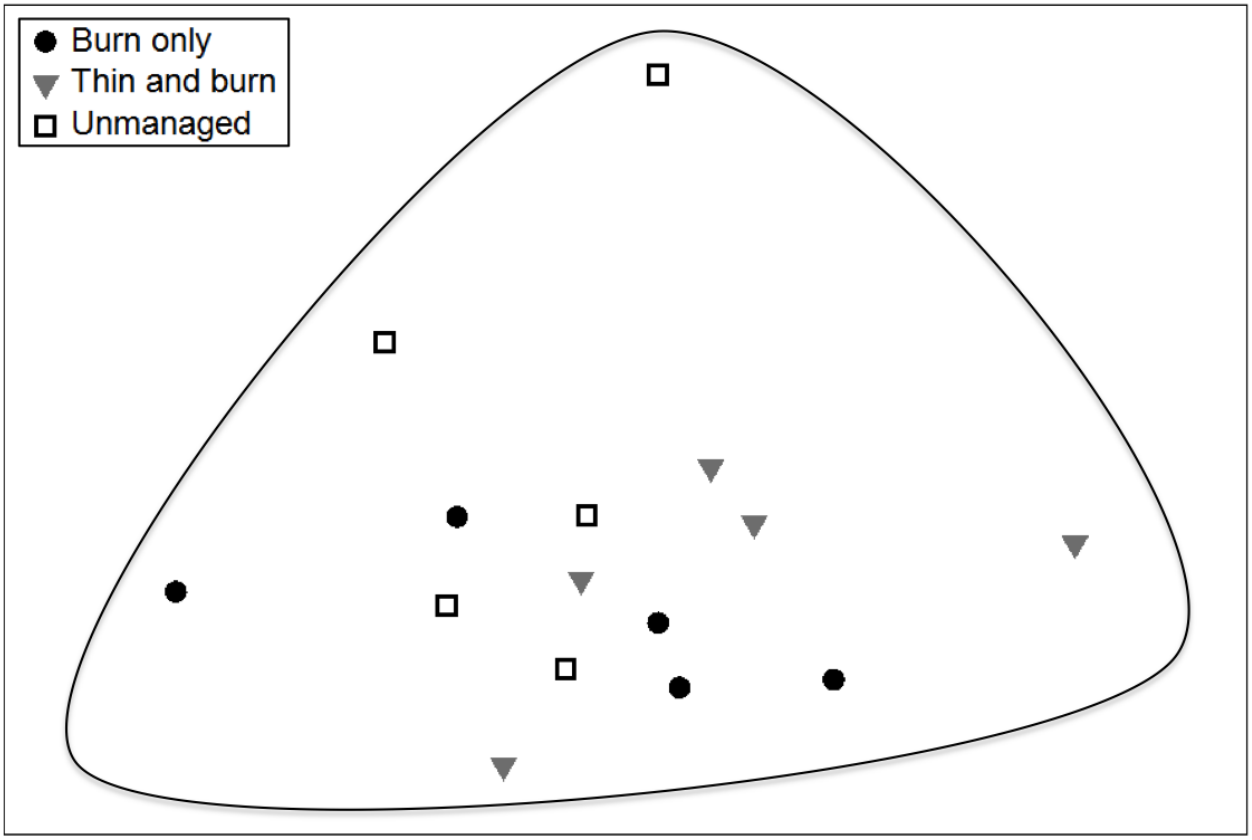


Figure 15B. Two-dimensional MDS ordinations of bee communities among restoration treatments in 2012. Increasing distance between points corresponds to decreasing similarity between bee communities of individual treatment replications, and vice versa. Community comparisons were made using Bray-Curtis similarity matrix values generated from replicate means across multiple dates within a season. Lines encircling points correspond to statistical groupings of treatments resulting from pairwise comparisons according to ANOSIM. Stress value of the two-dimensional ordination was 0.15.

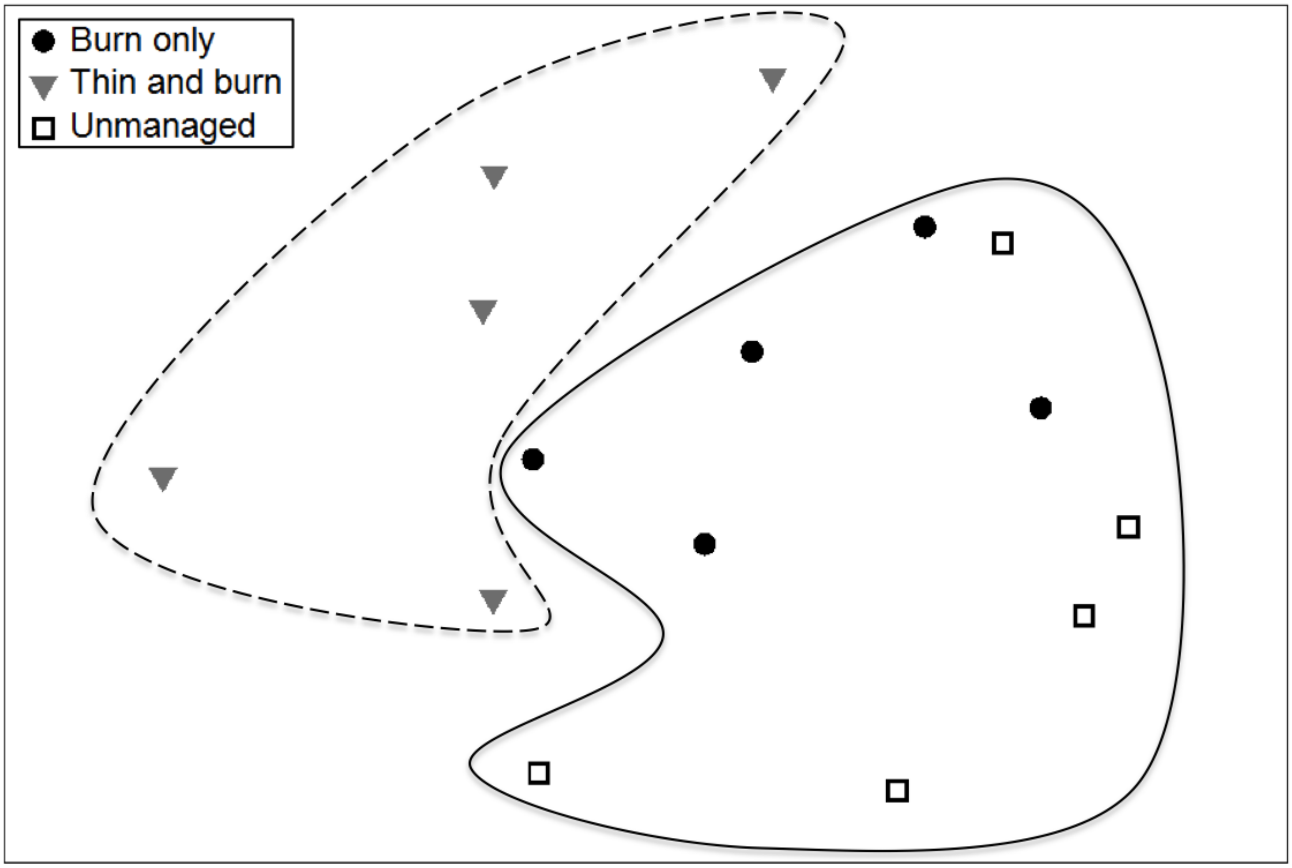


Figure 16A. Diagram of 2011 variable and treatment relationships indicated by Spearman's rank correlation. Biotic variables (i.e. bee richness, bee abundance, floral richness, floral abundance) were measured biweekly. Lines connecting variables represent significant correlations between ranks at α=0.05. The thickness of each line is scaled with the magnitude of Spearman's ρ. Solid lines represent positive relationships among ranked variables, while dashed lines represent negative relationships.

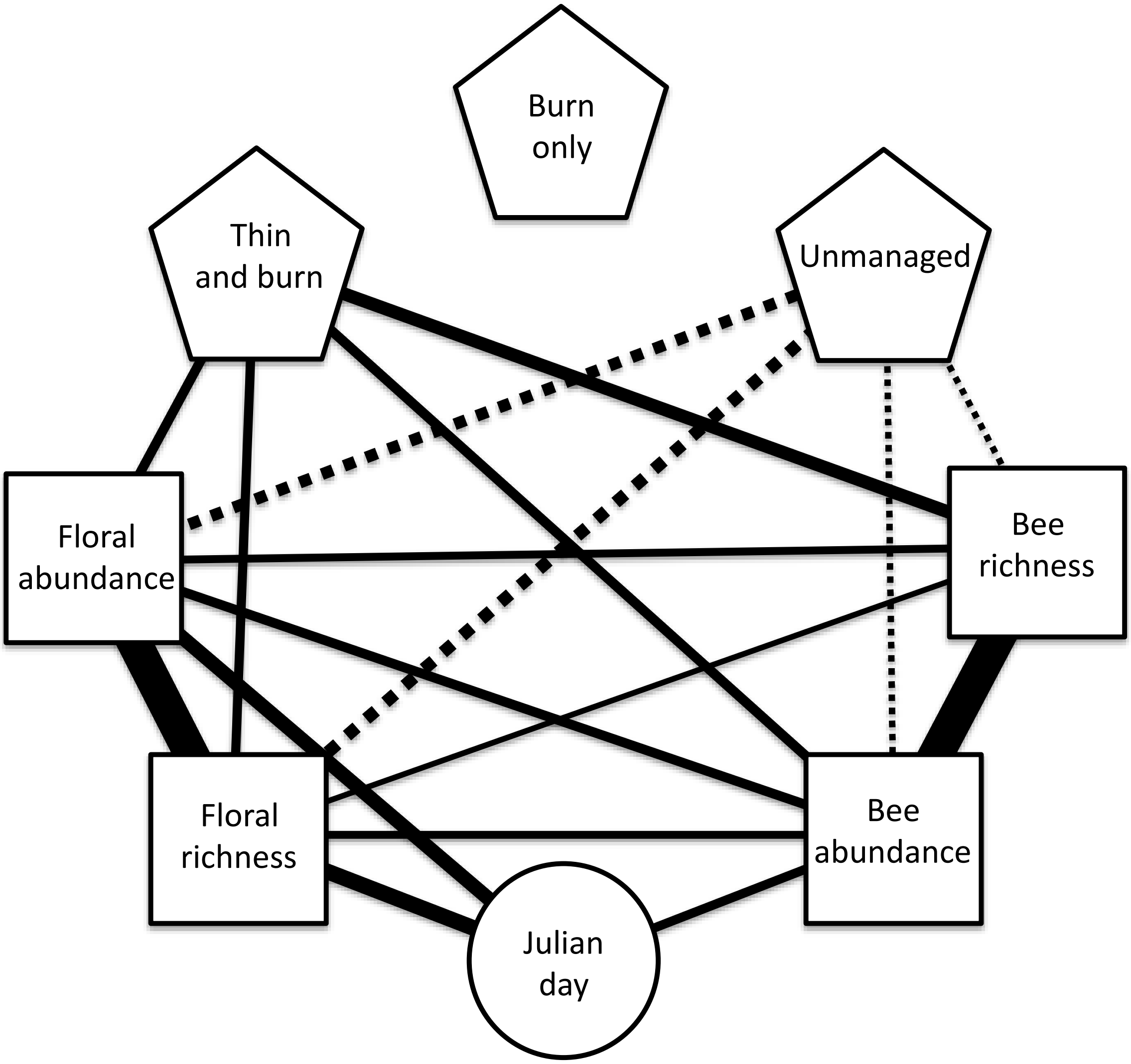


Figure 16B. Diagram of 2012 variable and treatment relationships indicated by Spearman's rank correlation. Biotic variables (i.e. bee richness, bee abundance, floral richness, floral abundance) were measured biweekly. Lines connecting variables represent significant correlations between ranks at α=0.05. The thickness of each line is scaled with the magnitude of Spearman's ρ. Solid lines represent positive relationships among ranked variables, while dashed lines represent negative relationships.

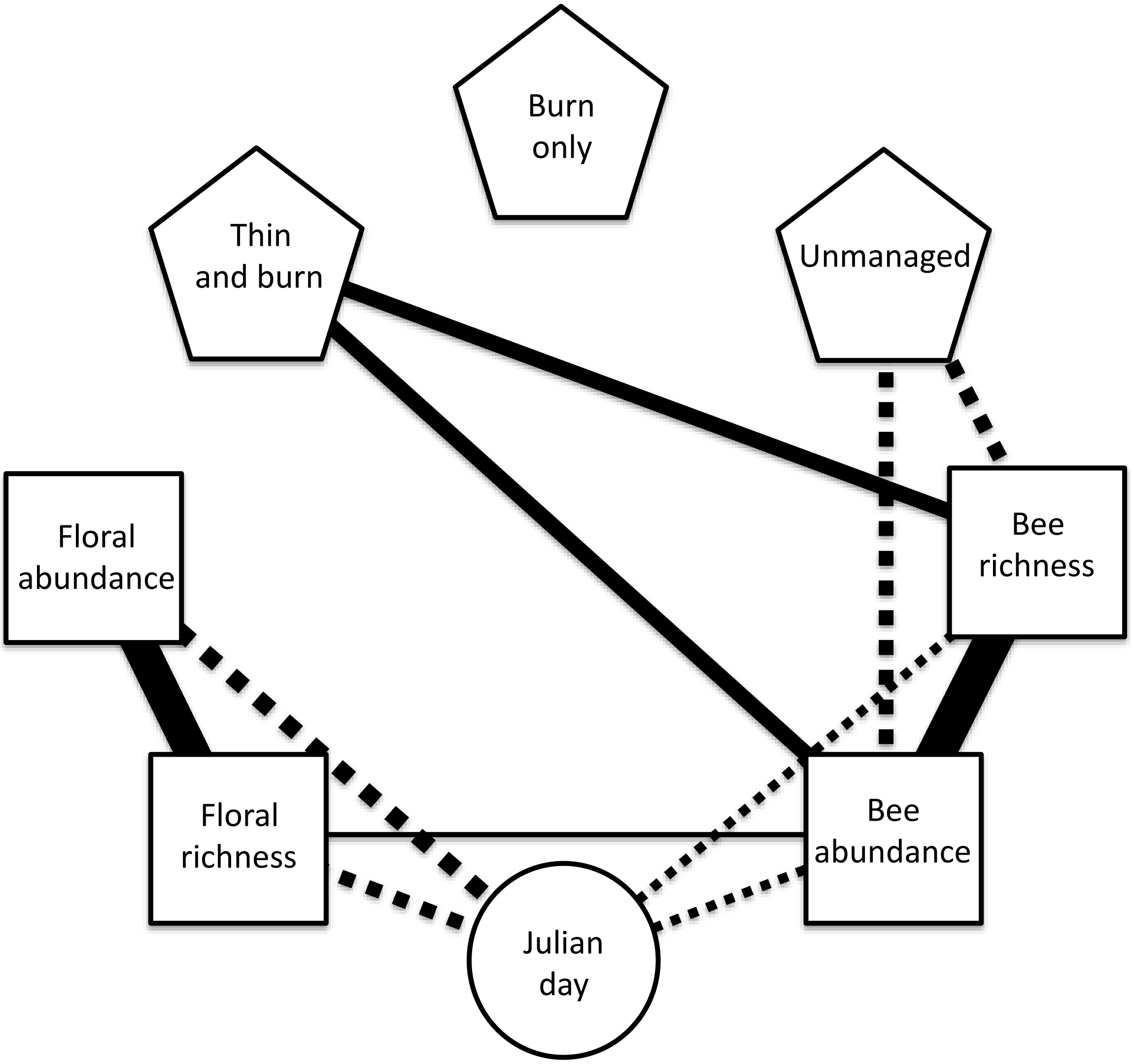


Figure 17A. Diagram of 2011 variable and treatment relationships indicated by Spearman rank correlation. Biotic variables (i.e. bee richness, bee abundance, floral richness, floral abundance) were averaged from biweekly measurement across the season, while abiotic variables (i.e. light, cover) were averaged across two sampling dates. Lines connecting variables represent significant correlations between ranks at α=0.05. The thickness of each line is scaled with the magnitude of Spearman's ρ. Solid lines represent positive relationships among ranked variables, while dashed lines represent negative relationships. Relationships between multiple levels of cover are not shown here due to their logical relationships and to simplify visual interpretation.

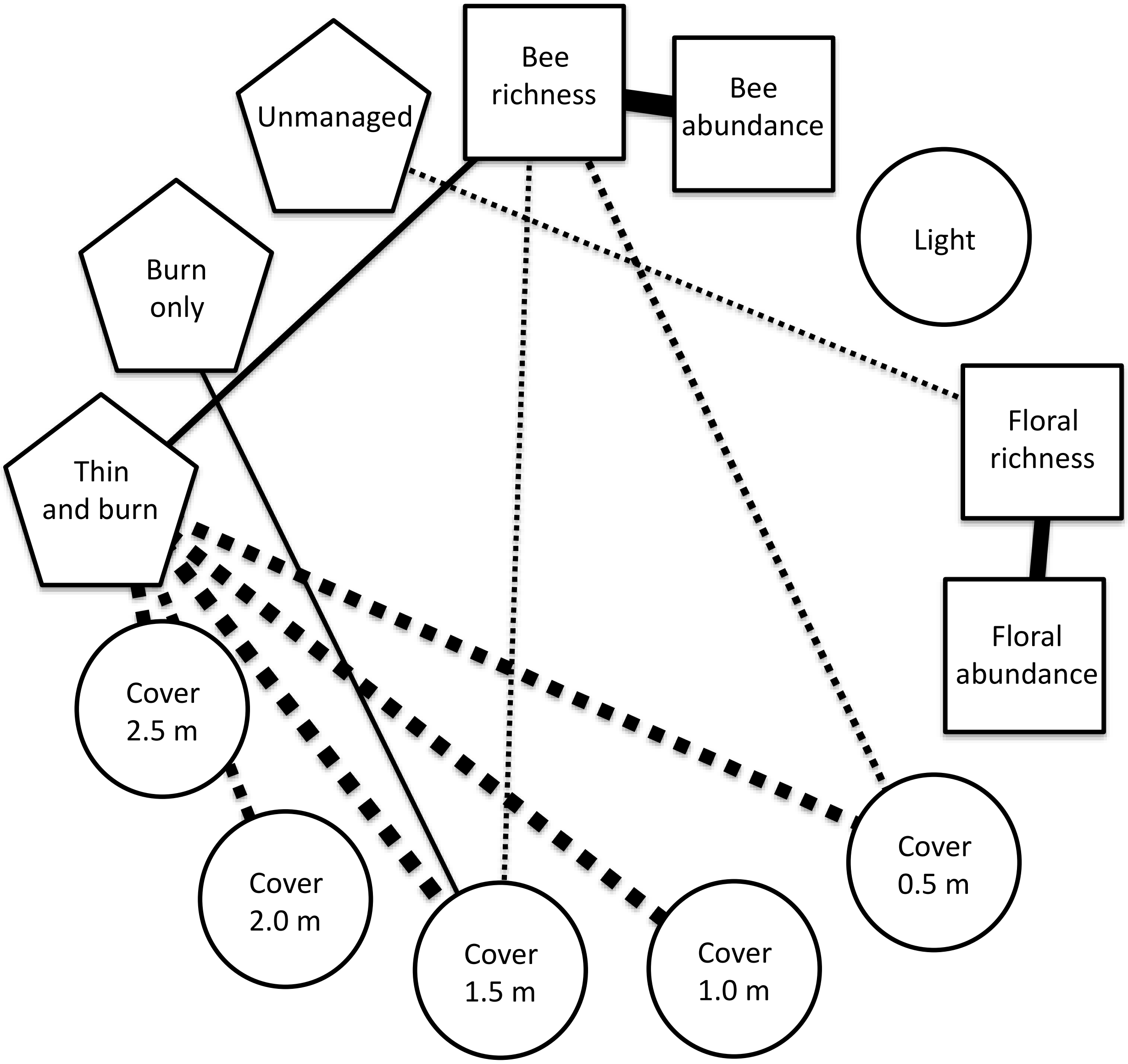
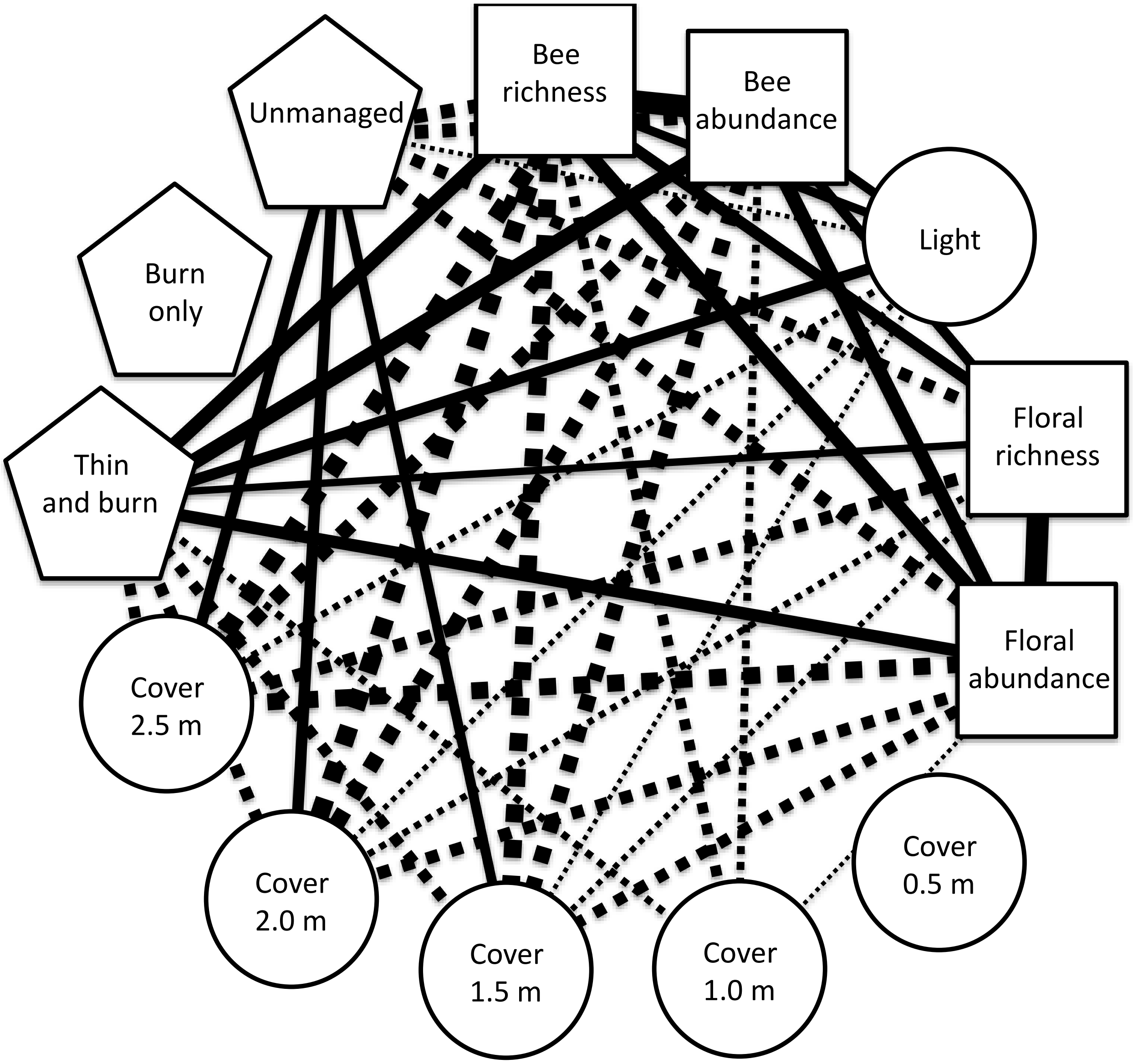


Figure 17B. Diagram of 2012 variable and treatment relationships indicated by Spearman rank correlation. Biotic variables (i.e. bee richness, bee abundance, floral richness, floral abundance) were averaged from biweekly measurement across the season, while abiotic variables (i.e. light, cover) were averaged across two sampling dates. Lines connecting variables represent significant correlations between ranks at α=0.05. The thickness of each line is scaled with the magnitude of Spearman's ρ. Solid lines represent positive relationships among ranked variables, while dashed lines represent negative relationships. Relationships between multiple levels of cover are not shown here due to their logical relationships and to simplify visual interpretation.



APPENDIX D

RECORD OF DEPOSITION OF VOUCHER SPECIMENS

RECORD OF DEPOSITION OF VOUCHER SPECIMENS

The specimens listed below have been deposited in the named museum as samples of those species or other taxa, which were used in this research. Voucher recognition labels bearing the voucher number have been attached or included in fluid preserved specimens.

Voucher Number: 2013-07

Author and Title of thesis:

Mitchell Carl Lettow

"Effects of two oak savanna restoration strategies on light, vegetative cover, flowering forbs, and pollinator communities"

Museum(s) where deposited:
Albert J. Cook Arthropod Research Collection, Michigan State University (MSU)

Specimens:

Table 7. List of bee and butterfly species of voucher specimens deposited at the MSU A. J. Cook Arthropod Research Collection

Family	Genus-Species	Life Stage	Quantity	Preservation
Halictidae	*Agapostemon sericeus*	Adult	1	Pinned
Halictidae	*Agapostemon texanus*	Adult	1	Pinned
Halictidae	*Agapostemon virescens*	Adult	1	Pinned
Andrenidae	*Andrena distans*	Adult	1	Pinned
Andrenidae	*Andrena nasonii*	Adult	1	Pinned
Andrenidae	*Andrena nivalis*	Adult	1	Pinned
Andrenidae	*Andrena perplexa*	Adult	1	Pinned
Apidae	*Anthophora bomboides*	Adult	1	Pinned
Apidae	*Apis mellifera*	Adult	1	Pinned
Halictidae	*Augochlora pura*	Adult	2	Pinned
Halictidae	*Augochlorella aurata*	Adult	2	Pinned
Apidae	*Bombus bimaculatus*	Adult	1	Pinned
Apidae	*Bombus impatiens*	Adult	1	Pinned
Apidae	*Ceratina calcarata*	Adult	1	Pinned
Apidae	*Ceratina strenua*	Adult	1	Pinned
Halictidae	*Halictus confusus*	Adult	1	Pinned
Halictidae	*Halictus ligatus*	Adult	1	Pinned
Halictidae	*Halictus rubicundus*	Adult	1	Pinned
Megachilidae	*Heriades variolosa*	Adult	1	Pinned
Megachilidae	*Hoplitis producta*	Adult	2	Pinned
Megachilidae	*Hoplitis truncata*	Adult	2	Pinned

Table 7 (cont'd).

Colletidae	*Hylaeus annulatus*	Adult	1	Pinned
Halictidae	*Lasioglossum bruneri*	Adult	1	Pinned
Halictidae	*Lasioglossum cattellae*	Adult	1	Pinned
Halictidae	*Lasioglossum coeruleum*	Adult	2	Pinned
Halictidae	*Lasioglossum coriaceum*	Adult	2	Pinned
Halictidae	*Lasioglossum cressonii*	Adult	2	Pinned
Halictidae	*Lasioglossum divergens*	Adult	1	Pinned
Halictidae	*Lasioglossum foveolatum*	Adult	1	Pinned
Halictidae	*Lasioglossum leucozonium*	Adult	2	Pinned
Halictidae	*Lasioglossum lineatulum*	Adult	1	Pinned
Halictidae	*Lasioglossum macoupinense*	Adult	1	Pinned
Halictidae	*Lasioglossum nelumbonis*	Adult	2	Pinned
Halictidae	*Lasioglossum nigroviride*	Adult	1	Pinned
Halictidae	*Lasioglossum oblongum*	Adult	1	Pinned
Halictidae	*Lasioglossum obscurum*	Adult	1	Pinned
Halictidae	*Lasioglossum pectorale*	Adult	2	Pinned
Halictidae	*Lasioglossum pilosum*	Adult	2	Pinned
Halictidae	*Lasioglossum subviridatum*	Adult	2	Pinned
Halictidae	*Lasioglossum timothyi*	Adult	1	Pinned
Halictidae	*Lasioglossum versans*	Adult	2	Pinned
Halictidae	*Lasioglossum versatum*	Adult	1	Pinned
Megachilidae	*Megachile campanulae*	Adult	1	Pinned
Megachilidae	*Megachile montivaga*	Adult	1	Pinned
Apidae	*Melissodes coreopsis*	Adult	1	Pinned
Apidae	*Melissodes desponsa*	Adult	2	Pinned
Apidae	*Nomada* (toothed) *sp. 1*	Adult	1	Pinned
Apidae	*Nomada* (toothed) *sp. 2*	Adult	1	Pinned
Apidae	*Nomada* (toothed) *sp. 3*	Adult	1	Pinned
Megachilidae	*Osmia pumila*	Adult	1	Pinned
Megachilidae	*Stelis lateralis*	Adult	1	Pinned
Hesperiidae	*Amblyscirtes vialis*	Adult	1	Pinned
Satyridae	*Enodia anthedon*	Adult	1	Pinned
Hesperiidae	*Epargyreus clarus*	Adult	1	Pinned
Satyridae	*Megisto cymela*	Adult	1	Pinned
Nymphalidae	*Nymphalis antiopa*	Adult	1	Pinned
Papilionidae	*Papilio cresphontes*	Adult	1	Pinned
Papilionidae	*Papilio glaucus*	Adult	1	Pinned
Papilionidae	*Papilio troilus*	Adult	1	Pinned
Hesperiidae	*Poanes hobomok*	Adult	1	Pinned
Nymphalidae	*Polygonia interrogationis*	Adult	1	Pinned
Nymphalidae	*Speyeria cybele cybele*	Adult	1	Pinned

Table 7 (cont'd).

Nymphalidae	*Vanessa virginiensis*	Adult	1	Pinned

APPENDIX E

SEED SET OF NATIVE SENTINEL PLANTS

Methods

In order to determine whether restoration methods affected realized pollination of understory forbs, we conducted a pollination experiment with potted native forb species. *Helianthus divaricatus* L. and *Rudbeckia hirta* L. were the forb species that we selected for experimentation based on commercial availability, obligate outcrossing, presence at MacCready Reserve in areas of high light availability, and their reported occupation of high quality oak savannas by other researchers.

We potted purchased plugs of both species, and maintained them in greenhouses until individual plants approached blooming. When each species of plants approached their bloom, we covered them with fine mesh intended to exclude pollinators and other insects. When plants were actively blooming (determined by presence of pollen on anthers) we took 60 individuals of similar progress in blooming, and randomly assigned four plants to each experimental plot. Two of each four assigned plants were designated as “open” and two were designated as “closed.” These 60 plants were transported to MacCready Reserve, and staked four plants into the ground at one randomly selected pollinator sampling station near the center of each plot. At this time, we removed mesh netting from open plants, while closed plants retained their mesh. We visited plots ~ two days after deployment, we watered plants using 1 l water for each plant, and subsequently made pollinator observations of open plants for four minutes per array. After four days, we returned to plots, covered open plants with mesh, and transported plants back to the greenhouse where they were left until seed set.

Following seed set, whole dried seed heads were collected from both closed and open plants of each species. All *H. divaricatus* seeds were counted, and separated into “empty” and “filled” categories based on visual differences, and a “pinch test.” *R. hirta* were spread onto trays, where a subsample of 25 seeds per plant were randomly selected. Empty seeds were assumed to not have been pollinated, while filled seeds were assumed to have been pollinated. Filled *H. divaricatus* seeds were visibly more distended, mottled with dark color, and remained firm upon pinching with forceps, while empty seeds lacked these features. Filled *R. hirta* seeds were jet black, distended, and resisted compression when pinched with forceps. We verified our visual distinction by dissecting seeds of both species, and additionally weighing 25 filled and empty *H. divaricatus* for comparison (Figure 26). Filled seeds from both species revealed starchy, full, white interiors, while empty seeds were shriveled, and void of starchy contents. Empty and filled seeds of each species were then counted, using the aforementioned criteria for distinction, and seeds of *H. divaricatus* were weighed. Seeds of *R. hirta* were too light to make meaningful comparisons with the lack of precision of our scales. We then calculated the mean number of filled seeds for closed and open plants of both species across all three treatments and years (Figures 27, 28, 29, and 30).

Figure 18. Mean weight ± SEM of visually separated “filled” and “empty” seeds of *Helianthus divaricatus* used in pollination experiment.

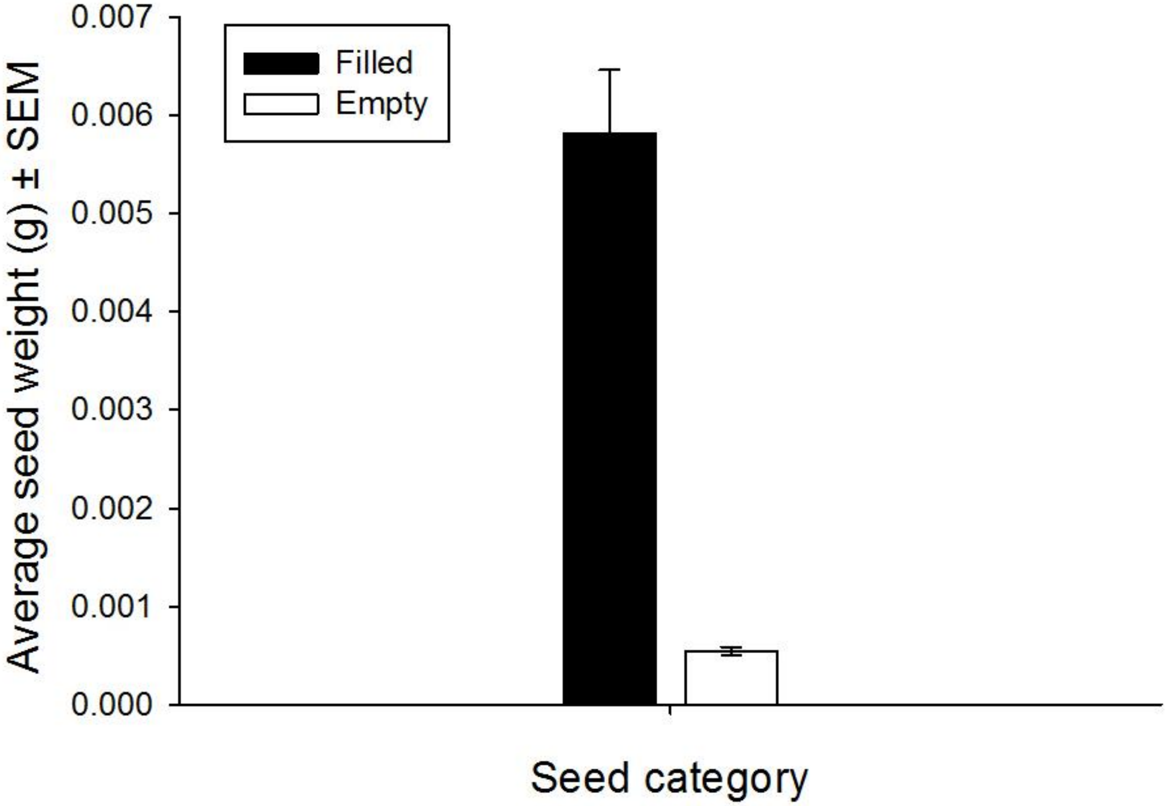


Figure 19A. Mean number of filled seeds ± SEM of *Helianthus divaricatus* from sentinel plant experiment between treatments in 2011. Open plants had no mesh covering inflorescences while closed plants excluded pollinators with mesh.

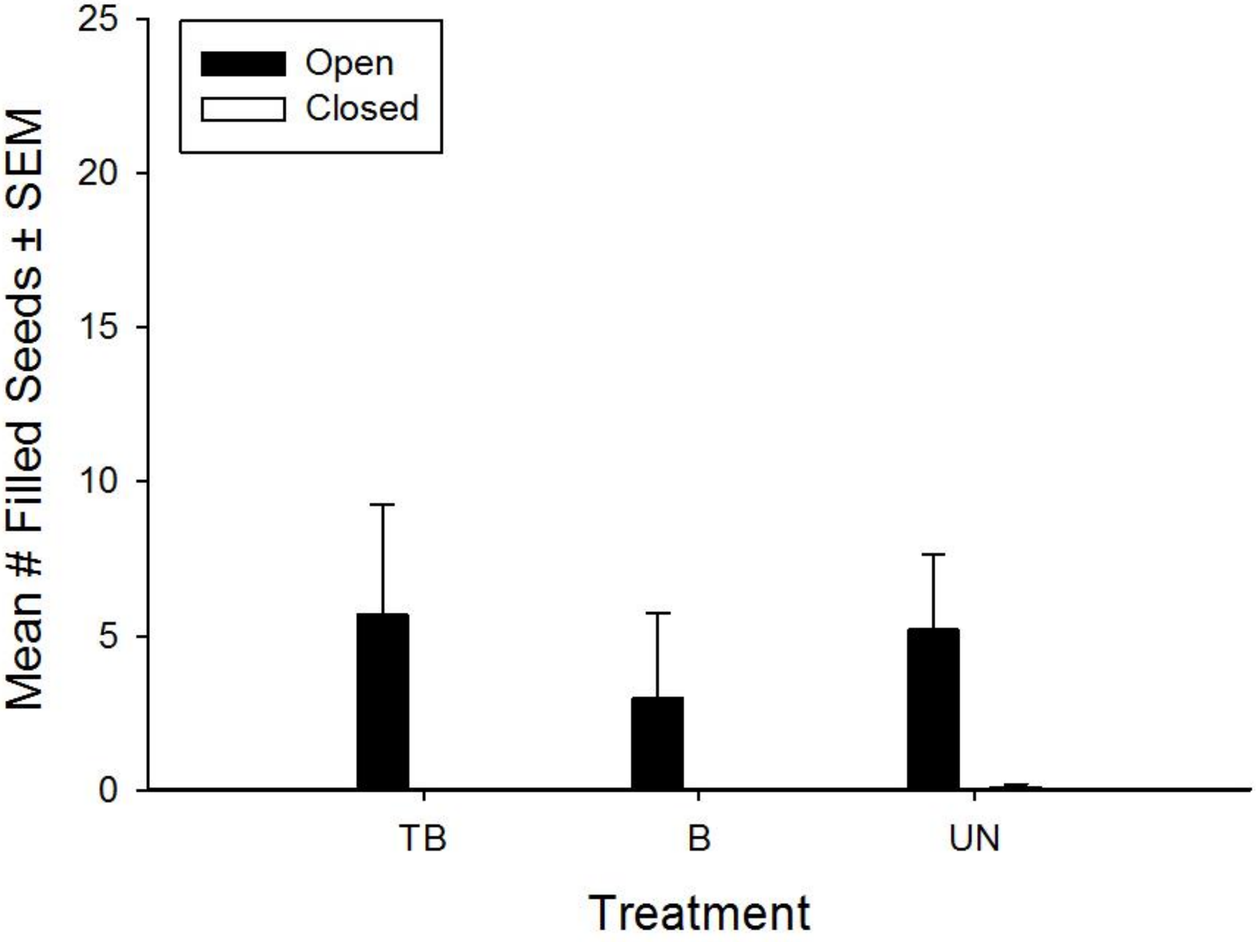


Figure 19B. Mean number of filled seeds ± SEM of *Helianthus divaricatus* from sentinel plant experiment between treatments in 2012. Open plants had no mesh covering inflorescences while closed plants excluded pollinators with mesh.

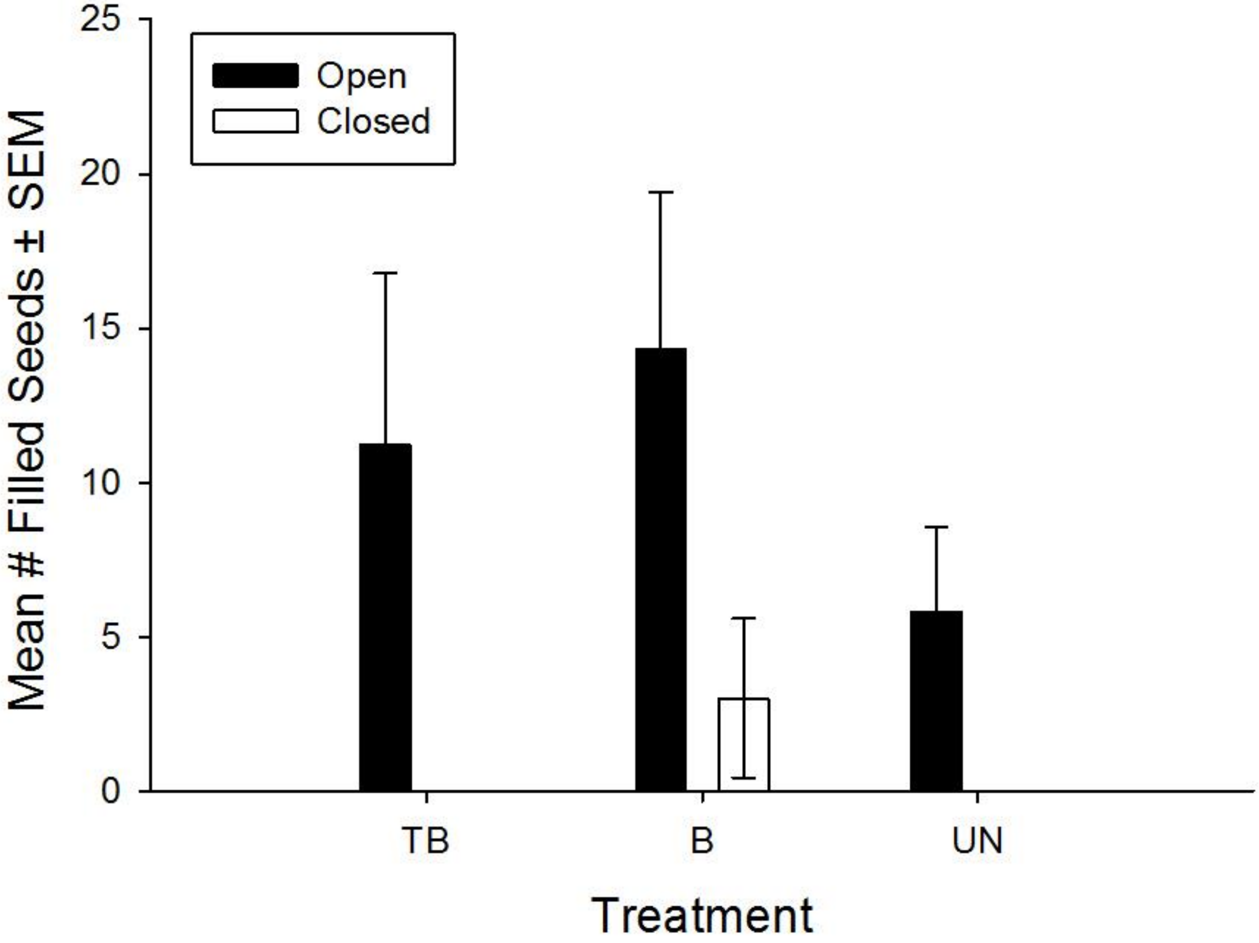


Figure 20A. Mean number of filled seeds ± SEM of *Rudbeckia hirta* from sentinel plant experiment between treatments in 2011. Open plants had no mesh covering inflorescences while closed plants excluded pollinators with mesh.

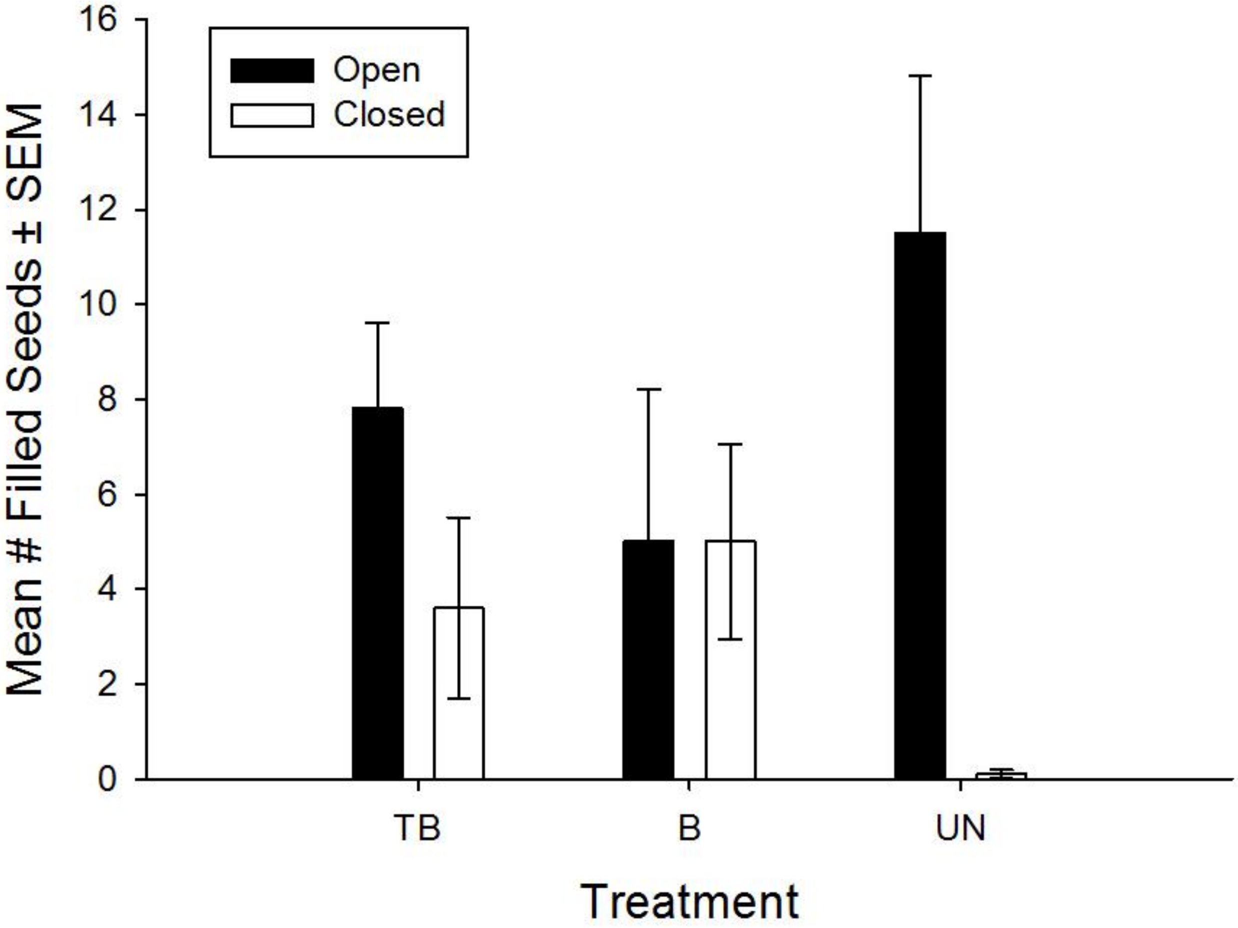
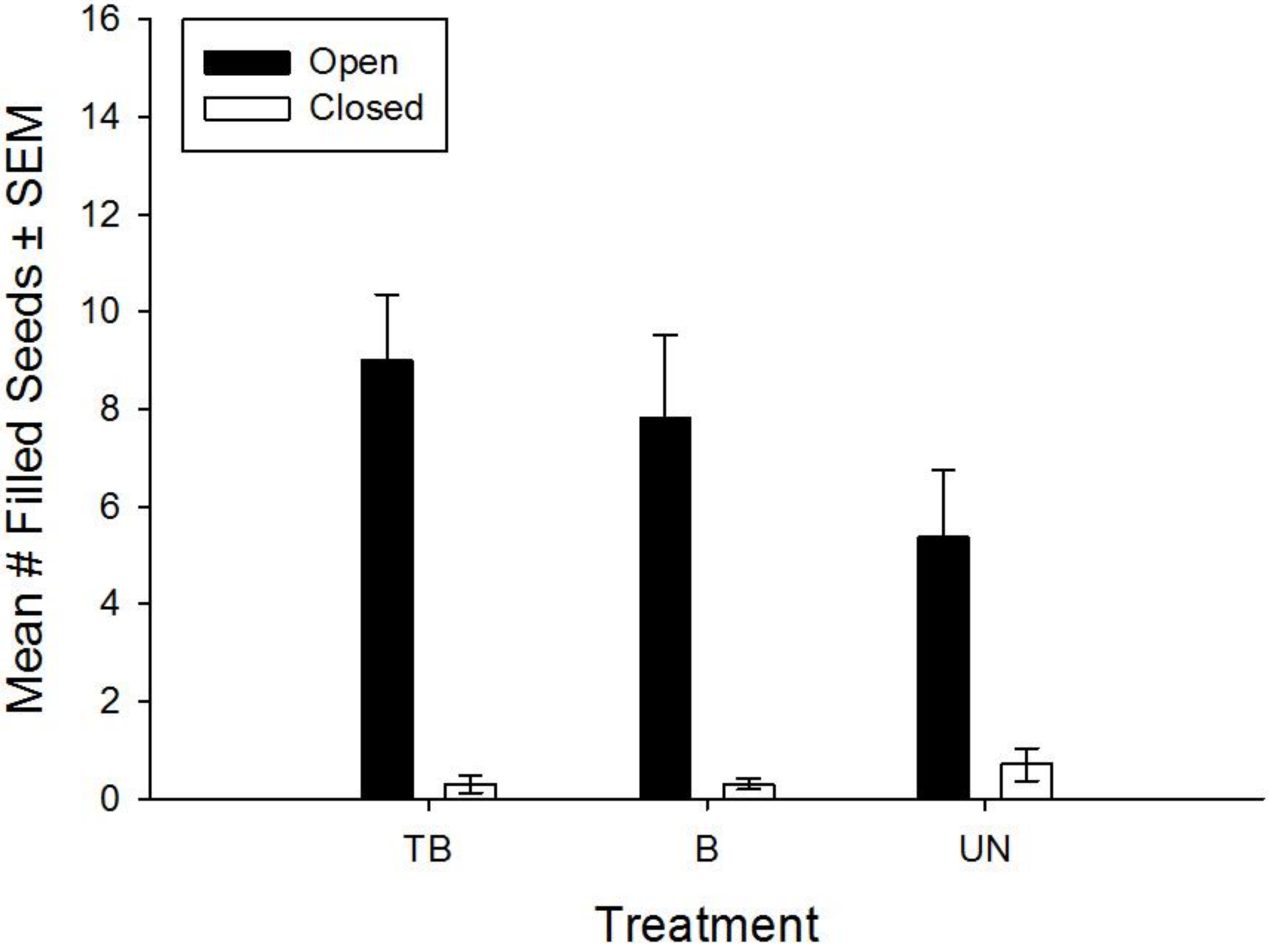


Figure 20B. Mean number of filled seeds ± SEM of *Rudbeckia hirta* from sentinel plant experiment between treatments in 2012. Open plants had no mesh covering inflorescences while closed plants excluded pollinators with mesh.



LITERATURE CITED

LITERATURE CITED

Abella, S. R. (2010). "Thinning Pine Plantations to Reestablish Oak Openings Species in Northwestern Ohio." Environmental Management 46(3): 391-403.

Abella, S. R., J. F. Jaeger, et al. (2001). "Restoring Historic Plant Communities in the Oak Openings Region of Northwest Ohio." Ecological Restoration 19(3): 155.

Abella, S. R., J. F. Jaeger, et al. (2004). "Fifteen years of plant community dynamics during a northwest Ohio oak savanna restoration." The Michigan Botanist 43: 117-127.

Abrams, M. D. (1992). "Fire and the Development of Oak Forests." Bioscience 42(5): 346-353.

Abrams, M. D. (1996). "Distribution, historical development and ecophysiological attributes of oak species in the eastern United States." Annales Des Sciences Forestieres 53(2-3): 487-512.

Abrams, M. D. and G. J. Nowacki (2008). "Native Americans as active and passive promoters of mast and fruit trees in the eastern USA." Holocene 18(7): 1123-1137.

Albert, D.A. 1995. Regional landscape ecosystems of Michigan, Minnesota, and Wisconsin: A working map and classification. Gen. Tech. Rep. NC-178. St. Paul, MN: USDA, Forest Service, North Central Forest Experiment Station, St. Paul, MN. http://nrs. fs.fed.us/pubs/242 (Version 03JUN1998). 250 pp.

Albrecht, M., P. Duelli, et al. (2007). "The Swiss agri-environment scheme enhances pollinator diversity and plant reproductive success in nearby intensively managed farmland." Journal of Applied Ecology 44(4): 813-822.

Albrecht, M., B. Schmid, et al. (2012). "Diverse pollinator communities enhance plant reproductive success." Proceedings of the Royal Society B-Biological Sciences 279(1748): 4845-4852.

Alexander, H. D., M. A. Arthur, et al. (2008). "Survival and growth of upland oak and co-occurring competitor seedlings following single and repeated prescribed fires." Forest Ecology and Management 256(5): 1021-1030.

Anderson, R. C. and L. E. Brown (1986). "Stability and Instability in Plant Communities Following Fire." American Journal of Botany 73(3): 364-368.

Anderson, R. C., S. L. Jones, et al. (2006). "Modifying distance methods to improve estimates of historical tree density from General Land Office survey records." Journal of the Torrey Botanical Society 133(3): 449-459.

Apfelbaum, S.I. and A.W. Haney. (1991). “Management of degraded oak savannah remnants in the upper Midwest: Preliminary results from three years of study.” In, G.V. Burger, J.E.

Ebinger, and G.S. Wilhelm (eds.), Proceedings of the Oak Woods Managment Workshop. Eastern Illinois Univeristy, Charleston.

Asbjornsen, H., L. A. Brudvig, et al. (2005). "Defining reference information for restoring ecologically rare tallgrass oak savannas in the Midwestern United States." Journal of Forestry 103(7): 345-350.

Au, L., D. E. Andersen, et al. (2008). "Patterns in bird community structure related to restoration of Minnesota dry oak savannas and across a prairie to oak woodland ecological gradient." Natural Areas Journal 28(4): 330-341.

Axelrod, D. I. (1985). Rise of the grassland biome in central North America. Botanical Review 51:163-201

Bader, B. J. (2001). "Developing a Species List for Oak Savanna/Oak Woodland Restoration at the university of Wisconsin-Madison Arboretum." Ecological Restoration 19(4): 242.

Baskerville, G. L. and P. Emin (1969). "Rapid Estimation of Heat Accumulation from Maximum and Minimum Temperatures." Ecology 50(3): 514-517.

Bayley, C. C. (1954). Western trip. An address given at Manlius, N.Y.”Bayley Wis. Mag. Hist., 37:237-39.

Beal, W. J. (1898). Seed dispersal. Boston, Massachusetts, The Anthenaeum Press.

Benadi, G., N. Bluthgen, et al. (2012). "Population Dynamics of Plant and Pollinator Communities: Stability Reconsidered." American Naturalist 179(2): 157-168.

Bock, C. E., Z. F. Jones, et al. (2007). "Relationships between species richness, evenness, and abundance in a southwestern Savanna." Ecology 88(5): 1322-1327.

Bowles, M. L. and J. L. McBride (1998). "Vegetation composition, structure, and chronological change in a decadent midwestern North American savanna remnant." Natural Areas Journal 18(1): 14-27.

Bowles, M., S. Apfelbaum, et al. (2011). "Canopy cover and groundlayer vegetation dynamics in a fire managed eastern sand savanna." Forest Ecology and Management 262(11): 1972-1982.

Bowman, D., J. Balch, et al. (2011). "The human dimension of fire regimes on Earth." Journal of Biogeography 38(12): 2223-2236.

Brawn, J. D. (2006). "Effects of restoring oak savannas on bird communities and populations." Conservation Biology 20(2): 460-469.

Bray, J. R. (1958). "The distribution of savanna species in relation to light intensity." Canadian Journal of Botany 36(5): 671-681.

Bray, J. R. (1960). "The composition of savanna vegetation in Wisconsin." Ecology 41(4): 721-732.

Brudvig, L. A. and C. M. Mabry (2008). "Trait-based filtering of the regional species pool to guide understory plant reintroductions in Midwestern oak savannas, USA." Restoration Ecology 16(2): 290-304.

Brudvig, L. A. and H. Asbjornsen (2005). "Oak regeneration before and after initial restoration efforts in a tall grass oak savanna." American Midland Naturalist 153(1): 180-186.

Brudvig, L. A. and H. Asbjornsen (2009). "The removal of woody encroachment restores biophysical gradients in Midwestern oak savannas." Journal of Applied Ecology 46(1): 231-240.

Brudvig, L. A. (2011). "The restoration of biodiversity: where has research been and where does it need to go?" American Journal of Botany 98(3): 549-558.

Brudvig, L. A., H. M. Blunck, et al. (2011). "Influences of woody encroachment and restoration thinning on overstory savanna oak tree growth rates." Forest Ecology and Management 262(8): 1409-1416.

Brudvig, L. and H. Asbjornsen (2007). "Stand structure, composition, and regeneration dynamics following removal of encroaching woody vegetation from Midwestern oak savannas." Forest Ecology and Management 244(1-3): 112-121.

Buddle, C. M., J. Beguin, et al. (2005). "The importance and use of taxon sampling curves for comparative biodiversity research with forest arthropod assemblages." Canadian Entomologist 137(1): 120-127.

Campbell, J. W., J. L. Hanula, et al. (2007). "Effects of prescribed fire and fire surrogates on floral visiting insects of the blue ridge province in North Carolina." Biological Conservation 134(3): 393-404.

Chapman, K. A. and R. Brewer (2008). "Prairie and Savanna in Southern Lower Michigan: History, Classification, Ecology." The Michigan Botanist 47(1): 1-50.

Chiang, J. M., M. A. Arthur, et al. (2005). "The effect of prescribed fire on gap fraction in an oak forest understory on the Cumberland Plateau." Journal of the Torrey Botanical Society 132(3): 432-441.

Choi, Y. D. (2007). "Restoration Ecology to the Future: A Call for New Paradigm." Restoration Ecology 15(2): 351-353.

Clark, J. S. (1988). "Effect of climate change on fire regimes in northwestern Minnesota." Nature 334(6179): 233-235.

Cole, K. L. and R. S. Taylor (1995). "Past and current trends of change in a dune prairie oak savanna reconstructed through a multiple-scale history." Journal of Vegetation Science 6(3): 399-410.

Colwell, R. K. and J. A. Coddington (1994). "Estimating terrestrial biodiversity through extrapolation." Philosophical Transactions of the Royal Society of London Series B-Biological Sciences 345(1311): 101-118.

Considine, C. D., J. W. Groninger, et al. (2013). "Fire History and Stand Structure of High Quality Black Oak (Quercus velutina) Sand Savannas." Natural Areas Journal 33(1): 10-20.

Cottam, G. (1949). "The Phytosociology of an Oak Woods in Southwestern Wisconsin." Ecology 30(3): 271-287.

Curtis, J. T. (1955). "A Prairie Continuum in Wisconsin." Ecology 36(4): 558-566.

Curtis, J. T. (1959). The Vegetation of Wisconsin. Madison, Wisconsin, University of Wisconsin Press.

Cutter, B. E. and R. P. Guyette (1994). "Fire frequency on an oak-hickory ridgetop in the Missouri Ozarks." American Midland Naturalist 132(2): 393-398.

Davis, M. A., D. W. Peterson, et al. (2000). "Restoring savanna using fire: Impact on the breeding bird community." Restoration Ecology 8(1): 30-40.

DeSantis, R. D., S. W. Hallgren, et al. (2011). "Drought and fire suppression lead to rapid forest composition change in a forest-prairie ecotone." Forest Ecology and Management 261(11): 1833-1840.

Dey, D., R. Guyette, et al. (2004). Fire history of a forest, savanna, and fen mosaic at White Ranch State Forest. Upland oak ecology symposium: history, current conditions, and sustainability, Asheville, NC: US Department of Agriculture, Forest Service, Southern Research Station, Missouri Department of Conservation.

Dicks, L. V., S. A. Corbet, et al. (2002). "Compartmentalization in plant-insect flower visitor webs." Journal of Animal Ecology 71(1): 32-43.

Dijkstra, F. A., K. Wrage, et al. (2006). "Tree Patches Show Greater N Losses but Maintain Higher Soil N Availability than Grassland Patches in a Frequently Burned Oak Savanna." Ecosystems 9(3): 441-452.

Dixon, K. W. (2009). "Pollination and Restoration." Science 325(5940): 571-573.

Droege, S. (2012). The Very Handy Manual: How to Catch and Identify Bees and Manage a Collection.

Eagle, A., E. M. Hay-Chmielewski, et al. (2005) Michigan's Wildlife Action Plan. Michigan Department of Natural Resources.

Evans, E. W. (1984). "Fire as a natural disturbance to grasshopper assemblages of tallgrass prairie." Oikos 43(1): 9-16.

Faberlangendoen, D. and J. R. Tester (1993). "Oak mortality in sand savannas following drought in East-Central Minnesota." Bulletin of the Torrey Botanical Club 120(3): 248-256.

Faberlangendoen, D. and M. A. Davis (1995). "Effects of fire frequency on tree canopy cover at Allison-savanna, East-Central Minnesota, USA." Natural Areas Journal 15(4): 319-328.

Fiedler, A. K., D. A. Landis, et al. (2012). "Rapid Shift in Pollinator Communities Following Invasive Species Removal." Restoration Ecology 20(5): 593-602.

Gibbs, J. (2011). "Revision of the metallic Lasioglossum (Dialictus) of eastern North America (Hymenoptera: Halictidae: Halictini)." Zootaxa(3073): 1-+.

Giles, V. and J. S. Ascher (2006). "A survey of the bees of the Black Rock Forest preserve, New York (Hymenoptera : Apoidea)." Journal of Hymenoptera Research 15(2): 208-231.

Glasgow, L. S. and G. R. Matlack (2007). "Prescribed burning and understory composition in a temperate deciduous forest, Ohio, USA." Forest Ecology and Management 238(1-3): 54-64.

Gleason, H. A. (1913). "Review: Relation of Prairie and Forest in Central Illinois." Journal of Ecology 1(2): 152-155.

Gleason, H. A. (1917). A prairie near Ann Arbor, Michigan. Rhodora. 19: 163-165.

Gleditsch JM, Carlo TA. 2011. Fruit quantity of invasive shrubs predicts the abundance of common native avian frugivores in central Pennsylvania. Diversity and Distributions 17: 244–253.

Gobster, P.H. 1994. "The Urban Savanna: Reuniting ecological preference and function." Restoration & Management Notes 12(1):64-71

Grimm, E. C. (1983). "Chronology and dynamics of vegetation change in the prairie-woodland region of Southern Minnesota, USA." New Phytologist 93(2): 311-350.

Grundel, R., N. B. Pavlovic, et al. (1998). "The effect of canopy cover and seasonal change on host plant quality for the endangered Karner blue butterfly ." Oecologia 114(2): 243-250.

Grundel, R., R. P. Jean, et al. (2010). "Floral and nesting resources, habitat structure, and fire influence bee distribution across an open-forest gradient." Ecological Applications 20(6): 1678-1692.

Grundel, R., R. P. Jean, et al. (2011). "A Survey of Bees (Hymenoptera: Apoidea) of the Indiana Dunes and Northwest Indiana, USA." Journal of the Kansas Entomological Society 84(2): 105-138.

Gutierrez, D., J. L. Leon-Cortes, et al. (2001). "Metapopulations of four lepidopteran herbivores on a single host plant, Lotus corniculatus." Ecology 82(5): 1371-1386.

Guyette, R.P. and B.E. Cutter. 1991. Tree-ring analysis of fire history of a post oak savanna in the Missouri Ozarks. Natural Areas Journal, 11:93-99.

Haney, A., M. Bowles, et al. (2008). "Gradient analysis of an eastern sand savanna's woody vegetation, and its long-term responses to restored fire processes." Forest Ecology and Management 256(8): 1560-1571.

Harding, J. (1997). Amphibians and Reptiles of the Great Lakes Region. Ann Arbor, Michigan, The University of Michigan Press.

Harrington, J. A. and E. Kathol (2009). "Responses of Shrub Midstory and Herbaceous Layers to Managed Grazing and Fire in a North American Savanna (Oak Woodland) and Prairie Landscape." Restoration Ecology 17(2): 234-244.

Hedtcke, J., J. Posner, et al. (2009). "Browsing for conservation: Springtime forage value of midstory shrubs of degraded oak savannas in southern wisconsin." Renewable Agriculture and Food Systems 24(4): 293-299.

Hegland, S. J., J. Dunne, et al. (2010). "How to monitor ecological communities cost-efficiently: The example of plant-pollinator networks." Biological Conservation 143(9):

2092-2101.

Heikens, A. L. and P. A. Robertson (1994). "Barrens of the Midwest: A Review of the Literature." Castanea 59(3): 184-194.

Henderson, R. (1995). Wisconsin's Biodiversity as a Management Issue, Oak Savanna Communities. Madison, Department of Natural Resources: 88-96.

Herman, K. D., L. A. Masters, M. R. Penskar, A. A. Reznicek, G. S. Wilhelm, W. W. Brodovich, and K. P. Gardiner. 2001. Floristic quality assessment with wetland categories and exapmles of computer applications for the state of Michigan. Michigan DNR, Wildlife Division, Natural Heritage Program, Lansing, MI.

Hoekstra, J. M., T. M. Boucher, et al. (2005). "Confronting a biome crisis: global disparities of habitat loss and protection." Ecology Letters 8(1): 23-29.

Houdeshell, H., R. L. Friedrich, et al. (2011). "Effects of Prescribed Burning on Ant Nesting Ecology in Oak Savannas." American Midland Naturalist 166(1): 98-111.

Hubbard, Bela. (1872) “A Michigan geological expedition in 1837.” Collections of the Pioneer Society of the State of Michigan, Volume 3

Hubbard, Bela. (1887). Memorials of a Half Century in Michigan and the Lake Regions. G. P. Putnam Sons.

Hubbard, Bela. Memorials of a Half-Century. New York: The Knickerbocker Press. 1887.

Hughes, F. M. R., A. Colston, et al. (2005). "Restoring riparian ecosystems: The challenge of accommodating variability and designing restoration trajectories." Ecology and Society 10(1).

Huffman, J. M. and P. A. Werner (2000). Restoration of Florida pine savanna: Flowering response of Lilium catesbaei to fire and roller-chopping. Natural Areas Journal 20(1): 12-23.

Hutchinson, T. F., R. E. J. Boerner, et al. (2005). Prescribed fire effects on the herbaceous layer of mixed-oak forests. Canadian Journal of Forest Research 35(4): 877-890.

Karnitz, H. and H. Asbjornsen (2006). "Composition and age structure of a degraded tallgrass
oak savanna in central Iowa." Natural Areas Journal 26(2): 179-186.

Kay, A. D., J. D. Schade, et al. (2007). "Fire effects on insect herbivores in an oak savanna: the role of light and nutrients." Ecological Entomology 32(6): 754-761.

Kevan, P. G. and H. G. Baker (1983). "Insects as flower visitors and pollinators." Annual Review of Entomology 28: 407-453.

Keeley, J. E. and C. J. Fotheringham (1998). "Mechanism of smoke-induced seed germination in a post-fire chaparral annual." Journal of Ecology 86(1): 27-36.

Kern, C. C., P. B. Reich, et al. (2012). "Do deer and shrubs override canopy gap size effects on growth and survival of yellow birch, northern red oak, eastern white pine, and eastern hemlock seedlings?" Forest Ecology and Management 267: 134-143.

King, R. S., K. E. Brashear, et al. (2007). "Red-headed woodpecker nest-habitat thresholds in restored savannas." Journal of Wildlife Management 71(1): 30-35.

Knapp, A. K., J. M. Blair, et al. (1999). "The keystone role of bison in north American tallgrass prairie - Bison increase habitat heterogeneity and alter a broad array of plant, community, and ecosystem processes." Bioscience 49(1): 39-50.

Knight, K. S., J. S. Kurylo, A. G. Endress, and J. R. Stewart. 2007. Ecology and ecosystem impacts of common buckthorn (Rhamnus cathartica): a review. Biol. Invasions 9: 925-937.

Kost, M.A., D.A. Albert, J.G. Cohen, B.S. Slaughter, R.K. Schillo, C.R. Weber, and K.A. Chapman. 2007. Natural Communities of Michigan: Classification and Description. Michigan Natural Features Inventory, Report No. 2007-21, Lansing, MI.

Kudo, G., T. Y. Ida, et al. (2008). "Linkages between phenology, pollination, photosynthesis, and reproduction in deciduous forest understory plants." Ecology 89(2): 321-331.

Leach, M. K. and L. Ross (1995). Midwest oak ecosystems recovery plan: A call to action. Midwest Oak Savanna and Woodland Ecosystems Conferences. Springfield, Missouri.

Leach, M. K. and T. J. Givnish (1999). "Gradients in the composition, structure, and diversity of remnant oak savannas in southern Wisconsin." Ecological Monographs 69(3): 353-374.

Lee, Y. and J. T. Legge. (2000). Special animal abstract for Sistrurus catenatus catenatus (eastern massasauga). Michigan Natural Features Inventory, Lansing, MI. 4 pp.

Mack, R.N. (2003). Plant naturalizations and invasions in the eastern United States: 1634-1860. Annals of the Missouri Botanical Garden 90: 77- 90.

Matthews, J. W., G. Spyreas, et al. (2009). "Trajectories of vegetation-based indicators used to assess wetland restoration progress." Ecological Applications 19(8): 2093-2107.

McEwan, R. W., T. F. Hutchinson, et al. (2007). "Temporal and spatial patterns in fire occurrence during the establishment of mixed-oak forests in eastern North America." Journal of Vegetation Science 18(5): 655-664.

Memmott, J. (1999). "The structure of a plant-pollinator food web." Ecology Letters 2(5): 276-280.

Menz, M. H. M., R. D. Phillips, et al. (2011). "Reconnecting plants and pollinators: challenges in the restoration of pollination mutualisms." Trends in Plant Science 16(1): 4-12.

Montoya, D., L. Rogers, et al. (2012). "Emerging perspectives in the restoration of biodiversity-based ecosystem services." Trends in Ecology & Evolution 27(12): 666-672.

Muir, J. (1913). The Story of my Boyhood and Youth. Nature Writings, New York, The Library of America 7.

Nelson, C. R., C. B. Halpern, et al. (2008). "Thinning and burning result in low-level invasion by nonnative plants but neutral effects on natives." Ecological Applications 18(3): 762-770.

Nicolai, V. (1991). "Reactions of the fauna on the bark of trees to the frequency of fires in a North-American savanna." Oecologia 88(1): 132-137.

Nielsen, M. C. (1999). Michigan Butterflies & Skippers: A field guide and reference. East Lansing, MI, Michigan State University Extension.

Nielsen, S., C. Kirschbaum, et al. (2003). "Restoration of midwest oak barrens: Structural manipulation or process-only?" Conservation Ecology 7(2).

Nowacki, G. J. and M. D. Abrams (2008). "The demise of fire and "Mesophication" of forests in the eastern United States." Bioscience 58(2): 123-138.

Nuzzo, V. A. (1986). "Extent and status of Midwest oak savanna: presettlement and 1985." Natural Areas Journal 6(2): 6-36.

Nuzzo, V. A., W. McClain, et al. (1996). "Fire impact on groundlayer flora in a sand forest 1990-1994." American Midland Naturalist 136(2): 207-221.

O'Connor, R. P. (2006). A Land Managers Guide to Prairies and Savannas in Michigan: History, Classification, and Management. Lansing, Michigan.

O'Connor, R. P., M. A. Kost, et al. (2009). Prairies and Savannas in Michigan:

Rediscovering Our Natural Heritage. East Lansing, Michigan, Michigan State University Press.

Ollerton, J., R. Winfree, et al. (2011). "How many flowering plants are pollinated by animals?" Oikos 120(3): 321-326.

Packard, S. 1988b. Just a few oddball species: restoration and the rediscovery of the tallgrass savanna. Restoration and Management Notes 6(1):13-20.

Packard, S. and C. F. Mutel (2005). The Tallgrass Restoration Handbook, Society for Ecological Restoration International.

Packard, Steve, "Just a Few Oddball Species: Restoration and the Rediscovery of the Tallgrass Savanna", Restoration and Management Notes, Vol. 6, No. 1 (Summer 1998).

Panzer, R. and M. W. Schwartz (1998). "Effectiveness of a vegetation-based approach to insect conservation." Conservation Biology 12(3): 693-702.

Panzer, R., K. Gnaedinger, et al. (2010). "The Prevalence and Status of Conservative Prairie and Sand Savanna Insects in the Chicago Wilderness Region." Natural Areas Journal 30(1): 73-81.

Pavlovic, N. B., R. Grundel, et al. (2006). "Groundlayer vegetation gradients across oak woodland canopy gaps." Journal of the Torrey Botanical Society 133(2): 225-239.

Pavlovic, N. B., S. A. Leicht-Young, et al. (2011). "Short-term effects of burn season on flowering phenology of savanna plants." Plant Ecology 212(4): 611-625.

Petchey, O. L. and K. J. Gaston (2006). "Functional diversity: back to basics and looking forward." Ecology Letters 9(6): 741-758.

Peterson, D. W. and P. B. Reich (2001). "Prescribed fire in oak savanna: Fire frequency effects on stand structure and dynamics." Ecological Applications 11(3): 914-927.

Peterson, D. W., P. B. Reich, et al. (2007). "Plant functional group responses to fire frequency and tree canopy cover gradients in oak savannas and woodlands." Journal of Vegetation Science 18(1): 3-12.

Pickens, B. A. and K. V. Root (2008). "Factors affecting host-plant quality and nectar use for the Karner blue butterfly: Implications for oak savanna restoration." Natural Areas Journal 28(3): 210-217.

Polziehn, R. O., J. Hamr, et al. (2000). "Microsatellite analysis of North American wapiti (Cervus elaphus) populations." Molecular Ecology 9(10): 1561-1576.

Proctor, E., E. Nol, et al. (2012). "Responses of insect pollinators and understory plants to silviculture in northern hardwood forests." Biodiversity and Conservation 21(7): 1703-1740.

Pruka, B.W. 1994. Distribution of understory plant species along light and soil depth gradients in an upland oak savanna remnant in southern Wisconsin. M.S. Thesis (Land Resources), University of Wisconsin, Madison. 271 pp.

Pyne, S. J. (1983). "Indian Fires." Natural History 92(2): 6-&.

Rabe, A. J. and D. E. Soltis (1999). "Pollen tube growth and self-incompatibility in Heuchera micrantha var. diversifolia (Saxifragaceae)." International Journal of Plant Sciences 160(6): 1157-1162.

Reich, P. B., D. W. Peterson, et al. (2001). "Fire and vegetation effects on productivity and nitrogen cycling across a forest-grassland continuum." Ecology 82(6): 1703-1719.

Rentch, J. S. (2010). "Relationship between treefall direction, slope-aspect, and wind in eight old-growth oak stands in the Central Hardwood Forest, USA." Journal of the Torrey Botanical Society 137(4): 391-400.

Ritchie, M. E., D. Tilman, et al. (1998). "Herbivore effects on plant and nitrogen dynamics in oak savanna." Ecology 79(1): 165-177.

Roseberry, J. L. and A. Woolf (1998). "Habitat-population density relationships for white-tailed deer in Illinois." Wildlife Society Bulletin 26(2): 252-258.

Ruiz-Jaen, M. C. and T. M. Aide (2005). "Restoration success: How is it being measured?" Restoration Ecology 13(3): 569-577.

Russell, F. L. and N. L. Fowler (1999). "Rarity of oak saplings in savannas and woodlands of the eastern Edwards Plateau, Texas." Southwestern Naturalist 44(1): 31-41.

Ryndock, J. A., G. E. Stratton, et al. (2012). "Differences in Spider Community Composition among Adjacent Sites during Initial Stages of Oak Woodland Restoration." Restoration Ecology 20(1): 24-32.

Schetter, T. A. and K. V. Root (2011). "Assessing an Imperiled Oak Savanna Landscape in Northwestern Ohio using Landsat Data." Natural Areas Journal 31(2): 118-130.

Sheffield, C., A. Pindar, et al. (2013). "The potential of cleptoparasitic bees as indicator taxa for assessing bee communities." Apidologie: 1-10.

Shuey, J. A. (1997). "Conservation status and natural history of Mitchell's satyr, Neonympha mitchellii mitchellii French (Insecta: Lepidoptera: Nymphalidae)." Natural

Areas Journal 17(2): 153-163.

Siemann, E., J. Haarstad, et al. (1997). "Short-term and long-term effects of burning on oak savanna arthropods." American Midland Naturalist 137(2): 349-361.

Simpson, J. W., R. E. J. Boerner, et al. (1994). "48 years of landscape change on 2 contiguous Ohio landscapes." Landscape Ecology 9(4): 261-270.

Smith, K. G., J. H. Withgott, and P. G. Rodewald. (2000). Red-headed Woodpecker (Melanerpes erythrocephalus). In The Birds of North America, No. 518 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia and American Ornithologists' Union, Washington, D.C.

Steffan-Dewenter, I. and T. Tscharntke (1997). "Early succession of butterfly and plant communities on set-aside fields." Oecologia 109(2): 294-302.

Stevens, W. K. (1995). Miracle Under The Oaks. New York, New York, Pocket Books.

Summerville, K. S., R. M. Steichen, et al. (2005). "Restoring lepidopteran communities to oak savannas: Contrasting influences of habitat quantity and quality." Restoration Ecology 13(1): 120-128.

Swengel, A. and S. Swengel (2007). "Benefit of permanent non-fire refugia for Lepidoptera conservation in fire-managed sites." Journal of Insect Conservation 11(3): 263-279.

Swengel, A. B. and S. R. Swengel (2001). "Effects of prairie and barrens management on butterfly faunal composition." Biodiversity and Conservation 10(10): 1757-1785.

Swink, F. and G. S. Wilhelm. 1994. Plants of the Chicago Region, 4th ed. Indiana Academy of Science, Indianapolis, IN.

Tester, J. R. (1989). "Effects of fire frequency on oak savanna in East-Central Minnesota." Bulletin of the Torrey Botanical Club 116(2): 134-144.

Tews, J., U. Brose, et al. (2004). "Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures." Journal of Biogeography 31(1): 79-92.

Thomas, S. C., C. B. Halpern, et al. (1999). "Plant diversity in managed forests: Understory responses to thinning and fertilization." Ecological Applications 9(3): 864-879.

Towne, E. G., D. C. Hartnett, et al. (2005). "Vegetation trends in tallgrass prairie from bison and cattle grazing." Ecological Applications 15(5): 1550-1559.

Transeau, E. N. (1935). "The Prairie Peninsula." Ecology 16: 423-437.

Trimble, S. W. and A. C. Mendel (1995). "The cow as a geomorphic agent - A critical-review." Geomorphology 13(1-4): 233-253.

Urbanek, R. E., C. K. Nielsen, et al. (2012). "White-tailed Deer (Odocoileus virginianus Zimm.) Herbivory in Herbaceous Plant Communities in Northeastern Illinois." Natural Areas Journal 32(1): 6-14.

Vestal, A. G. (1936) Barrens vegetation in Illinois. Illinois State Academy of Science Transactions. 19:79-80.

Waltz, A. E. M. and W. W. Covington (2004). "Ecological restoration treatments increase butterfly richness and abundance: Mechanisms of response." Restoration Ecology 12(1): 85-96.

White, A. S. (1983). "The effects of 13 years of annual prescribed burning on a Quercus ellipsoidalis community in Minnesota." Ecology 64(5): 1081-1085.

Williams, Ephraim. (1886) “Personal Reminiscences.” Mich. Historical Collection

Williams, N. M. (2011). "Restoration of Nontarget Species: Bee Communities and Pollination Function in Riparian Forests." Restoration Ecology 19(4): 450-459.

Williams, N. M., E. E. Crone, et al. (2010). "Ecological and life-history traits predict bee species responses to environmental disturbances." Biological Conservation 143(10): 2280-2291.

Winfree, R. and C. Kremen (2009). "Are ecosystem services stabilized by differences among species? A test using crop pollination." Proceedings of the Royal Society B-Biological Sciences 276(1655): 229-237.

Wolf, A. T. and J. S. Ascher (2008). "Bees of Wisconsin (Hymenoptera: Apoidea: Anthophila)." The Great Lakes Entomologist 41: 129-168.

Wolf, J. (2004). "A 200-year fire history in a remnant oak savanna in southeastern Wisconsin." American Midland Naturalist 152(2): 201-213.