Spider Community Response to Disturbances

DISSERTATION

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Abstract

Ecosystem restoration efforts that emulate natural disturbance processes and the legacies provided by these disturbances are thought to be the most successful, but without a clear understanding of how ecosystems regenerate after these disturbances we do not have a good framework to design effective restoration practices or the information to evaluate the success of these restoration efforts. In order to obtain more holistic views of ecological restoration there needs to be an integration of plant and animal metrics utilized to evaluate success of practices. I advocate that spiders are a good choice of indicator organism to bridge this gap.

My research focused specifically on the spider community response to a variety of disturbances, ranging from natural-- stand replacing fires in jack pine stands of northern Lower Michigan and catastrophic wind disturbance in mixed-hardwood forests of northeastern Ohio, to human based-- prescribed burning of grasslands in central Ohio. Specifically, my research questions are: 1. What is the spider community responses and/or succession in response to disturbances? 2. What do changes in spider community composition and structure reveal about habitat structure and changes in post-disturbance ecosystem development? 3. Do those spiders that are disturbance specialists share similar life traits that we can use to classify all spiders on a spectrum from disturbance specialist to disturbance avoiders?
I found that there are succession responses of the spider community, and that the vegetation structure and succession stage are primary drivers of those changes. These differences affected the diversity, abundance, and overall spider community composition. Additionally, I found that many species/families/guilds of spiders are indicator species of habitat successional stages.

By studying the changes in spider communities (including community composition, diversity and abundance) we can gain insights into the development of ecosystems impacted by disturbances, as well as insights into many aspects of the habitat structure and quality. This information, in turn, can be applied to active ecosystem to provide more holistic evaluations.
Dedicated to all the spiders,

especially those

that lost their lives in the name of science.
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research to be completed.
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Chapter 1: Introduction

Ecological restoration is an intentional activity that assists in the recovery of an ecosystem (Society for Ecological Restoration International Science and Policy Working Group 2004), and can include activities ranging from minor (prescribed natural regeneration) to major interventions (complete reconstruction) (Clewell et al. 2007). The practice, by its very nature, uses the past as a reference but needs to also be focused on the future. One key to understanding the past, specifically the events and legacies that create and maintain the structure and function of ecosystems, are natural disturbances. Natural disturbances are discrete events that alter the ecosystem structure, resource availability, or physical conditions (White and Pickett 1985). Although the word disturbance implies negativity, many disturbances are seen as an integral part of ecosystems (Turner et al. 2001). Disturbances do not themselves occur in isolation, and we must consider not only the individual event, but the possible synergistic and multiplicative effects (Turner and Dale 1998), as well as the long lasting legacies and residuals of those disturbances (Turner et al. 2001). Many (if not most) ecosystems are dependent on some form of natural disturbance for system regulation (White and Pickett 1985). Thus, in order to assist ecosystems in recovery natural disturbances and their legacies must be considered. Additionally, if natural disturbance is not a viable option there are opportunities to emulate disturbances (Perera and Buse 2007).
One possible downfall or limitation in evaluating the success of restoration practices is the tendency to evaluate only the plant community. McAlpine et al. (2016) found that of the 1,020 peer review journal articles they examined 67% focused solely on plants, and only 24% were mixed, looking at both plants and animals. This focus on the plant community exclusively is an example of the “Field of Dreams Myth” (Hilderbrand et al. 2005, McAlpine et al. 2016), the idea that if we create the appropriate structure (plants) that the animal community will self-assemble (Bradshaw 1983). Although subsequent evaluations of the plant community are relevant, they may not be revealing of the overall functionality of the ecosystem (Wheater et al. 2000), and ecological restoration aims to restore functional communities (Young et al. 2005), not just the structural basis for these communities. Additionally, in many cases restoration professionals intentionally establish the plant community, so using this as the primary or single source of evaluating success could likely lead to obtaining measures of positive success in error.

There are several common characteristics of disturbances, regardless of their origin or type. They create heterogeneity, may have long lasting effects, have both indirect and direct impacts, and for some ecosystems are necessary for their maintenance and persistence. By considering a wide range of disturbances we will be able to draw conclusions that apply to multiple systems that are subjected varied disturbances. Therefore, without a clear understanding of how the overall ecosystem functioning is impacted by disturbances lack a strong framework to determine management choices,
design effective restoration practices, and provide the means to evaluate the success of these management and restoration efforts.

In order to obtain a more holistic view of ecological restoration, McAlpine et al. (2016) suggest there needs to be an integration of plant and animal metrics utilized to evaluate success of restoration practices. I advocate that spiders are a good choice of organism to bridge this gap.

Spiders are abundant in most ecosystems and are highly diverse (Beccaloni 2009, Wise 1993). Worldwide there are over 46,000 described species of spiders (World Spider Catalog, 2017), with over 3700 inhabiting North America (Ubick et al. 2005). Spiders also live in almost any terrestrial ecosystems; the arctic, deserts, tidal zones, and mountain tops (Foelix 2011). Despite their diminutive nature, spiders fill an important ecosystem role. As one of the most numerous and higher level predators of the arthropod world (Warren et al. 1987) they have been shown to be good biocontrol agents of many pest and invasive species (Wise 1993) and are important natural enemies in many agro-ecosystems (Buddle et al. 2004).

Most spiders are generalist predators, with a few that are very specialized (Foelix 2011). They are also a diverse group with multifaceted methods of prey capture, each that can serve as an indicator to the habitat in which they reside or utilize. They are also prey for many animals; including birds, reptiles, amphibians, fish and mammals (Foelix 2011). Spiders have been shown to be higher in protein, cysteine, and taurine (Ramsay and Houston 2003) than other potential forest arthropods. Arnold et al. (2007) demonstrated that the higher level of taurine in nestling blue tits increased their spatial learning,
memory, and risk taking behavior; traits that may lead to the increased success of the nestlings. Additionally, adult birds have been seen to actively select spiders for feeding to their nestlings irrespective of relative abundances (Ramsay and Houston 2003). Webs constructed by spiders are used by some bird species as nesting material (Brunetta and Craig 2010), and some animals even use spider webs as sources of easy food, stealing the spider’s prey (Lucas 1893, Weber 2002). Spiders are known to be pioneer colonizers in areas that have been recently altered or disturbed (Bradley 2004, Hodkinson et al. 2001). Unlike many insects, spiders do not have strong host plant associations (Bell et al. 1999), but rather seem to respond more strongly to environmental and micro-spatial variables (Greenstone 1984). They are sensitive and respond quickly to environmental conditions (Marc et al. 1999), making them a good choice as bioindicators, especially when looking at disturbances. Lastly, there are fewer societal and ecological constraints compared to vertebrate studies (Kremen et al. 1993).

Little is known, however, about the response of spider communities to disturbance (Moretti et al. 2002), and even less is known about the linkages between spider community composition and ecosystem structure (Work et al. 2004). Being one of the earliest colonizers it has been hypothesized that spiders may be a valuable source for trapping water and nutrients to a newly disturbed site (Hodkinson et al. 2001). Some studies have shown that relative abundances and richness can be similar among sites of differing disturbances and ages (Work et al. 2004) the community composition in these sites can provide valuable insights into succession of spider communities (Buddle et al. 2000). Bultman and Uetz (1982) in their seminal work noted “understanding the ecology
of spider communities may significantly enhance our understanding of energy and nutrient dynamics in forest ecosystems.” Therefore, by expanding our knowledge of the spider community response to disturbances we will have additional tools for evaluating and monitoring restoration practices that use or emulate natural disturbances. We can think of disturbances conceptually (figure 1.1) as changes to the historical habitat inducing changes in vegetation structure and composition, shifts in abiotic conditions, and alterations to the food resources and predator community. These in turn will alter the spider community, and we would see changes over time as the habitat undergoes succession.

My dissertation focuses specifically on the spider community response to a variety of disturbances, ranging from natural stand replacing wildfires in jack pine stands of northern Lower Michigan and catastrophic wind disturbance in mixed-hardwood forests of northeastern Ohio, to human mediated disturbances such as prescribed burning of grasslands. My overall research questions are:

A. What are the spider community responses and/or succession in response to disturbances?
   - Are there similarities in spider communities and succession in response to different types of disturbance?

B. What do changes in spider community composition and structure reveal about habitat structure and changes in post-disturbance ecosystem development?
• Are there specific species that are good indicators of post-disturbance successional stages?

C. Do those spiders that are disturbance specialists share similar life traits that we can use to classify all spiders on a spectrum from disturbance specialist to disturbance avoiders?

• Are these disturbance specialists consistent across a variety of disturbance types, including natural and human?

By studying the changes in spider communities, including species, diversity, and abundance, we can gain insights into the natural development of areas impacted by disturbances, as well as insights into many aspects of the habitat. This information, in turn, can be applied to active restoration of habitat that will help improve our evaluations to be from a more holistic ecosystem approach.

In Chapter 2 I provide a review of spider community response to natural and anthropogenic disturbance. This review is focused on those disturbance regimes that are often utilized or emulated in ecological restoration. I consider many natural (e.g., fire, flooding, catastrophic wind disturbance, volcanic activity, landslides, and drought) and human induced (e.g., mining, urbanization, agriculture, grazing, and mesophication) disturbances.

In Chapter 3 I highlight the use of spider guilds in response to stand-replacing wildfire in northern Lower Michigan. One of the potential limitations to using spiders as bioindicators is the difficulty, even for trained arachnologists, to identify to specimens to species (Clausen and Henning 1986). One alternative is to assign spider to guilds, and
Uetz et al. (1999) determined that guilds cluster based on web use, web type, and microhabitat conditions, thus spiders can be categorized into guilds by hunting strategy (Cardoso et al. 2011). This chapter evaluates the changes in spider community composition at a guild level as it relates to changes in habitat structure.

Building on the results in Chapter 3, I focus on the species of the ground hunting spider guild within the same study system of northern Lower Michigan in Chapter 4. Here, I report a detailed study on the species specific responses to succession in post-wildfire jack pine forests. The ground hunting spider guild is of particular interest as they are easily sampled by passive pitfall trapping, allowing for a high volume of samples to be collected with minimal human effort.

Chapter 5 also examines the relationships between spiders and fire, however in this chapter I explore the impacts to the spider community from prescribed burning in a restored grassland. Grassland ecosystems are important as they provide many valuable services, such as: soil conservation, water quality enhancement, wildlife habitat, and biodiversity (Risser 1996). Wildfires, usually in the fall and ignited by lightning (Risser 1996, Steinauer and Collins 1996), were important natural disturbances that have been shown to prevented the encroachment of woody vegetation (Molles 2008, Hartley 2007), increases nutrient cycling, and create conditions that promote seed germination (Kozlowski and Ahlgren 1974). Prescribed burning is an important and inexpensive restoration and management tool (Whelan 1995, Zelhart and Robertson 2009) in these systems that have been extensively modified with EuroAmerican settlement.
In *Chapter 6* the role of catastrophic wind in forest stands and its impact on spider communities is evaluated. Catastrophic winds, which include gales, windstorms, cyclonic storms, and tornadoes (Everham and Brokaw 1996), have been shown to play an important role in the successional dynamics of forests (Bouget and Duelli 2004, Long 2009). This study utilizes a natural forest stand located in Wooster, Ohio at the Secrest Arboretum that was impacted by an EF-2 tornado in 2011, and a companion reference stand that suffered minimal impact.

Finally, the overall conclusions and trends observed across these various studies are discussed in *Chapter 7*. Here I evaluate the observed overall trends to the spider community from disturbances. I look for overall traits and specific characteristics that may help explain specific spider’s responses. By comparing the similarities and the differences of the spider community response we should be able to provide a more holistic approach to ecological restoration.
Figure 1.1: Conceptual diagram of the impacts of disturbance on the spider community.
References


Chapter 2: Spider Community Response to Ecosystem Disturbance:

A Review

Abstract:

Ecological restoration, by its very nature, uses the past as a reference but is future focused. One key to understanding the past is natural disturbance. Many (if not most) ecosystems are dependent on some form of natural disturbance for system regulation. Therefore, in order for restoration practices to be successful we need an in depth understanding of the response of the ecosystem to the historical natural disturbance regime. One possible downfall or limitation in evaluating the success of restoration practices is the tendency to evaluate only the plant community or a single target organism. In order to obtain more ecosystem wide views of ecological restoration there needs to be an integration of plant and animal metrics utilized to evaluate the success of restoration practices. I advocate that spiders are a good choice of organism to bridge this gap. Here I review the literature of spider community response across a broad range of disturbances and habitats. By developing an understanding of the dynamics of spider communities across a variety of ecosystems and disturbances we can add an important metric to the tool box of restoration practitioners for monitoring and evaluating their
work, providing a more holistic approach. It is clear that additional research is needed. Specifically, we need a clear understanding of the spider species that occupy native habitats, and a clearer understanding of the underlying drivers of community composition. With this knowledge we can provide valuable insights to restoration ecologists and promote approaches that take into consideration the complete ecosystem to management and restoration.

Introduction:

Ecological restoration is an intentional activity that assists in the recovery of an ecosystem (Society for Ecological Restoration International Science and Policy Working Group 2004), and can include activities ranging from minor (prescribed natural regeneration) to major intervention (complete reconstruction) (Clewell et al. 2007). The practice, by its very nature, uses the past as a reference but needs to also be future focused. One key to understanding the past, specifically the events and legacies that create and maintain ecosystems, is natural disturbance.

Natural disturbances are discrete events that alter the ecosystem structure, resource availability, or physical conditions (White and Pickett 1985). Many (if not most) ecosystems are dependent on some form of natural disturbance for system regulation (White and Pickett 1985). Thus, in order to assist ecosystems in recovery, natural disturbances and their legacies must be considered. Additionally, if natural disturbance is
not a viable option there are opportunities to emulate disturbances (Perera and Buse 2007).

In order for restoration practices to be successful, though, we need to have a comprehensive, ecosystem wide, understanding on the response of the ecosystem to the historical natural disturbance regime, otherwise we do not have the tools needed to assess the effectiveness of those restoration practices that are put into place either using the natural disturbance itself or emulating those disturbances.

One possible downfall or limitation in evaluating the success of restoration practices is the tendency to evaluate only the plant community. McAlpine et al. (2016) found that of the 1020 papers they reviewed 67% focused solely on plants, and only 24% were mixed, looking at both plants and animals. This focus on the plant community exclusively is an example of the “Field of Dreams Myth” (Hilderbrand et al. 2005), the idea that if we create the appropriate structure (plants) that the animal community will self-assemble (Bradshaw 1983). In many cases the restoration professionals intentionally establish the plant community, therefore using it as the single source of evaluating success could likely lead to obtaining measures of positive success in error. Although subsequent evaluations of the plant community are relevant, they may not be revealing of the functionality of the ecosystem (Wheater et al. 2000).

In order to obtain more holistic views of ecological restoration there needs to be an integration of plant and animal metrics utilized to evaluate success of practices (McAlpine et al. 2016). I advocate that spiders are a good choice of organism to bridge this gap.
Spiders are abundant in most ecosystems and are highly diverse (Beccaloni 2009). There are considered one of the top predators of the arthropod world (Warren et al. 1987), yet also serve as prey for many other organisms (Foelix 2011). Many are pioneer colonizers of recently disturbed sites (Bradley 2004; Marx et al. 2012), and may determine the initial spatial patterns of developing plant and animal communities (Hodkinson et al. 2001). Spiders have shown clear successional trends (Lowrie 1948; Muma and Muma 1949). Unlike many of the insects, spiders do not have strong host plant associations (Bell et al. 1999; Sanderson et al. 1995; Woodcock et al. 2005), but rather seem to respond more strongly to environmental and micro-spatial variables (Gibson et al. 1992; Greenstone 1984). Therefore, spider communities will change in response to successional changes after disturbances (Bultman et al. 1982).

Here I will summarize some of the known responses of the spider community to ecological disturbances, specifically focusing on disturbances that are utilized or emulated in ecological restoration, as well as anthropogenic disturbances that may need to be considered from a restoration perspective. Specifically, I will look at natural and prescribed fire, forestry management, flooding, drought, catastrophic winds, landslides, volcanic activity, grazing and agriculture, mining, urbanization, and mesophication.

Fire

Fire can be considered a widespread phenomenon (Whelan 1995), and can be seen in a variety of habitats; from grasslands to forests. The physical environment after a
fire is usually extremely different than pre-fire conditions (Whelan 1995). Areas impacted by fire have high heterogeneity, with many islands of unburned or slightly burned patches (Chapin et al. 2002).

Most studies document a decline in richness and abundance of spiders post fire (Abbott et al. 2003; Gillette et al. 2008; Huhta 1971), regardless of habitat type; although Koponen (2005) showed that there was long term increase in spider richness of forested sites after a natural wildfire, and Haskins and Shaddy (1986) found an increase in spider diversity associated with prescribed burning of grassland sites. It is not surprising that studies have shown that some families (i.e. Gnaphosidae, Dictynidae, and Lycosidae) seem to benefit from fire, whereas others (Antrodiaatidae, Thomisidae, Cybaeidae, and Linyphiidae) seemed to be negatively impacted (Niwa and Peck 2002). There is some evidence to support the idea that some species are fire specialists (Buddle et al. 2006; Gillette et al. 2008). For example, Buddle et al. (2006) found five species of spiders that were strong indicators of young (1-2 years post-fire) pyrogenic stands, and Gillette et al. (2008) found six indicators of burned sites compared to only two species as indicators for old-growth patches. Carrel (2003) demonstrated that burrowing wolf spiders (Genus: Geolycosa) are dependent on gaps that are created by recurrent wildfire, and this group of spiders are lacking in fire excluded sites. Moretti et al. (2002) also found that burned sites contained a unique spider species composition; 47% of species were exclusively found in burned sites (19.5% repeated burns, 12.5% single burn, and 14.8% in both single and repeated burns), whereas only 10.9% of species were found exclusively in unburned sites (Figure 2.1).
Seasonality of the burn must also be considered. Often times prescribed burning takes place in seasons outside of the historic regime for reasons such as safety, management of smoke, and logistical constraints (Knapp et al. 2009). Carrel (2008a) found that *Argiope* spp. were effectively eliminated by summer burns, and Johnson et al. (2008) found that there is a decrease in Tetragnathidae after winter burns. Interestingly, Rose and Goebel (2015) found evidence to support the hypothesis that spiders may be able to survive fire in situ (Warren et al. 1987), when a Lycosidae was captured a month after a prescribed grassland burn with evidence of burn injuries to his extremities. Additionally, Carrel (2008b) documented survivorship of burrowing wolf spiders; where over 90% of the monitored large *Geolycosa hubbelli* Wallace, 1942 and *Geolycosa xera archboldi* McCrone, 1963 survived five days post fire.

Brennan et al. 2006, demonstrated that vegetation variables (such as understory density, litter depth, and canopy cover) explained almost 70% of the variation in spider family richness. Ryndock et al. (2012) noted that canopy openness and herbaceous vegetation taller than 50cm were significant drivers of changes to the spider community. Niwa and Peck (2002) concluded that reduction of small trees and shrubs due to fire altered the spider community. Leaf litter depth and complexity are also important variables (Bell et al. 2001, Bultman and Uetz 1982). Therefore, vegetation structure seems to be one of the primary drivers of the changes in spider communities post fire.
Clear-cutting is a one method used to emulate stand replacing disturbances (Maclean 2007). Vegetation structure seems to be a dominant driver of changes in the spider community within managed areas. Sites managed for higher heterogeneity have higher spider species richness (Finch 2005). Barbaro et al. (2005) found that across a variety of taxa (birds, Carabid beetles, and spiders) that tree height was the best predictor variable for richness; and specifically for spiders, shrub and oak density were important factors. Oxbrough et al. (2005) found that lower field vegetation (herbaceous vegetation shorter than 50cm) and canopy closure were important drives of the changes in the spider community. Pearce et al. (2004) found that each of the stand types (conifer, mixed wood, deciduous, and clear-cut) had different spider communities; specifically that some species that had strong associations with deciduous leaf litter and feathermoss habitats, which should be considered in management plans. It has also been noted that there are significantly different spider communities when comparing burned sites to those clear-cut (Buddle et al. 2006; Larrivee et al. 2005), therefore, the authors concluded that clear-cutting does not provide the same microhabitat variation and is therefore is not functionally equivalent to burning (Buddle et al. 2006).
Flooding, like most disturbances, creates heterogeneous habitats (Naiman and Decamps 1997). Flooding events, coupled with low flow (or drought-like conditions) influence the river ecosystem and the associated biological components (Lambeets et al. 2008). For example, large flood events may cause vegetation mortality, but deposit high levels of nutrients allowing for pioneer plant species to establish (Hughes 1997). The shifts in the nutrients, hydrology, and plant communities all influence the fauna occupying these habitats.

Bonn et al. (2002) and Bonte et al. (2002) both found that structure was a more important driver of spider community than flood regime, although Malt (1995) stated that spiders were a good indicator of flood regimes. This may be due to the impact that flooding can have on the plant community. Riparian systems, which are subjected to regular fluxes of flood and drought, tend to be highly productive systems (Marx et al. 2012). Bell et al. (1999) documented that Leptorhoptrum robustum Westring, 1851 and Pachygnatha clercki Sundevall, 1823 can be considered hydrophiles. Lambeets et al. (2008) found that Pardosa agricola Thorell, 1856, a riparian specialist, survived being submerge for over 100 hours, although individuals tried to escape simulated flooding in a laboratory setting.

Drought

Few studies have looked at the overall response of spider communities to drought; those that have only considered the short-term impacts. Lensing et al. (2005) manipulated
plots to mimic precipitation patterns; creating drought and high rainfall treatments. Some families showed no response to treatment (Lycosidae, Thomisidae, and Theridiidae), but Gnaphosidae showed increased activity/density in the drought plots. Buchholz (2010) manipulated grassland plots to simulate a small scale drought. This study did not detect any response of the spider community to drought conditions (increased mean and max temperature, and decreased mean humidity) during the study. It was hypothesized that spiders may have wider ecological amplitudes to cope with changing conditions than previously assumed (Buchholz 2010).

Some species of spiders have adaptations to help prevent water loss from evapotranspiration. Spiders can keep lung atria closed, entering a state of oxygen deficit (Marx et al. 2012). Their resistance to desiccation (Agnew and Smith 1989), and additionally, many spider species enclose their eggs within a silken cocoon that has been shown to regulate moisture levels (Marx et al. 2012).

Catastrophic Wind

Little has been published in regards to the impact of catastrophic wind and spider communities. Spiller and Losos (1998) had an opportune moment when a hurricane struck the island they had just completed surveying for spiders. They noted that the spider population was significantly reduced (79% lower) after the hurricane, but recovered to pre-hurricane abundances within a year, although some species were considered locally extinct and new species were detected.
Rose and Goebel (unpublished) found that abundance and richness both increased after a tornado in a mixed-wood forest patch of northeastern Ohio, compared to an unimpacted reference stand. At the family level Lycosidae and Linyphiidae showed a significant increase in abundance in the tornado impacted stand, whereas Dictynidae showed the opposite response, with higher abundances in the reference stand.

Landslides

Landslides have much in common with other disturbances (Walker and Shiels 2013). There is an initial negative effect on biota (Walker and Shiels 2013), and they create heterogeneous microhabitats (Walker and Shiels 2013). True landslide specialists do not exist, but many species found in landslide patches are exclusively found in disturb habitats (Walker and Shiels 2013). Arthropod studies in landslide habitats are sparse (Walker and Shiels 2013).

Volcanic Activity

Few studies have looked at the impact of volcanic activity on spiders. One notable exception is the work of Crawford et al. (1995) in the aftermath of the May 1980 eruption of Mt. St. Helens in Washington State. In the first year post-eruption the only spiders found were those capable of ballooning. Ballooning is a method of transportation utilized by some spiders where a line of silk is ejected into the wind, and when enough silk has
been released the spider is lifted into the air and carried by the wind (Foelix 2011). Some of the spiders found in the Mt. St. Helens sites were assumed to have traveled distances of 50km or more to get to the site. Anecdotally, after the eruption of Krakatoa, which is also assumed to have cleared the landscape of all animal life, the first (and only) living creature found during the May 1884 expedition was a spider on the south side of Rakata (Thornton 1997).

Grazing/Agriculture

Anthropogenic land use for agriculture and grazing is common and increasing in area, with millions of acres occupied by crop systems in the United States each year (Young and Edwards 1990). Spiders are the most abundant predator of soybean crop field ecosystems (Ferguson et al. 1984). They are beneficial in agroecosystems as they tend to maintain pest insect populations at acceptable levels (Agnew and Smith 1989), and limit the initial exponential growth seem in many insect pest populations (Riechert and Lockely 1984).

Approximately half of the known spider families in the United States have been found to occur in crop fields (Young and Edwards 1990). It is likely that only spiders with the ability to disperse well would be found in field crops (Young and Edwards 1990). Crop fields tend to have a higher abundance of wandering spiders and a lower abundance of web building spiders (Young and Edwards 1990). In homogenized systems of their host plants, specialist herbivores will respond strongly (Rypstra et al. 1999);
whereas, in systems with increasing architectural diversity of plants (such as seen in natural succession) there is an increase in spider richness (Gibson et al. 1992). Complex habitats are hypothesized to have a greater array of microclimate features, food sources, and retreat sites, and therefore promote the colonization and establishment of robust natural enemy communities (Rypstra et al. 1999). Ferguson et al. (1984) did find higher abundances of spiders in double cropped fields when compared to single homogenized crop fields. Not only is the homogenized system more likely to see exponential growth of specialized herbivores, there may be a lower abundance of spiders to counter that.

Domestic grazing tends to have a greater impact on the vegetation than native herbivores (Warui et al. 2005). Ungrazed areas have been shown to allow for greater accumulation of litter layers and diverse vegetation, which increases the spider community diversity (Gibson et al. 1992) and abundance (Morris 1968). Some level of herbivory by mammals can benefit spider communities. For example, animal dung can attract prey (Janetos 1986) and serve as fertilizer for plants; promoting increased structural height (Maelfait and De Keer 1990). In contrast, cattle’s grazing was shown to lower spider diversity and abundance when compared to plots with native herbivory (Warui et al. 2005).

Among spider communities there is an observed decrease in richness and diversity with increased farm management, grazing, and trampling (Curtis et al. 1990; Downie et al. 1999; Gibson et al. 1992, ), with mixed results for spider abundance; Jansen et al. (2013) found no decline in abundance, whereas Gibson et al. (1992) recorded a significant decline in abundance. In general, there is an overall negative impact of land use in agroecosystems and rangelands on the spider community (Prieto-
Benitez and Méndez 2011), including the family Zodariidae, that were shown to increase in abundance with reduced grazing activity (Churchill 1998). Additionally, there is an increase in spider abundance in farming utilizing organic vs. traditional techniques (Schmidt et al. 2005) as well as an increase in abundance of a wolf spider (*Pardosa milvina* Hentz, 1844) in sites utilizing conservation tillage compared to conventional tillage (Marshall and Rypstra 1999).

Agricultural practices impact the spider community in varying ways. Pesticide treatments can reduce the predatory importance of spiders in orchards (Nyffeler and Benz 1987). The ability of spiders to survive harvesting activities, or the subsequent soil alternations, has not been investigated in the United States (Young and Edwards 1990). Mining

In post-mining sites that were open land areas with spontaneous vegetation post-reclamation, Mrzljak and Wiegleb (2000) demonstrated that vegetation structure parameters were significant in determining the spider community, but found that previously un-mined sites had different spider communities and no convergence was detected, even after 70 years.

Wheater *et al.* (2000) looked at disused quarry areas compared to natural dales and a restored blast pile. In comparing the vegetation it was found that the restored site showed greater similarity to the natural dales than the disused quarries; which was likely due to the selection of specific plants in an attempt to emulate the natural dale. In
comparison the spider community was significantly different in the restored site compared to both the disused quarries and the natural dales (Figure 2.2); demonstrating that evaluating the plant community alone may not provide an accurate measure of success of restoration efforts from an ecosystem wide perspective.

Urbanization

Our world is urbanizing; there is an increase in human habitation with extensive modification to the landscape (McDonnell and Pickett 1990). This increase in urbanized habitat creates sharply contrasting fragmentation of the natural areas (Tscharntke et al. 2002). Fragment size, location, and the surrounding matrix can all contribute to how these fragments function ecologically (Tscharntke and Brandl 2004).

Miyashiata et al. (1998) showed that spider species richness and density increases with an increase in forest fragment size in urbanized areas. In contrast Magura et al. (2010a) showed an increase in richness in urban forest areas, attributed to species from the surrounding matrix being more able to penetrate disturbed sites. Varet et al.’s (2011) study on urbanization showed that boundaries areas between urban and rural contained intermediate assemblages, with some species present across the entire gradient. Copley and Winchester (2010) found increases in diversity in regenerating forests, but higher abundance in the contrasting ancient sites. Although it has also been demonstrated that forest species, which may have narrower tolerance limits, are sensitive to urbanization this may be due to moisture retention of the substrate rather than habitat type (Greenstone
Buddle et al. (2004) showed that wider forest patches have higher diversity of ground-dwelling spiders than narrower forest patches, and that loss of complexity in hedgerows, due to the exotic shrub Lonicera maackii, had the lowest ground-dwelling spider diversity. Uetz (1979) looked specifically at leaf litter composition and found that with increasing depth and/or complexity of leaf litter there was an overall increase in spider diversity and abundance. This may also influence the spider density, as many species in temperate areas over winter in leaf litter (Foelix 2011). Gibb and Hochuli (2002) compared small and large fragments of heath and woodlands and found no difference in richness based on size of fragment, but did find that the assemblages were different; specifically noting that the smaller fragment assemblages were not just subsets of the larger fragment assemblages.

Shochat et al. (2004) evaluated the effects of human modification by looking at a range of habitats from agricultural to industrial and found that there was a decrease in spider diversity with increased anthropogenic influence. Horváth et al. (2002) looked specifically at edge effect and found that spider richness at the edge was significantly greater than that of meadow or forest interior. This can be explained by spiders that are specifically suited for edge habitat as well as spiders from adjacent habitats being able to penetrate the edges but not the core of alternate habitats. Greenstone (1984) looked at web spider species in meadow versus scrub areas and found that vegetation height accounted for 71% of the variation in spider species diversity and 40% of species richness. Kajak et al. (2000) found that spider diversity was higher in natural fens than in
managed grasslands, showing that soil moisture, plant complexity and management practices appeared to be the most important factors in shaping the spider community. The general trend appears to be a loss of richness or diversity, sensitive species being most strongly affected, with increasing urbanization and fragmentation, additionally vegetation structure and ground moisture seem to have major roles. This trend is not exclusive to spiders; studies have also shown a decrease in abundance and diversity with urbanization in ground beetles (Magura et al. 2010b), butterflies (Blair and Launer 1997), and stream insects (Smith and Lamp 2008).

Mesophication

Multiple anthropogenic influences (e.g., fire suppression, land-use changes, and high deer density) in eastern hardwood forests have interacted synergistically and resulted in a shift from fire-tolerant, shade-intolerant species to those dominated by fire-sensitive, shade-tolerant species (Abrams 1998; Nowacki and Abrams 2008). As result of this shift there is an overall mesophication of eastern forests: a positive feedback cycle whereby conditions continually improve for shade-tolerant mesophytic species (namely red maple (Acer rubrum)) and deteriorate for shade-intolerant, fire-adapted species (notably oak (Quercus spp.) and hickory (Carya spp.)) (Nowacki and Abrams 2008). Ryndock et al. (2012) investigated the impacts of restoration of oak woodland impacted by mesophication. Their study showed that restoration efforts of thinning and burning
had a positive effect on the spider diversity. This study did note that comparisons to a native reference site were not possible as none existed in the area.

Overall Summary and Discussion

Ecological restoration is complex, and everything is interconnected and must “fit together in a holistic manner” (Clewell et al. 2007). Often the plant community is manipulated and/or planted in an attempt to establish a target community. By using this same plant community as a metric of success restoration ecologist can erroneously obtain results implying a successful overall restoration. There is a need to establish and evaluate restoration from a more comprehensive viewpoint (McAlpine et al. 2016).

Spiders are a highly diverse group, and in all situations there will be winners and losers. Euryoecious species seem to do well in frequently disturbed habitats (Marx et al. 2012), and some species have strong associations to particular habitat structures (Gillette et al. 2008; Greenstone 1983; Moretti et al. 2002; Niwa and Peck 2002). Diverse spider communities help buffer the effect of exponential growth of insect pest populations (Riechert 1981) and can have an immediate impact on immigrating and exotic pests (Symondson et al. 2002). Spiders are not host-plant specialized (Bell et al. 1999), and seem to respond more directly to micro-spatial heterogeneity and vegetation structure (Greenstone 1984), where each stratum provides unique opportunities for retreats and predator-prey interactions (Marx et al. 2012). By developing an understanding of the dynamics of spider communities across a variety of ecosystems and disturbances we can
add an important metric to the tool box of restoration practitioners for monitoring and evaluating their work, providing an ecosystem wide approach.

It is clear that additional research is needed. We need a clear understanding of the spider species that occupy native habitats, and a clearer understanding of the underlying drivers of community composition. With this knowledge we can provide valuable insights to restoration ecologists and promote integrated approaches to management and restoration.
Figure 2.1: Adaptation of the Venn diagram from Moretti et al. (2002). Absolute number ± SD of the exclusive spider species and relative percentages as a function of the fire treatment for each patch with the numbers of species in more than one category are noted in the overlapping areas.
Figure 2.2: DECORANA biplot of vegetation (x-axis) compared to spider (y-axis) in Natural Dale (ND), Disused Quarry (DQ), and Restoration Blast Piles (RB) from Wheater et al. 2000.


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Chapter 3: Spider guild community compositional changes in response to natural jack pine succession in northern Lower Michigan

Abstract

The fire-dependent jack pine forests of Michigan, which serve as the breeding ground for the endangered Kirtland’s warbler (KW), are the focus of conservation and restoration efforts. In an attempt to increase KW habitat current forest management practices, however, have been shown to simplify landscape structure. Without a holistic understanding of how these ecosystems naturally respond to wildfire we have limited abilities to measure the success of restoration practices that emulates fire and post-fire succession. One indicator of ecosystem function is the spider community. Spiders were sampled in 12 former wildfire sites in northern Lower Michigan to quantify the spider guild community. Sites were all relatively unaltered by human activity, and were categorized as either young (2-7 years post-fire) or mature (23-41 years post-fire). A total of 7,947 spiders were collected, representing all eight guilds. I observed a higher diversity (Shannon Diversity Index) in mature versus young stands (P=<0.001, 0.018), and significant differences in the spider guild community composition between the age classes (MRPP=0.001). RDA analysis demonstrated that live and dead jack pine
understory density, stand age, and fuel loadings were significant drivers of the spider
guild community. These differences in the spider guild communities suggest that
heterogeneous structure associated with naturally regenerated stands provide a variety of
microclimates, prey availability, and habitat structures; providing suitable habitat to
maintain a high diversity of spiders across stands ages. Consequently, current
management practices in place to enhance KW by simplifying the landscape may be
negatively influencing other important ecosystem structures and functions.

Introduction

The jack pine forests of northern Lower Michigan, which serve as the breeding
grounds for the endangered Kirtland’s warbler (KW) (*Setophaga kirtlandii*) (Spaulding
and Rothstein 2009), are an area of conservation concern. Fire is one of the key processes
of successful regeneration for jack pine (Simard and Blank 1982). Prior to EuroAmerican
settlement these forests experienced a wildfire approximately once every 60 years
(Cleland *et al.* 2004), and without fire jack pine stands often convert into hardwood
forests (Solomon 1998). The Michigan Department of Natural Resources established
Kirtland’s warbler (KW) management units in 1957 (Solomon 1998) after a marked
decline in the population densities were noted, most likely due to the implementation of
fire suppression activities (Michigan Department of Natural Resources *et al.* 2014). KW
have been shown to preferentially choose jack pine stands that are 5-24 year old for
breeding territories (Probst and Weinrich 1993), and with fire suppression there was loss
of suitably aged jack pine stands. Subsequently, KW was listed as endangered in 1973, and in 1976 a plan was enacted to assist in its recovery (Michigan Department of Natural Resources et al. 2014).

Due to the increasing human population and risks associated with prescribed burns (Solomon 1998) forest management focused on emulating fires by means, including the use of commercial clear-cutting and artificial jack pine regeneration utilizing an open weave planting arrangement in which systematically elliptical openings are incorporated in rows of jack pines planted at 1.2m intervals (Houseman and Anderson 2002). This, along with management of Brown-headed Cowbirds, which parasitize KW nests, resulted in an astounding recovery for the KW (Michigan Department of Natural Resources et al. 2014).

These management techniques, put into place to cater to the single species (KW), create jack pine stands that differ in habitat structure and connectivity when compared to naturally regenerating stands (Corace et al. 2010). The elliptical openings, created as part of the open weave plantation, lack the connectivity that the open habitat retains in naturally regenerating stands (Houseman and Anderson 2002). The use of a V-plow to produce wide furrows in the soil, to prepare sites for jack pine planting (Kepler et al. 1996), also disturb the soil in a manner uncharacteristic of the natural disturbance regime. Although these management practices have proven successful for KW there is concern that these techniques simplify not only the individual stands they are implemented within (Spaulding and Rothstein 2009), but the landscape as a whole (Tucker et al. 2016), with unknown consequences to many components of the ecosystem and its functionality.
Spiders are one of the best groups to study when investigating community structure and natural succession (Barnes 1953). Spiders, which are abundant in most terrestrial ecosystems (Wise 1993), play important ecosystem roles. As one of the most numerous and higher level predators of the invertebrate world (Warren et al. 1987) they have been shown to be good biocontrol agents of many pest (including invasive species) (Wise 1993) and are considered important natural enemies in many ecosystems (Buddle et al. 2004). They are an extremely diverse group, and are mostly generalist predators (Foelix 2011). Additionally, they serve as prey and sources of resources for many other animals (Foelix 2011). For example, Ramsay and Houston (2003) found spiders to be higher in protein, cysteine, and taurine than other arthropods. Higher level of taurine in nestling blue tits increased their spatial learning, memory, and risk taking behavior; traits associated with increased success (Arnold et al. 2007). Spider webs also are a resource utilized by some bird species for nesting material (Brunetta and Craig 2010), and as sources of easy food, as birds and other animals have been observed to steal prey from spiders’ webs (Lucas 1893, Weber 2002). As pioneer species, many spiders quickly colonize areas that have been recently altered or disturbed (Bradley 2004, Hodkinson et al. 2001). Unlike many insects, however, spiders do not have strong host plant associations (Bell et al. 1999), and are sensitive and respond quickly to changing environmental conditions (Marc et al. 1999) and micro-spatial variables (Greenstone 1984). Finally, spiders are easily sampled, and as there are fewer societal and ecological constraints compared to vertebrate studies (Kremen et al. 1993).
One of the considerations noted when studying spider communities, though, is the difficulty, even for arachnologists, to identify specimens to species (Clausen 1986), and the difficulty of modeling all species individually (Hawkins et al. 1989). One alternative to working with species level data is to assign spider to guilds. Although predominately generalist predators of invertebrates, spiders do not constitute a single functional group (Marc et al. 1999), but rather can be categorized into guilds by hunting strategy (Cardoso et al. 2011). Uetz et al. (1999) determined that spiders cluster functionally based on web use, web type, and microhabitat conditions, supporting their use in ecological studies. Michalko and Pekár (2016) found that different guilds of spiders occupied different trophic niches, and therefore guilds can be used as a proxy of functional diversity. Thus, guilds, due to the broader ecological scale they respond to, are useful (Bultman et al. 1982). Additionally, juveniles (often a large percentage of the spiders sampled) can be assigned to guilds based on family level identification, whereas species-level assessments must exclude juvenile specimens as they cannot be consistently identified (New 1999).

In this study I explore the succession of the spider community, at the guild level, in naturally regenerating jack pine stands of northern Lower Michigan. Specifically, my objectives are: 1) Compare the diversity of the spider community at a guild level between young and mature stands; 2) Determine if there are shifts in the spider guild community associated with natural jack pine succession; 3) Identify any guild specific responses to natural jack pine succession; and 4) Compare any detected shifts in spider guild community composition with recorded changes in fuel loadings and habitat variables.
Methods

Site Selection

I utilized 12 sites located within 9 wildfires in northern Lower Michigan (Figure 3.1) previously established in a study examining the effects of forest succession on fuel loadings in jack pine forests. All sites developed following wildfires occurring as recently as 2011 and the oldest having burned in 1972, and all are relatively undisturbed by recent human activity (e.g., no artificial jack pine regeneration). The sites were categorized as either young (2-7 years post-fire) or mature (21-41 years post-fire). Due to the restrictions associated with sampling jack pine stands occupied by KW, I did not include jack pine stands between the ages of 8 and 20 years old as all naturally regenerated jack pine stands in the study area that developed following wildfire were occupied by KW.

Using ArcGIS (version 9.0) 25 random points were selected within each site. Using a histogram of the distances between points distance associated site specific transect lengths were calculated for each sampling window; transects ranged between 90-150m long. Of these 25 random points six were randomly selected as the starting point for a sampling transect. A random cardinal direction was chosen for each transect prior to sampling. In cases where there was an overlap with any other transect or the random direction would have placed any portion of the transect outside of the selected site the transect was adjusted clockwise to the next cardinal direction. Along each transect
sampling plots were established at distances equal to 0%, 15%, 30% and 50% of the total transect length.

Spider Sampling

A sampling quadrat of 1 m² was established at the center of each sampling plot. At this sampling quadrat the spiders were sampled using visual sampling, vegetation beating, and leaf litter extraction. Five pitfall traps (for a total of 60 pitfall traps) were installed in each site along an independent transect (40-m minimum length) such that they did not overlap with any other spider sampling quadrat.

Understanding sampling techniques is an important aspect to arthropod research as there is potential for biases and errors (Leather and Watt 2005). Each spider sampling method targets specific guilds of spiders. For example, pitfall trapping is more likely to capture ground active spiders (such as the ground hunting guild) than vegetation beating, which targets orb building and foliage hunting spiders. Therefore, I used four spider sampling techniques in an attempt to capture the spider diversity. Visual Sampling (V) entails collecting any spiders visually observed within the sampling quadrat within a 15 minute timeframe. Collected spiders were placed in 70% ethanol, and stored for identification. Vegetation Beating (B) occurred once visual sampling was completed by placing a tarp over the ground and vegetation in the same sampling quadrat is struck with a wooden pole for 60 seconds. Any spiders falling to the tarp were collected and stored in 70% ethanol for identification. Leaf Litter Extraction (L) is completed by collecting the
leaf litter in each quadrat in Ziploc bags and returned to the lab. At time of collection the volume of each bag is estimated, and the mass of the litter is recorded. At the lab the litter is placed in a Berlese funnel for three days to allow for extraction of invertebrates. After three days the invertebrates were sorted and stored in 70% ethanol for identification. These three sampling techniques, visual (V), vegetation beating (B), and leaf litter extraction (L), will be referred to collectively as the VBL sampling henceforth. At each pitfall trap location I excavated an area large enough for a one gallon flower pot to fit snuggly with the top rim of the pot level with the natural ground. As a catch container a 0.9-L deli food container with ~5 cm of propylene glycol/dish soap solution was placed in the flower pot. Propylene glycol was selected as a killing and preserving agent as it is considered less harmful to other wildlife than the alternatives (specifically ethylene glycol). Dish soap was added to reduce surface tension on the solution, causing any trapped invertebrates to sink into the solution. A wooden trap, following the design of Bradley (2004), was installed over the catch container and flower pot. The roof and base were constructed of ¼” plywood. In the center of the base a 7.62 cm hole was cut in which a solo cup with the bottom removed was installed to serve as a funnel, guiding the invertebrates to the catch container. To reduce mammalian disturbances a 0.6-m x 0.6-m piece of chicken wire was secured over the top of the trap with landscape pins. The traps were serviced regularly throughout the season (June 3rd -September 23rd, 2013), and spiders and other invertebrates were separated and stored in 70% ethanol until identification.
A Nikon SMZ 1270 stereomicroscope was used for spider identification. Identification to family was completed following Ubick et al. (2005) and the World Spider Catalog (2017). Guilds can be assigned based on family level identification as many spiders in the same family use the same hunting strategy (Michalko and Pekár 2016). Guild assignment followed Cardoso et al. 2011; except for Pisauridae, which I assigned to the “Other Hunter” guild as the species present in northern Lower Michigan are not considered sheet web weavers. Additionally, for families that have representatives in more than one guild, I assigned guild placement based on sampling technique. For example, Linyphiidae and Dictynidae captured using visual and beating techniques were assigned to the sheet web weaver and space web weaver guilds, and to other hunters and ground hunters, respectively, when collected using leaf litter extraction and pitfall trapping (Table 3.1). Voucher specimens were donated to The Ohio State University Museum of Biodiversity.

Habitat and Weather Variables

Stand habitat variables included stand age (years since wildfire), percent canopy cover, ground cover, vegetation structure, and geographic location. Percent canopy cover (above 3m) was estimated by the researcher standing in the center of the plot using an ocular tube. I used a modified version of the vegetation structure methods outlined in Kearns and Rodewald (2013). At each sampling quadrat and pitfall trap location the ground cover at the corner of the 1m² was categorized as live vegetation, leaf litter,
sand/soil, woody debris, or moss. Vegetation structure was characterized by placing a 3m long pole at the corner of each area, the number of vegetation hits was recorded at 0.5m intervals starting at the ground. These were categorized as forbs, fern, grass, and trees, shrubs, and vines by species. Additionally, dead woody vegetation was recorded as either dead jack pine or dead other. To assist in characterizing the understory plant density the total number of all vegetation hits was also calculated for each 0.5-m increment.

Fuel Loadings

Fuels were sampled using a modified US Forest Service Forest Inventory and Analysis (FIA) approach. From each sample plot three 7.3 m (24 ft) transects were established arrayed at 30°, 150°, and 270°. Along each of these transect downed and live fuels were measured using the following:

1,000-hr fuels - Along the entire 7.3 m of each transect, all downed wood that was > 8 cm in diameter where it intersected the transect was measured. For each downed wood piece we identified the species, and diameter of the piece at the intersection (DX; cm), diameter of the piece at the small end (DS; cm), diameter of the piece at the large end (DL; cm), total length (L; m) and decay class (classes 1-5 following the FIREMON CWD decay class descriptions).

100-hr fuels – Along a 3.1 m (10 ft) section of each transect beginning at 4.26 m (14 ft) from the sample plot center, all pieces intersecting the transect that were between 2.51-8.00 cm in diameter were counted.
10-hr fuels – Along a 1.8 m (6 ft) section of each transect beginning at 5.49 m (18 ft) from the sample plot center, all pieces intersecting the transect that were between 0.61-2.50 cm in diameter were counted.

1-hr fuels – Along a 1.8 m (6 ft) section of each transect beginning at 5.49 m (18 ft) from the sample plot center, all pieces intersecting the transect that were between < 0.61 cm in diameter were counted.

Duff/litter – At 7.3 m (24 ft) from the beginning of each transect the duff and litter depth was measured (cm) and the % litter in the duff estimated.

Live vegetation – Live fuels were measured in a 2m2 (1m by 2m) quadrat placed 90° and 3.7 m (12 ft) from the sample plot center. Within each quadrat, the following were estimated: 1) % cover of live woody shrubs and trees (LS); 2) % cover of live herbaceous plants (LH); 3) % cover of dead herbaceous plants (DH); 4) average height of woody shrubs and trees (HW; cm); and 5) average height of herbaceous plants (HH; cm).

Statistical Analyses

Each sampling quadrat or pitfall trap was treated as an independent replicate. According to Woodcock (2005) if one has sufficient spacing (min 10-m) between sampling locations they can be considered independent. Additionally I noted several other studies that have also treated individual traps/sampling quadrats as independent (Moore et al. 2002, Moretti et al. 2002, Obrist and Duelli 1996).
Prior to analyses all early instars and young juveniles (not identifiable to family) were excluded. For guild level analyses one guild (Sensing Web Weavers) was excluded as only one individual was collected, and for family level analyses any family represented by less than 5 individuals were also excluded. VBL spiders were pooled by sampling quadrat. Pitfall samples were analyzed separately from the VBL sampling as they were at different locations, pooled by pitfall trap, and adjusted to per-trapping-day to account for differences in sampling days and trap disturbances.

Shannon Diversity Index (H’) was calculated for each pitfall trap and sampling quadrat at the guild level using BiodiversityR (Kindt and Coe 2005). Comparisons of H’ and overall spider abundance between the young and mature stands were then analyzed using t-tests for each of the sampling types (VBL and pitfall trapping). These analyses were completed using R (R Core Team 2013).

The overall differences in the spider community composition between age classes and stand age at the guild level were determined using Multi-response Permutation Procedures (MRPP), a nonparametric procedure that tests a-priori groups for differences in composition (McCune et al. 2002). To further explore the patterns in spider guilds a non-metric multidimensional scaling (nMDS) ordination plot was performed with Bray-Curtis distance matrix using the vegan package in R (R Core Team 2013).

Indicator analysis by stand age category (young vs. mature) was also used to determine guild and family specific responses (Dufréne and Legendre 1997) utilizing the Monte-Carlo procedures (4999 permutations) within PCOrd version 5 (McCune and
Mefford 1999). Additionally, indicator analysis was run using the individual stand ages and both guild and family level identification to provide further detailed information.

Redundancy Analysis (RDA) was performed using Canoco 4.5 to determine the site characteristics that were the primary drivers of the changes in the spider guild community. For the VBL sampling the fuel loading data for each location was used. As the pitfall traps were situated away from the fuels sampling plots I summarized the fuel data by site and used the fuel means for analysis.

Results

An overall total of 7,947 spiders were collected representing 28 families and from all eight guilds identified by Cardoso et al. (2011); 4,164 by pitfall and 3,783 by VBL (Table 3.2). Both the mature and the young stands had representatives from 26 families. Atypidae and Eutichuridae were only found in the young stands, and Amaurobiidae and Theridiosomatidae were only found in mature stands (Table 3.3), although, it should be noted that all four of these families were captured in low numbers and were not utilized in family level analyses. Perry Holt (25 year old stand) and Luzerne (21 year old stand), mature stands, had the highest family richness with 21 families collected, while Hughes Lake 2 (7 year old stand), a young stand, had the lowest richness with only 17 families collected.

Shannon Diversity Index (H’) was significantly higher in the mature stands when compared in both VBL (P<0.001) and pitfall sampling (P= 0.018) (Figure 3.2a and 3.2b).
The mean $H'$ of the young stand was $0.83\pm0.04$ (SE, n=156) for VBL sampling and $0.55\pm0.04$ (SE, n=25) for pitfall sampling, whereas the mean $H'$ in the mature stand was $1.04\pm0.02$ (SE, n=242) for VBL sampling and $0.71\pm0.05$ (SE, n=35) for pitfall sampling. Abundance was significantly higher in the mature stands for VBL sampling ($P<0.001$), whereas there was no significant difference in overall spider abundance between the age classes with pitfall sampling ($P=0.515$) (Figure 3.2c and 3.2d). Mean abundance of young stands was $6.68\pm0.44$ (SE, n=156) spiders per quadrat for VBL sampling and $0.74\pm0.09$ (SE, n=25) spiders per trapping day for pitfall sampling. Whereas the mean abundance in matures stands was $11.30\pm0.51$ (SE, n=242) spiders per quadrat for VBL sampling and $0.81\pm0.06$ (SE, n=35) spiders per trapping day for pitfall sampling.

MRPP suggests that the spider guild community was significantly different between stand age class for VBL sampling ($P=0.001$), but not for pitfall sampling ($P=0.258$). This may be due to the high proportion of spiders collected from the ground hunting guild (78% of the total pitfall catch) with no significant difference in overall abundance between the age classes. Ground hunting and other hunters made up over 92% of the pitfall samples, and the specialist guild was not represented in these samples; in contrast, only 7% of the VBL specimens were from the ground hunting guild. The nMDS plots (stress=0.233 for the VBL samples, stress = 0.076 for the pitfall samples) showed large areas of overlap, but differences are noted (Figure 3.3). For example, in both sampling techniques one of the drivers of the differences in the communities seems to be the dominance of orb weavers in the young stands, and other hunters in mature stands.
Indicator analysis found that six of the eight guilds, and 70% of the families utilized in the analyses were significant indicators of an age class and/or stand age, with an additional 8% that had a nearly significant trend (Table 3.4 and 3.5). Looking at the guild level sampling six of the seven guilds used for analyses were an indicator of stand age or age class for at least one set of sampling techniques. The guild not represented was the specialists, which was solely represented by the family Mimetidae in these data. Note, that Mimetidae was not an indicator in any of the family level analyses, and this may be due to the relatively low number collected from that family for this study (< 1% of the total catch). Of the 28 families collected 18 were found to be a significant indicators. Of the ten families collected that were not indicators five were excluded from analyses due to low catch numbers. The indicators that were common to both sampling techniques represented the same age class in both analyses (Guilds: Sheetweb weavers and Ambush Hunters and families: Dictynidae, Theridiidae, and Agelenidae as indicators of Mature stands.) In contrast, there were some differences in the stand age indicators based on sampling technique. At the guild level Other Hunters were an indicator of the 23 year old stand in VBL and 5 year old stands in pitfall sampling. At the family level, Salticidae was an indicator of 23 year old stands in the VBL sampling and 41 year old stands with the pitfall samples. Dictynidae was found to be an indicator of the 25 year old stand when utilizing the VBL samples, but of the 41 year old stand with the pitfall samples. The fact that Dictynidae was found to be indicators of different stand ages based on sampling technique was not surprising. There are two subfamilies of Dictynidae that were collected for this study, Cicurininae and Dictyninae. Cicurininae are known to live near the ground,
and function as ground spiders, whereas Dictyninae occur in a variety of habitats ranging from branch tips to leaf litter (Bennett 2005), therefore I hypothesize that VBL sampling would target Dictyninae, whereas pitfall sampling would target Cicurininae, which could explain those differences. Similarly, Agelenidae was found to be an indicator of the 41 year old stand with the VBL sampling, and the 26 year old stand with the pitfall samples. Agelenidae has species that are known for building funnel web retreats within vegetation (such that they would be more likely targeted by VBL sampling), whereas genera recently moved to Agelenidae from Amaurobiidae (i.e. Wadotes and Coras) are more prone to living at the ground level and therefore would be more likely trapped by pitfalls. Therefore, species level identification would help to resolve these issues and likely provide further insights.

RDA analysis demonstrated that for VBL sampling live and dead jack pine understory density, stand age, as well as the fuel loading characteristics were drivers of the changes in the spider community (P= 0.002, first axis explains 20.3% of the variation, and the second axis explains 1.7% of the variation) (Figure 3.4A). The x-axis appears to represent stand age, with more mature stands to the right. This is supported by the fact that ambush hunters, other hunters, and sheetweb weavers were all found to be indicators of mature stands. In contrast, the y-axis appears to represent the fuel loadings and understory plant composition. This is supported as orb weavers, which were indicators of young stands, are known to respond more directly to understory plant density as they need appropriate locations to secure their webs (Mcnett and Rypstra 2000). For pitfall sampling, similarly, live and dead jack pine understory density, stand age, and fuel
characteristics were also important drivers, as well as percentage canopy cover (P=0.048, first axis explains 29.4% of the variation, and the second axis explains 3.8% of the variation)(Figure 3.4B). Once again, the x-axis appears to represent stand age, with mature stands to the right. This is supported by spaceweb weavers, ambush hunters, and sheetweb weavers being indicators of mature stands. The y-axis appears to represent canopy cover and jack pine density.

Discussion

In wildfire regenerated stands habitat structure (e.g., live and dead jack pine densities, and fuel characteristics) were strong drivers of the spider guild community. These findings supports those of Larrivée et al. (2005), who found that web building spiders were associated with mature stands, whereas hunting spiders were associated with open habitat types, like those found in the young jack pine stands. Although, it should be noted that Larrivée et al. (2005) was sampling in 2001, comparing a burned sites to an “undisturbed” sites, with undisturbed referring to those sites that were not part of a 1999 wildfire and clear-cutting operations. My results differ, which may be partially due to the more robust guild assignment used. I found that Space Web Weavers and Sheet Web Weavers were indicators of mature stands, and no guilds were indicators of young stands. In contrast, when the indicator analysis was run using stand age I did find that Orb Weavers and Sheet Web Weavers (collected with VBL sampling) were indicators of the 5 and 7 year post-fire stands respectively, and Other Hunters (collected with pitfall
sampling) were an indicator of the 5 year post-fire stands. Interestingly, Larrivée et al. (2005) did note that two Linyphiidae species (Sheet Web Weaver guild) were mainly found in the burn sites, which are consistent with my results. Otherwise, all guilds reported as indicators were for mature stands (those 21 or more years post-fire).

Buddle et al. (2000) stated that spider communities converged at approximately 30-years post fire in mid-boreal stands when comparing clear-cut stands with wildfire stands, although the wildfire stands followed a different trajectory to the clear-cut stands. Specifically, they found that some species (referred to as fire specialists) were only found in young fire initiated stands. In comparison, I did not find any guilds or families as indicators of my youngest stand (2 years post-fire), but I did have several family level indicators of 5 years post-fire. I also had families and guilds that were indicators of the most mature stand (41 years post-fire) that I sampled, demonstrating that not only are some specialized of recently burned sites, but also of mature stands. These differing results may be due to the fact that jack pine has a fire rotation of 50 years (Meyer 2010), compared to a 39 year fire rotation in the mid-boreal forest (Murphy 1985) studied by Buddle et al. (2000), where a shorter fire rotation may be advantageous to those that are specialize for young stands. Spiders are known to respond quickly to changes in habitat structure and microclimate conditions (Marc et al. 1999).

Fires are considered a natural and necessary part of the ecology of many forest ecosystems (Hutto 2008, Koponen 2005), as is the case with the jack pine forests (Simard and Blank 1982). Fire influences the dynamics of the forest both directly and indirectly (Oliver and Larson 1996). The most conspicuous direct influence of fire is mortality of
adult vegetation (Whelan 1995). Indirectly, the physical conditions post fire are very different from pre-fire; such as vegetation structure, soil temperature, wind speed, water runoff, erosion, etc. (Whelan, 1995). Fires do not burn evenly (Kozlowskie and Ahlgren 1974, Oliver and Larson 1996), with many islands of unburned or slightly burned patches interspersed in areas of high fuel consumption (Chapin et al. 2002), creating a diversity of mosaics of vegetation structures.

Implications

The Endangered Species Act (ESA) is a single species focused and is reactive rather than proactive (Simberloff 1998), providing protection to individual species only once numbers have dropped dangerously low. It is clear that the first step should be to evaluate and determine the causes of that specific species decline to assist with determining what actions need to be taken to prevent further decline and encourage recovery. Although focusing on a single species can lead to an understanding of the drivers of its decline, many other species are often overlooked (Lindenmayer et al. 2007), leading to a failure to maintain biodiversity (Simberloff 1998) and ecosystem functionality. Thus, a more holistic approach is needed.

Changes in vegetation structure are one of the primary drivers of the changes in spider communities post-fire (Bultman and Uetz 1982, Bell et al. 2001, Niwa and Peck 2002, Brennan et al. 2006, Ryndock et al. 2012). Overall, my results show that there are successional shifts in the spider guild communities in jack pine stands, and these shifts
are associated with changes in habitat structure. As assignment to guilds directly relates to their hunting strategies (Cardoso et al. 2011) it also relates to their habitat use. Guild level spider community analysis has many advantages for investigations of succession and functional diversity (Corcuera et al. 2016). The combined ease of guild assignment with family level identification and their response to changes in environmental conditions demonstrates the usefulness of spider guilds as bioindicators of habitat structure and ecosystem function, providing a more comprehensive approach to understanding ecosystems.

Acknowledgements

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Figure 3.1: Map of northern Lower Michigan showing the post-wildfire jack pine stand locations (young=white, mature=grey) and the sampling sites (black dots). Site name (year of fire) located adjacent to site.
Figure 3.2: Comparison of spider guild Shannon Diversity Index $H'$ a) VBL Sampling ($P < 0.001$) b) Pitfall Sampling ($P = 0.018$), and Abundance c) VBL Sampling ($P < 0.001$) d) Pitfall Sampling ($P = 0.515$), in post-wildfire regenerating jack pine stands of northern Lower Michigan.
Figure 3.3: Non-metric multidimensional scaling plot of shifts in the spider guild community in post-wildfire jack pine stands. A. VBL sampling (stress=0.233) B. Pitfall sampling (stress= 0.076). White= young stands (2-7 years post-fire), grey= matures stands (>21 years post-wildfire).
Figure 3.4: RDA biplots of the spider guild community response to habitat and fuel structure in post-wildfire jack pine stands of northern Lower Michigan. A. VBL sampling (P=0.002, first axis explains 20.3% of the variation, and the second axis explains 1.7% of the variation). B. Pitfall sampling (P=0.048, first axis explains 29.4% of the variation, and the second axis explains 3.8% of the variation).
Table 3.1: Guild assignment by family and sampling technique for spiders collected in post-wildfire jack pine stands of northern Lower Michigan.

<table>
<thead>
<tr>
<th>Family</th>
<th>Visual/Beating</th>
<th>Leaf Litter Extraction/Pitfall</th>
</tr>
</thead>
<tbody>
<tr>
<td>Agelenidae</td>
<td>Sheet Web Weaver</td>
<td>Sheet Web Weaver</td>
</tr>
<tr>
<td>Amaurobiidae</td>
<td>Sheet Web Weaver</td>
<td>Sheet Web Weaver</td>
</tr>
<tr>
<td>Anyphaenidae</td>
<td>Other Hunter</td>
<td>Other Hunter</td>
</tr>
<tr>
<td>Araneidae</td>
<td>Orb Web Weaver</td>
<td>Orb Web Weaver</td>
</tr>
<tr>
<td>Atypidae</td>
<td>Sensing Web Weaver</td>
<td>Sensing Web Weaver</td>
</tr>
<tr>
<td>Clubionidae</td>
<td>Other Hunter</td>
<td>Other Hunter</td>
</tr>
<tr>
<td>Corinnidae</td>
<td>Ground Hunter</td>
<td>Ground Hunter</td>
</tr>
<tr>
<td>Dictynidae</td>
<td>Space Web Weaver</td>
<td>Ground Hunter</td>
</tr>
<tr>
<td>Eutichuridae</td>
<td>Other Hunter</td>
<td>Other Hunter</td>
</tr>
<tr>
<td>Gnaphosidae</td>
<td>Ground Hunter</td>
<td>Ground Hunter</td>
</tr>
<tr>
<td>Hahniidae</td>
<td>Sheet Web Weaver</td>
<td>Sheet Web Weaver</td>
</tr>
<tr>
<td>Linyphiidae</td>
<td>Sheet Web Weaver</td>
<td>Other Hunter</td>
</tr>
<tr>
<td>Liocranidae</td>
<td>Ground Hunter</td>
<td>Ground Hunter</td>
</tr>
<tr>
<td>Lycosidae</td>
<td>Ground Hunter</td>
<td>Ground Hunter</td>
</tr>
<tr>
<td>Mimetidae</td>
<td>Specialist</td>
<td>Specialist</td>
</tr>
<tr>
<td>Miturgidae</td>
<td>Other Hunter</td>
<td>Other Hunter</td>
</tr>
<tr>
<td>Mysmenidae</td>
<td>Space Web Weaver</td>
<td>Space Web Weaver</td>
</tr>
<tr>
<td>Oxyopidae</td>
<td>Other Hunter</td>
<td>Other Hunter</td>
</tr>
<tr>
<td>Philodromidae</td>
<td>Other Hunter</td>
<td>Other Hunter</td>
</tr>
<tr>
<td>Phrurolithidae</td>
<td>Ground Hunter</td>
<td>Ground Hunter</td>
</tr>
<tr>
<td>Pisauridae</td>
<td>Other Hunter</td>
<td>Other Hunter</td>
</tr>
<tr>
<td>Salticidae</td>
<td>Other Hunter</td>
<td>Other Hunter</td>
</tr>
<tr>
<td>Tetragnathida</td>
<td>Orb Web Weaver</td>
<td>Orb Web Weaver</td>
</tr>
<tr>
<td>Theridiidae</td>
<td>Space Web Weaver</td>
<td>Space Web Weaver</td>
</tr>
<tr>
<td>Theridiosomatidae</td>
<td>Orb Web Weaver</td>
<td>Orb Web Weaver</td>
</tr>
<tr>
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<td>Ambush Hunter</td>
<td>Ambush Hunter</td>
</tr>
<tr>
<td>Titanoecidae</td>
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<td>Space Web Weaver</td>
</tr>
<tr>
<td>Uloboridae</td>
<td>Orb Web Weaver</td>
<td>Orb Web Weaver</td>
</tr>
</tbody>
</table>
Table 3.2: Spider families collected in the post-wildfire jack pine stands of northern Lower Michigan, total number caught total by sampling technique.

<table>
<thead>
<tr>
<th>Family</th>
<th>Total</th>
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</tr>
<tr>
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<td>755</td>
</tr>
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</tr>
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</tr>
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Table 3.3: Spider families found in each post-wildfire jack pine stand in northern Lower Michigan by site and age class.

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<th>Young</th>
<th>Mature</th>
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<td></td>
<td>Site</td>
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<td>Young</td>
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<td>Amaurobiidae (Amau)</td>
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<td>Anyphaenidae (Anyp)</td>
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</tr>
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</tr>
<tr>
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</tr>
<tr>
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<td>X</td>
</tr>
<tr>
<td>Dictynidae (Dict)</td>
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</tr>
<tr>
<td>Eutichuridae (Euti)</td>
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</tr>
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<td>Pisauridae (Pisa)</td>
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<td>Salticidae (Salt)</td>
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<td>Tetragnathidae (Tetr)</td>
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<td>X</td>
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<tr>
<td>Theridiosomatidae (Thds)</td>
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<th>Thomisidae (Thom)</th>
<th>Titanoecidae (Tita)</th>
<th>Uloborididae (Ulob)</th>
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<th># of sites family found in</th>
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Table 3.4: Spider guild indicator analysis by age class and stand age for VBL and pitfall traps in post-wildfire jack pine stands of northern Lower Michigan.

<table>
<thead>
<tr>
<th>Guild</th>
<th>Age Class</th>
<th>Stand Age</th>
<th>P-value</th>
<th>Age Class</th>
<th>Stand Age</th>
<th>P-value</th>
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<tbody>
<tr>
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<td>Mature</td>
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<td>19.500</td>
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<tr>
<td>OtherHunter</td>
<td>Mature</td>
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<td>19.000</td>
<td>23.000</td>
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<tr>
<td>GroundHunter</td>
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<td>15.100</td>
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<tr>
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<td>OrbWeavers</td>
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<table>
<thead>
<tr>
<th>Guild</th>
<th>Age Class</th>
<th>Stand Age</th>
<th>P-value</th>
<th>Age Class</th>
<th>Stand Age</th>
<th>P-value</th>
</tr>
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<td>na</td>
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<tr>
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<td>21.000</td>
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<td>SheetWebWeavers</td>
<td>Mature</td>
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<td>26.000</td>
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<tr>
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<td>0.018</td>
<td>33.0</td>
<td>5</td>
<td>0.016</td>
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Table 3.5: Spider family level indicator analysis by age class and stand age for VBL and pitfall traps in post-wildfire jack pine stands of northern Lower Michigan.

<table>
<thead>
<tr>
<th>VBL Sampling</th>
<th>Age Class</th>
<th>P-value</th>
<th>Stand Age</th>
<th>P-value</th>
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<td>Family</td>
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<td>IV</td>
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</tr>
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<td>Theridiidae</td>
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<td>&lt;0.001</td>
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<td>Dictynidae</td>
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<td>Mature</td>
<td>&lt;0.001</td>
<td>24.6</td>
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<td>Oxyopidae</td>
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<td>Agelenidae</td>
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<td>Anyphaenidae</td>
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<td>Young</td>
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<td>Tetragnathida</td>
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<td>Uloboridae</td>
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<td>Thomisidae</td>
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<td>Clubionidae</td>
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<th>Stand Age</th>
<th>P-value</th>
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<tbody>
<tr>
<td>Family</td>
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<td>IV</td>
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<td>Dictynidae</td>
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<td>Thomisidae</td>
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<td>Agelenidae</td>
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<td>Lycosidae</td>
<td>na</td>
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References


Probst, J. R. 1986. A review of factors limiting the Kirtland’s warbler on its breeding grounds. American Midland Naturalist 87-100


Chapter 4: Ground hunting spider guild response to stand replacing fires and natural jack pine succession

Abstract

Fire-dependent jack pine forests of northern Michigan are the breeding ground for the endangered Kirtland’s warbler (KW) and as such are the focus of conservation and restoration efforts. As part of the KW recovery plan, many jack pine forests have been managed as dense plantations to increase KW habitat. These management practices, however, tend to simplify forest and landscape structure, often to the detriment of other species. In this study, I examined the changes in the ground hunting spider guild (GHSG) with natural jack pine succession following wildfire. I established a network of pitfall traps across 12 former wildfire sites in northern Lower Michigan to quantify changes in GHSG diversity and community structure. All former wildfire sites were relatively unaltered by human activity, and were classified as either young (2-7 years post-fire) or mature (23-41 years post-fire). I observed a higher diversity (Shannon Diversity Index) of GHSG in mature (H’=2.12) versus young (H’=1.49) stands (p<0.01), and significant differences in the GHSG community composition between age classes (MRPP=0.001). Non-metric multidimensional scaling ordination revealed strong separation between young and mature stands, with several important drivers influencing GHSG abundance,
including stand age, and understory vegetation composition. These differences in the
GHSG community, and relationship to environmental and habitat factors, suggest that
heterogeneous structure associated with naturally regenerated stands likely provide a
variety of microclimates, prey availability, and habitat structures that influence the
GHSG and provide suitable habitat to maintain a high diversity of spiders across stands
ages.

Introduction

By its very nature the Endangered Species Act (ESA) is single-species focused
and is reactive rather than proactive in terms of conservation (Simberloff 1998), looking
to protect an individual species only once its numbers have dropped dangerously low. In
these cases, the first step is to evaluate and determine the causes of that specific species
decline to determine what actions need to be taken to prevent further decline and
encourage recovery. Although evaluating the decline in a single species can lead to a
clear understanding of the specific drivers of decline, the details of many other species
are overlooked (Lindenmayer et al. 2007), as the ESA does not promote holistically
evaluating ecosystems (Cole 1992). Therefore management practices put into place are
often solely focused on that one target organism, reducing our ability to maintain
biodiversity (Simberloff 1998), and ecosystem functionality (Rohlf 1991).

One example where the ESA has been successful in halting species decline is with
Kirtland’s warbler (Setophaga kirtlandii KW) in the jack pine forests of northern Lower
Michigan. The jack pine forests associated with extensive glacial outwash plains have been an area of considerable restoration attention as they are the breeding grounds for the endangered Kirtland’s warbler (Spaulding & Rothstein 2009). Wildfire is an important disturbance associated with natural jack pine forests (Simard & Blank 1982) as many jack pines have pyriscence serotinous cones (Cleland et al. 2004), meaning that high temperatures (like those occurring in a stand replacing wildfire) are necessary to melt the waxy covering of the cone to release the seeds. The pre-EuroAmerican settlement jack pine forests of northern Lower Michigan have been documented to have fire rotation of approximately 60 years (Cleland et al. 2004). Without fire jack pine stands often succeed into hardwood stands (Solomon 1998), and following the implementation of fire suppression that resulted in the conversion of natural jack pine forests to hardwood forests, there was also a marked decline in the population densities of Kirtland’s warblers (Michigan Department of Natural Resources et al. 2014). To counteract this decline, the Michigan Department of Natural Resources established Kirtland’s warbler management units in 1957 (Solomon 1998), and in 1973 KW was listed as endangered under the ESA legislation, and a plan was enacted to assist in its recovery in 1976 (Michigan Department of Natural Resources et al. 2014). The primary focus of the recovery plan focused on enhancing habitat, as KWs prefer dense jack pine stands 5-24 years of age (Probst & Weinrich 1993). Due to the increasing human population and risks associated with prescribed burning (Solomon 1998) most jack pine forest management associated with restoring KW populations shifted to management focused on emulating fires by means of clear-cutting and artificial jack pine regeneration utilizing an open weave planting
arrangement to emulate the outcomes of wildfires; the trees are planted at 1.2m intervals with systematically incorporated elliptical openings (Houseman & Anderson 2002). This, along with management of Brown-headed Cowbirds parasitizing Kirtland’s warbler’s nests, lead to an astounding recovery for the Kirtland’s warbler (Michigan Department of Natural Resources et al. 2014).

Although management practices implemented to promote KW habitat have proven successful, it has created jack pine forests that are uncharacteristic of naturally regenerating stands (Corace et al. 2010). The openings created as part of open weave plantations lack the connectivity that the open habitat retains in naturally regenerating stands (Houseman & Anderson 2002), a trait that could be detrimental to many animals using those openings as corridors or primary habitat. Preparation for jack pine planting also involves the use of a V-plow to produce wide furrows in the soil (Kepler et al. 1996), which could be destructive to many soil dwelling animals, as well as plant roots and seeds. There is now growing concern that these techniques simplify not only the individual stands they are implemented within (Spaulding & Rothstein 2009), but the landscape as a whole (Tucker et al. 2016), with unknown effects on many biological aspects of these systems; including biodiversity and ecosystem functioning.

Despite their diminutive nature, spiders play an important ecosystem role. They are one of the most numerous and higher level predators of the arthropod world (Warren et al. 1987) and are abundant in most terrestrial ecosystems (Wise 1993). They have been documented to be good biocontrol agents of many pest and invasive species (Wise 1993) and are considered important natural enemies in many agro-ecosystems (Buddle et al.
They are mostly generalist predators, but there are a few that are very specialized (Foelix 2011). They are an extremely diverse group with multifaceted methods of prey capture, each that can serve as an indicator to the habitat in which they utilize. They also serve as prey for many animals; including birds, reptiles, amphibians, fish, and mammals (Foelix 2011); including KW (Deloria-Sheffield et. al 2001) and other species or birds, mammals, reptiles, amphibians, and insects present in jack pine habitats (Beal 1915; Blanchard 1928; Hamilton 1941; Evans 1964; Best 1977; Pinkowski 1978; Thornhill 1978; Brown 1979). Ramsay and Houston (2003) documented that spiders are higher in protein, cysteine, and taurine than other potential forest arthropods. Arnold et al. (2007) found that the higher level of taurine in nestling blue tits increased their spatial learning, memory, and risk taking behavior; traits associated with increased success of the nestlings, and adult birds were shown to actively select spiders for feeding to their nestlings irrespective of relative abundances (Ramsay & Houston 2003). Additionally, webs are a resource utilized by some bird species as nesting material (Brunetta & Craig 2010), and in some cases it was observed that animals use spider webs as sources of easy food, stealing the spider’s prey (Lucas 1893; Weber 2002).

Spiders are also known to be pioneers to areas that have been recently altered or disturbed (Bradley 2004; Hodkinson et al. 2001). Furthermore, while spiders do not have strong host plant associations (Bell et al. 1999), they do respond more strongly to environmental and micro-spatial variables (Greenstone 1984). They are sensitive and respond quickly to environmental conditions (Marc et al. 1999), and there are fewer societal and ecological constraints compared to vertebrate studies (Kremen et al. 1993).
Specifically, the ground hunting spider guild (GHSG) are a good choice of study organisms as they have a shown to be important in the structure and function of many terrestrial communities (Mallis and Hurd 2005), have been shown to change with vegetation succession (Bultman & Uetz 1982), and are easily sampled using pitfall trapping.

The purpose of this study is to evaluate the changes in the GHSG community in response to succession in naturally regenerating jack pine stands of northern Lower Michigan. Specifically, my objectives are: 1) Compare the diversity of the ground hunting spider community between young and mature stands; 2) Determine if there are shifts in the ground hunting spider guild community associated with changes in jack pine succession; and 3) Examine species and habitat variables associated with species specific responses to jack pine succession.

Methods

Site Selection

Twelve sites within nine wildfires located in northern Lower Michigan were examined, all located from 44.36321° to 45.18327°, and -84.6990° to -83.80666° (Figure 4.1). All sites were located on xeric sandy Grayling outwash soil types. Sites were categorized as young (2-7 years post-fire) or mature (21-41 years post-fire) as they relate to KW occupancy. I did not include jack pine stands between the ages of 8 and 20 years.
old as all naturally regenerated jack pine stands in the study area that developed following wildfire were occupied by KW, and as such had highly restricted accessibility. All sites were relatively undisturbed by human activity (i.e. no artificial jack pine regeneration, limited road and energy development).

Spider Sampling

To characterize the ground hunting spider guild community, I installed five pitfall traps along a transect with a minimum distance between other traps or any edge or path of 10 meters. For each trap a hole was dug such that a one gallon flower pot fit snugly with the top rim of the pot level with the natural ground. As a catch container a 0.9-L deli food container with ~5 cm of propylene glycol/dish soap solution was placed in the flower pot. Propylene glycol was selected as a killing and preserving agent as it is considered less harmful to other wildlife than the alternatives (specifically ethylene glycol). Dish soap was added to reduce surface tension on the solution, causing any trapped invertebrates to sink into the solution. A wooden trap, following the design of Bradley (2004), was installed over the catch container and flower pot. The roof and base were constructed of ¼” plywood. In the center of the base a 7.6-cm hole was cut in which a solo cup with the bottom removed was installed to serve as a funnel, guiding the invertebrates to the catch container. To reduce mammalian disturbances a 0.6-m x 0.6-m piece of chicken wire was secured over the top of the trap with landscape pins. The traps were serviced regularly throughout the season (June 3rd -September 23rd, 2013), and
spiders and other invertebrates were separated and stored in 70% ethanol until identification.

A Nikon SMZ 1270 stereomicroscope was used for spider identification. Identification to genus was completed following Ubick et al. (2005), and identification to species utilized multiple resources available from the World Spider Catalog (2017). Voucher specimens have been donated and are housed at The Ohio State University Museum of Biodiversity.

Habitat Variables

A variety of habitat variables were collected, including stand age (number of years since wildfire), percent canopy cover, ground cover, vegetation structure, and geographic location. Vegetation structure methods were adapted from the vegetation characterization methods outlined in Kearns and Rodewald (2013). Percent canopy cover (above 3m) was estimated using an ocular tube. A 1-m² sample quadrat was centered over each pitfall trap and the ground cover at the corner of each quadrat was categorized as live vegetation, leaf litter, sand/soil, woody debris, or moss. Vegetation structure was characterized by placing a 3-m pole at the corner of each 1-m² quadrat, and the number of vegetation hits will be recorded at 0.5m intervals starting at the ground. These were categorized as forbs, fern, grass, and trees, shrubs, and vines by species. Additionally, standing dead and downed woody debris was recorded as either dead jack pine or dead
other. To assist in characterizing the understory plant density the total number of all vegetation hits was also calculated for each 0.5-m increment.

Statistical Analyses

Prior to analyses all early instars and juveniles (not identifiable to species), and species represented by only one specimen (singleton) were excluded from analyses. I considered each pitfall trap as an independent replicate and samples were adjusted to per-trapping-day. Woodcock (2005) demonstrated that for spiders where one has sufficient spacing between pitfall traps (i.e., minimum of 10 m), they can be safely considered independent. Furthermore, research conducted by Perry et al. (2017) demonstrated that less than 5% of spiders moved over 12 m, suggesting that daily movements are restricted to distances smaller than 12 m. Additionally, I noted that several other studies also treated individual traps as independent (Obrist & Duelli 1996; Moore et al. 2002; Moretti et al. 2002).

Ground hunting spider abundance, species richness, evenness (J), and Shannon diversity index (H’) were calculated for each trap using BiodiversityR (Kindt & Coe 2005). Each of these variables was then evaluated to determine if they followed a normal distribution using a Shapiro Wilks test. Comparisons between the young and mature stands were then analyzed using a t-test (for normally distributed variables) and Mann-Whitney-Wilcoxon test (for non-normally distributed variables). The habitat structure variables (other than grass density, and understory vegetation 0-0.5-m), GHSG
abundance and evenness were found to have a non-normal distribution (Shapiro Wilks test p-value<0.05), and therefore comparisons were made with the Mann-Whitney-Wilcoxon test. Understory vegetation density (0-0.5m), grass density, GHSG richness and Shannon diversity index were found to follow a normal distribution (Shapiro Wilks test p-value >0.05), and were compared using a t-test. These analyses were completed using R (R Core Team 2013).

Indicator species analysis by stand category (young vs. mature) was used to determine species specific responses (Dufréne & Legendre 1997) utilizing the Monte-Carlo procedures (4999 permutations) within PCOrd software (McCune & Mefford 1999). Additionally, an indicator species analysis was performed using the individual stand ages to provide more detailed information on the succession of the ground hunting spider guild species.

The overall differences in the ground hunting spider guild community composition were determined using Multi-response Permutation Procedures (MRPP). Finally, to further explore the patterns in ground hunting spider guild community a non-metric multidimensional scaling (nMDS) ordination plot was performed with Bray-Curtis distance matrix calculated on per-trapping-day abundances by trap and ENV Fit was applied to determined environmental drivers of the changes in the ground hunting spider guild community. These analyses were completed in R (R Core Team 2013).
Results

Changes in the habitat structure between young and mature stands

I observed that in the youngest stands (two years post-wildfire) that many of the dead jack pine snags were still standing, but by seven years post-fire that many of those dead trees had fallen creating abundant woody debris (Figure 4.2a). Young stands have jack pine up to 1.4 m tall, and were characterized by having a higher densities of grass (t=3.13, p=0.003), cherry (W=544.4, p=0.041), blueberry (W=654.5, p=<0.001), and oak (W=535, p=0.019). In contrast, mature stands have jack pine 5.5-20 m tall, with areas of clumped jack pine growth with open grassy area (Figure 4.2b). I found a higher canopy closure (%) in mature stands than young stands (W=215, p<0.001). I observed no statistically significant difference in litter ground cover between age classes (W=380, p=0.124), and there was a trend toward more standing dead vegetation (W=339.5, p=0.066) in the mature stands compared to the young stands. Wintergreen and moss were not observed in the young stands at any of my sampling locations, but were found at multiple mature sampling locations. Coarse woody debris (CWD) was not significantly different between the age classes (W=460.5, p=0.463).
Ground hunting spider community composition

A total of 3,219 spiders from the ground hunting spider guild were collected, and 1,748 (54%) were determined to be mature adults and identifiable to species. These individuals represented 6 families, 25 genera, and 56 species. The most commonly captured species were from Lycosidae (\textit{Pardosa distincta} (393 individuals, 22%) and \textit{Trabeops aurantiaca} (151 individuals, 9%)), and Dictynidae (\textit{Lathys foxi} (117 individuals, 7%)) (Table 4.8).

I did not find a significant difference \( (W = 350, p = 0.19) \) in overall ground hunting spider abundance, as young stands had a median abundance of 0.22 (n=25, IQR=0.22) and mature stands had a median abundance of 0.28 (n=35, IQR=0.17) (Figure 4.3a). Mean spider richness (11.77±1.05 (n=35, CI0.95)) was significantly greater in the mature stands than the young stands (8.80±2.33 (n=25, CI0.95)) \( (t = -2.51, df = 58, p = 0.01) \) (Figure 4.3b). I also found a significantly higher evenness (J) in mature stands (median J of 0.91(n=35, IQR=0.07)), compared to young stands (median J of 0.84(n=25, IQR=0.16)) \( (W = 274, p = 0.01) \) (Figure 4.3c). Mature stands also had a significantly greater Shannon Diversity Index \( (H' = 2.12±0.12 \text{ (n=35, CI0.95)}) \) than the young stands \( (H' = 1.49±0.31 \text{ (n=25, CI0.95)}) \) \( (t=-4.18, df = 58, p= 0.0001) \) (Figure 4.3d).

Nine indicators species of young stands and fifteen indicators species of mature stands were found (Table 4.1). Looking at indicator species analysis by stand age three indicators were found for 2 year old stands, seven indicators for 5 year old stands, two for 21 year old stands, three for 23 year old stands, three for 25 year old stands, three for 26
year old stands, and nine for 41 year old stands (Table 4.2). There appears to be an overall trend with species from the family Lycosidae as indicators of young stands, species in the family Corinnidae having indicators in both young and mature stands, and species in the families Gnaphosidae, Dictynidae, Liocranidae, and Phrurolithidae tended to be indicators of mature stands.

Relationship between GHSG and habitat structure

Multiple Response Permutation Procedures (MRPP) suggest a significant difference between the ground hunting spider community between young and mature wildfire-regenerated jack pine stands (p = 0.001). Using Non-metric multidimensional scaling (nMDS) I observed strong separation among pitfall samples from the young and mature sample sites (stress of 0.185) (Figure 4.4). The young stands cluster to the left side of the plot, whereas the mature stands are towards the right side. There is a small area of overlap, but in general there is a demonstrated difference in the ground hunting spider community by stand age. This seems to be driven the higher number of Lycosids in young stands, compared to more Gnaphosids in mature stands.

By adding ENVFit to the nMDS I found twelve habitat variables that influence the ground hunting spider guild community composition (Figure 4.4). Stand age (p =0.001) is almost parallel with the x-axis, supporting the clustering of the young stands to the left and mature to the right. Canopy closure (p =0.001) ground cover of litter (p =0.04), ground cover by wintergreen (p= 0.042), and standing dead vegetation (p= 0.08)
are associated with stand age, demonstrating an increase in these variables with successional age. In comparison, understory vegetation of oak (p=0.07), ground cover of grass (p=0.01), and understory vegetation 0-0.5 m (p= 0.004) are associated with the young stands. The y-axis appears to be a combination of ground cover by moss (p= 0.018), total understory vegetation 1-1.5 m (p= 0.02), and coarse woody debris (CWD) (p =0.10). Latitude (p= 0.007) was also found to be influential.

Discussion

There are successional changes in the ground hunting spider guild community, with higher diversity and changes in the community composition related to natural stand successional development of jack pine forests post-wildfire, although no difference in overall abundance was detected. This is in contrast to the findings of Mallis and Hurd (2005), who did not detect any relationship between successional age and any measure of ground-dwelling spider diversity. Interestingly, they did show that the majority of ground-dwelling spider species collected were specialists, and only found in one site type. Therefore, although the diversity within the sites was similar, the community composition changed with habitat succession. Ground beetles (Carabidae) have been shown to respond differently to disturbance in jack pine stands. Ground beetles were shown to have an increase in abundance and diversity following disturbance, although it is noted that some mature forest specialists become locally extinct for at least two years.
after the disturbance, leading to a conclusion that mature habitat needs to be conserved in these systems (Beaudry et al. 1997).

Buddle et al. (2000) evaluated the changes in the forest spider community in response to wildfire and harvesting in Alberta, Canada. Similarly, they noted no significant difference in relative spider abundance with succession, but did detect shifts in the spider community. In general, they found that Lycosidae (wolf spiders) were associated with, and dominated, younger stands, and Liocranidae (Spiny-legged sac spiders) were associated with mature stands. My results suggest that Liocranidae are associated with mature stands, and many of the Lycosids were more strongly associated with young stands, although there were some clear exceptions to this general trend (for example: *Trabeops aurantiaca* (Lycosidae), which was an indicator of mature stands in my study).

The most abundant species I collected was *Pardosa distincta*, a small Lycosid, known to inhabit open fields and grassy areas (Kaston 1981; Wolff 1981), and grassy clearings within woodlands (Dondale and Redner 1990). I found this species to be indicators of young stands, and nMDS showed *P. distincta* to be correlated to higher levels of grass cover and understory vegetation below 0.5 m. This is consistent with their known habitat affiliations, and supports the assertion by Buddle et al. (2000), that they are negatively correlated with leaf litter. Although I found that *P. distincta* dominated the young stands, they were also found to inhabit, albeit at lower numbers, mature jack pine stands (although it should be noted that they were not detected in the most mature stand). Mature jack pine stands are characterized by densely clumped patches of jack pines.
interspersed with open areas containing grass and sedge communities. Therefore, an open habitat species would be able to find available habitat within a mature jack pine stand at a lower frequency.

In contrast, my second most abundant species, *Trabeops aurantiaca* (Lycosidae), was an indicator of mature stands. *T. aurantiaca* has been found to be associated with oak woodlands and savannahs (Steffen & Draney 2009), as well as pine woodlands (Dondale & Redner 1990). The nMDS demonstrated that *T. aurantiaca* is correlated with an increase in canopy closure, standing dead vegetation, and leaf litter cover, similar to the results of Buddle et al. (2000) who observed that litter depth and CWD was positively correlated with *Trochosa terricola* abundance. In wildfire-regenerated jack pine stands of northern Lower Michigan *T. terricola* was also found to be an indicator of mature stands, and nMDS shows it associated with higher amounts of canopy closure and standing dead vegetation.

Buddle (2000) compared the life histories of *Pardosa mackenziana* and *Pardosa moesta*, he concluded that *P. moesta* prefers open habitats, and rapidly colonized newly disturbed areas through short distance dispersal. In contrast, he found that *P. mackenziana* prefer closed canopy sites, but that the two species do co-occur in habitats with both open and closed areas. Similarly, I found that *P. moesta* was an indicator of young stands, whereas *P. mackenziana* was an indicator of mature stands. I only had one young site where I found both *P. moesta* and *P. mackenziana* (Howes Lake 2), and *P. mackenziana* was only represented by one male in this site.
Lathys foxi was the third most abundant species observed in this study. This small Dictynidae has been collected in other studies from woodland leaf litter samples (Elliott 1930; Kaston 1981). Little is known about the life history and habitat associations of this species. In the current study L. foxi was an indicator of mature stands, and nMDS showed that it was associated with similar habitat variables as T. aurantiaca (positively correlated with standing dead vegetation, canopy closure, and leaf litter). Less than 2% of the L. foxi collected were collected from young stands, demonstrating their strong association with mature stands. Leaf litter depth has been shown to influence the spider community, with the strongest driver of changes in the spider community being depth of litter (rather than leaf heterogeneity) and the increase in habitat that it provides (Bultman & Uetz 1982).

Of the 56 species collected, 35 were significant indicators (p <0.1) of either stand category and/or specific stand ages. Considering that seven species were represented by singletons, and not used in analyses, over 71% of the species analyzed are indicator species, with 61% as indicators of specific stand ages, and 49% as indicators by category. This demonstrates the strong associations that spider species in the ground hunting guild have with specific development stages of jack pine and its associated habitat structure. I found nine indicators associated with the most mature stand (41 years post-fire), which raises concerns as there has been a significant loss of mature stands on the landscape (Tucker et al. 2016). Overall, Buddle et al. (2000) suggest that spider communities vary following wildfire due to wide range of microhabitats available; specifically noting that CWD increases micro-habitat heterogeneity. Deadwood biomass has been shown to be critical habitat for spiders and beetles in sites with limited overstory (Work et al. 2014).
This could lead to the conclusion that CWD is a keystone structure (Tews et al. 2004), and should be maintained in systems in order to promote high biodiversity.

Overall, heterogeneity has been shown to be influential many species (Tews et al. 2004; Barbaro 2005), although ground beetles (Carabidae) failed to show significant responses to habitat complexity (Langellotto & Denno 2004). There are five factors that have been hypothesized to change with increasing habitat heterogeneity that may influence spider communities: 1) increased prey abundance 2) refuge from predation 3) ability to locate and capture prey 4) microclimate preferences and 5) availability of alternative resources (i.e. nectar) (Langellotto & Denno 2004). It has been noted that with increased vegetation diversity there is an increases herbivorous prey (Ziesch & Roth 2013), although herbivorous invertebrates may not represent the entire prey base for spiders (Langellotto & Denno 2004). It has also observed that with increased litter depth there is an increase in prey richness (Uetz 1979). Cannibalism is a significant contributor to spider mortality of Schizocosa ocreata spiderlings, although habitat complexity was not found to significantly influence cannibalism rates (Wagner & Wise 1996). In contrast, Uetz (1979) concluded that habitat heterogeneity could reduce interspecific predation, creating a higher diversity of species in more complex litter habitat. Web building spiders appear to select web sites based on vegetation characteristics, and maintain fidelity to those sites only if sufficient prey is captured (McNett & Rypstra 2000). Additionally, patches higher in prey abundance may offer greater choices to foraging techniques utilized by a variety of spiders (Uetz 1979). Spider communities have been shown to be influenced by shading and moisture gradients (Entling et al. 2007), and temperature
Distinct spider communities have been shown to be associated with and respond to microhabitat structures (Greenstone 1984; Barton et al. 2017). Lastly, although spiders are usually considered obligate predators, there are many reported cases of use of alternative resources, such as nectar and pollen (Pollard & Beck 1995; Jackson et al. 2001; Taylor & Pfannenstiel 2008; Taylor & Bradley 2009; Chen et al. 2010). Thus, it may be a combination of all five factors hypothesized by Langellotto and Denno (2004). The results of this study demonstrate that the heterogeneous stand structure associated with naturally regenerated jack pine stands maintain a diversity of ground hunting spider species across stand ages, something that may be lost by the simplification of the landscape by current management practices.

Implications

Solomon (1998) stated that the endangered species recovery is the ultimate measure of success. Although intensive jack pine management has led to a tremendous recovery for KW (Corace et al. 2010) it is unclear if this single-species focus has had negative effects on other flora and fauna. Due to the nature of single species management we often lack the data to adequately determine the impacts to other species and the ecosystem as a whole, to clearly understand the success and/or failures management techniques cause. Specifically in the jack pine stands of northern Lower Michigan it was shown that each age class (young, KW occupied, and mature) had unique bird community compositions (Corace et al. 2010), although this study was
evaluating post-clearcut stands, and not post-wildfire. Additionally, many other species are not even studied well enough for us to know their status (Simberloff 1998). Concern over a particular species can stimulate interest in restoration efforts and encourage community involvement (Lindenmayer et al. 2000) especially if the target organism is “cute and cuddly” (Lindenmayer et al. 2007). In the case of the KW this is particularly true, with regional festivals that generate revenue for the area from ecotourism (Solomon 1998). For many other species, however, the opposite can occur, where the public instead resents the species being protected, for example, in the case of the spotted owl the protection was characterized as a choice between the environment and jobs (Solomon 1998).

Hilderbrand et al. (2005) describes the field of dreams myth as the idea that if the correct physical structure is created that the biotic composition will self-assemble, “if you build it, they will come”. There is a longstanding assumption that by conserving habitat for a single or focal species that the other biota using that ecosystem are also conserved, by assuming that the responses of other taxa will be the same as the target organism (Lindenmayer et al. 2000). McAlpine et al. (2016) noted that focusing on single target species and/or the plant community can cause restoration practices to fall victim to the “field of dreams” myth (Hilderbrand et al. 2005). Species differ in their specific habitat requirements, which limits the usefulness of using a single species as surrogates for others (Lindenmayer et al. 2000). Therefore, a prudent use of a mixture of strategies to provide more comprehensive insights (Lindenmayer et al. 2007) should include the evaluation of many different taxa.
Acknowledgements

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Figure 4.1: Map of northern Lower Michigan showing the post-wildfire jack pine stand locations (young=blue, mature=red) and the sampling sites (black dots). Site name (year of fire) located adjacent to site.

Figure 4.2: Young (a; 7 year post fire) and mature (b; 25 years post fire) jack pine stands in northern Lower Michigan.
Figure 4.3: Ground hunting spider guild comparisons between young (white) and mature (grey) post wild-fire jack pine stands (a) overall abundance, $p=0.19$ (b) Richness $p=0.01$ (c) Evenness $p=0.01$ and (d) Shannon Diversity Index (H’) $p<0.001$. (ns=not significant, *$p<0.05$, ***$p<0.001$)
Figure 4.4: Non-metric multidimensional scaling (nMDS) of the post-wildfire jack pine ground spider community by age class (Stress of 0.1853), young=white, and mature=grey
Table 4.1: Indicator species for the ground hunting spider guild by age class (young/mature) of post wild-fire jack pine stands of northern Lower Michigan. Indicator value (IV) and p-value for each indicator.

<table>
<thead>
<tr>
<th>Species Abbreviation</th>
<th>Species Family</th>
<th>Species</th>
<th>Age Class</th>
<th>Indicator Value (IV)</th>
<th>p-value</th>
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Table 4.2: Indicator species for the ground hunting spider guild by stand age (number of years post-fire) in jack pine stands of northern Lower Michigan. Indicator value (IV) and p-value for each indicator.

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Young stands (year since fire and site)  | Mature stands (year since fire and site)


Beal FEL. 1915. Food habits of the thrushes of the United States (No. 280). US Department of Agriculture.


Franklin JF, Lindenmayer D, MacMahon J A, McKee A, Magnuson J, Perry DA, Waide R, Foster D. 2000. Threads of continuity: there are immense differences between even-aged silvicultural disturbances (especially clearcutting) and natural disturbances, such as windthrow, wildfire, and even volcanic eruptions. Conservation in Practice 1(1):8-17.


Chapter 5: Short-term Impacts of Prescribed Burning on the Spider Community (Order: Araneae) in a Small Ohio Grassland

Abstract.

Prescribed burning is a management tool that is widely accepted for prairie management and restoration, yet little is known how burning may impact the spider community. Although it is generally thought that prescribed burning may alter the spider community composition and structure, few studies have examined these shifts in a controlled manner with both a burned grassland and a nearby unburned companion grassland. On October 25, 2014 we conducted a prescribed burn of a grassland at the Gwynne Conservation Area, London, Ohio. Spiders were sampled using pitfall traps for four weeks pre-burn and six weeks post-burn in both the treatment grassland and adjacent unburned grassland. A total of 298 spiders were collected from 16 families, over 60% of which were in the family Lycosidae. Overall, we found the prescribed burn did not significantly alter the abundance or diversity of spiders collected, and interestingly it appears the community composition of the unburned grassland changed more over the

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sample period than the burned grassland. Anecdotal observations also suggest that some spiders are capable of surviving the fire in situ. As we continue to study these communities, we will develop a better understanding of role that prescribed burning plays in regulating the structure and composition of the spider communities. Such information is important to develop process-based restoration and management practices in grassland ecosystems.

Introduction

Grassland ecosystems provide many valuable services, including but not limited to: soil conservation, water quality enhancement, wildlife habitat, and biodiversity (Risser 1996). Worldwide vast areas of grasslands have been lost to a variety of human land use (Steinauer and Collins 1996). Those grasslands that remain are highly fragmented (Risser 1996) and more susceptible localized extinction events and invasion by non-native species (Risser 1996), thus leading to the conclusion that grassland systems should one of the top priorities of conservation and restoration efforts (Sampson and Knopf 1994).

Before these restoration efforts begin, however, we need to better understand the natural disturbance regimes and the influence these disturbances have on ecosystem structure and composition, as restoration efforts that emulate natural disturbances and their legacies are more successful (Long 2009). In grasslands, frequent wildfires, usually in the fall and ignited by lightning (Risser 1996, Steinauer and Collins 1996), were
important natural disturbances. Fire in grasslands helps reduce the encroachment of woody vegetation (Molles 2008, Hartley 2007), increases nutrient cycling, and create warm soil conditions that promote seed germination (Kozlowski and Ahlgren 1974). Thus, prescribed burning of grasslands has generally been shown to increase plant productivity (Kozlowski and Ahlgren 1974), and as a result is considered an important and inexpensive restoration and management tool (Whelan 1995, Zelhart and Robertson 2009). Yet, even with the known benefits of burning of grasslands, some are concerned that prescribed burns may negatively impact small isolated populations of invertebrates (Panzer 2002) or reduce beneficial arthropods such as pollinators and predators in the ecosystems (Warren et al 1987).

Despite their diminutive nature, spiders fill an important role in many ecosystems. As one of the most numerous and higher level predators of the arthropod world (Warren et al 1987) they have been shown to be good biocontrol agents of many pest and invasive species (Wise 1993) and are important natural enemies of pest insects in many agro-ecosystems (Buddle et al 2004). Spiders are a diverse group with multifaceted methods of prey capture, each that can serve as an indicator to the habitat in which they reside or utilize. They are also prey for many animals, including birds, reptiles, amphibians, fish and mammals (Foelix 2011). Spiders are also abundant in most ecosystems (Wise 1993), and are known to be pioneer colonizers in areas that have been recently altered or disturbed (Bradley and Ohio Biological Survey 2004, Hodkinson et al 2001). Spiders are also sensitive and respond quickly to environmental conditions (Marc et al 1999), making
them a good choice as bioindicators, especially when considering disturbances and their
effects on ecosystem structure and function.

In grassland habitats, it is expected that the number of invertebrates (including
spiders) would decrease significantly in the short term following a fire either directly (i.e.
mortality) (Reichert and Reeder 1972) or indirectly (i.e. change in habitat structure and
microclimate) (Hore and Uniyal 2008, Hartley 2007). Although some have hypothesized
that spiders may survive a burn by seeking refuge in the burrows or non-flammable plant
matter (Warren et al 1987, Jansen 2013), Bell et al (2001) suggested that this was
unlikely due to the sensitivity of even the most tolerant spider’s physiology to minor
changes in temperature. Rice (1932) found that fire temperatures were not severe enough
to kill animals that were hibernating in the bases of bunch grass during a spring burn in
Illinois, and Brennan et al (2011) found that Xanthorrhoea preissii (grass trees) can serve
as refugia for some invertebrates during fire, although significant mortality was detected.
Thus it seems that spiders may be responding to changes in habitat variables altered by
burning in addition to direct mortality as a result of the fire.

Taking advantage of a scheduled prescribed burn in a restored grassland in central
Ohio planned as a practical experience for students acquiring red card certification as part
of a wildland fire management course at The Ohio State University, traps were set up to
monitor the spider community in order to determine if there are the differences in the
spider community following a prescribed burning. Specifically, my primary objective
was to quantify the changes in spider species community composition, diversity, and
abundance following the prescribed burn, and compare these changes with an adjacent unburned grassland. We hypothesized that a large proportion of the spiders in a grassland treated with prescribed burning will suffer mortality as a result of the prescribed burn, and we would therefore observe a decrease in diversity and abundance in spiders in the time period immediately following a prescribed burn in the burned grassland, but that this decline would not be observed in the adjacent unburned grassland.

Methods

Study area

This study utilized 2 grassland areas at the Gwynne Conservation area, a 27-hectare (67 acre) demonstration/education area that is part of The Ohio State University’s Molly Caren Agricultural Center located in London, Ohio (39.95N, -83.45W). The administrators of the wildland firefighter training class (offered through The Ohio State University) selected the Big Bluestem Prairie (BBS~2 hectares) to be used for a prescribed burning training, scheduled to occur on October 25, 2014. This prairie was originally established in 1989 and was planted exclusively as *Andropogon gerardii* (big bluestem grass), although many other grass and forb species have naturally established in the site since establishment. The Prairie Planting (PP~0.8 hectares) was chosen as a companion site for this study. It is approximately 350-m southeast of BBS, was
established in 1986 as a mixed species prairie ecosystem, and was not subjected to any management practices during the spider sampling period.

Spider Sampling

To characterize the spider community, 5 pitfall traps were installed along a transect with a minimum distance between traps of 10 meters, and a minimum distance to the grassland edge of 10 meters. At each trap location a hole was dug such that a one gallon flower pot fit snuggly into the hole with the top rim of the pot level with the natural ground. A 0.9-L deli food container with ~5 cm of propylene glycol/dish soap solution was placed in the flower pot. Propylene glycol was selected as it helps to kill and preserve the specimens in the trap and is less harmful to other wildlife than the alternatives (specifically ethylene glycol). The dish soap acts to reduce surface tension on the solution, causing the caught invertebrates to sink into the solution. The wooden trap, following the design of Bradley (2004) was then placed securely over the catch container and flower pot. The roof and base were constructed using ¼” plywood. The base had a 7.62 cm hole cut into the center in which a solo cup with the bottom removed was inserted to serve as a funnel, guiding the invertebrates to the catch container. A 0.6-m x 0.6-m piece of chicken wire was secured of the top of the trap with landscape pins to reduce the chance of mammalian disturbance to the traps. Traps were installed on September 26, 2014, and samples were collected every 2 weeks thereafter. The traps in both grasslands were removed on October 24, and the prescribed burn occurred on
October 25. Following the prescribed burn the traps were reinstalled in both areas on October 26. Samples were collected weekly for the first 2 weeks post-burn, while subsequent samples were collected every 2 weeks through December 7, for a total sample period of 4 weeks of sampling prior to the burn, and 6 weeks of sampling following the burn. Spiders and other invertebrates separated and stored in 70% ethanol until identification.

Spiders were identified using a Nikon SMZ 1270 stereomicroscope. Identification to genus was completed following Ubick et al. (2005), and identification to species utilized resources available from the World Spider Catalog (2015).

Data Analyses

Prior to analysis all early instar juveniles (i.e., early stage of development) that were not identifiable past the family level were excluded from all analyses. We also excluded those families that represented less than 1% of the total catch over the entire study period. In addition, *Leucauge venusta* (family Tetragnathidae) was also excluded, as only one individual was trapped, and unlike the other Tetragnathids captured, which are ground dwelling spiders, *L. venusta* is an orb-web dwelling species.

In order to characterize the differences in the spider community each pitfall trap was treated as an independent replicate and samples were pooled as either pre- or post-treatment and adjusted to per-trapping-week. Pitfall traps can be considered independent if there is sufficient spacing between traps (Woodcock 2005) and several other studies
have also treated individual traps as independent (Moore *et al.* 2002, Moretti *et al.* 2002, Obrist and Duelli 1996) with a minimum distance of 10-m between traps. Furthermore, in order to provide the most meaningful analysis of these data, even without true replication, the use of inferential statistics can be used in order to provide the most meaningful results (Oksanen 2001).

Shannon Diversity Index (Kent and Cocker 1992) was calculated for each grassland overall, pre- and post-treatment overall, and pre- and post-treatment by grassland. Comparisons between the grasslands and the treatments were analyzed using Kruskal-Wallis tests in R (R Core Team 2013).

Species specific responses were analyzed using an indicator species analysis (Dufréne and Legendre 1997) utilizing the Monte-Carlo procedures (4999 permutations) with PCOrd software (McCune and Mefford 1999). Indicator species analysis is a statistical approach that uses species fidelity (relative frequency of a species within a group) and exclusivity (relative abundance of a species within a group) to classify species into groups that reflect environmental conditions represented by sample units. In addition, the overall differences in the spider community composition both before and after treatment were determined using Multi-response Permutation Procedures (MRPP). MRPP is a nonparametric procedure that is used to test a-priori groups for differences in composition. (McCune *et al.* 2002). Finally, to further explore the patterns in spider community, both before and after treatment, a non-metric multidimensional scaling (nMDS) ordination plot was performed with Bray-Curtis distance matrix calculated on per trap week abundances by trap using the vegan package in R (R Core Team 2013).
Ordination techniques organize sampling entities along gradients to explain the variability in the data, with nMDS being particularly useful as it reduces the assumption of linearity (McGarigal et al. 2000).

Results

There were observable changes in the vegetation structure of both grasslands during the study as the prescribed burn consumed most of the vegetation and litter in the BBS, and the PP structure was altered by snowfall and plant senescence (Figure 5.1). It should also be noted that the first frost (overnight low temperature of 0°C (32°F) or lower) to occur during the sampling period occurred on October 30, 2014 and additionally there was a snow fall event totaling 7.87 cm (3.1 inches) on November 17, 2014. There was a decline in average temperature highs and lows throughout the duration of the study, consistent with the change from fall to early winter.

A total of 298 spiders from 14 families and 29 species were collected. Over 80% (244) of these spiders were adults or juveniles with enough characteristics to identify to species, genus, or morphospecies, while the remaining nearly 20% (54) were only identifiable to family (Table 5.1). Lycosidae (61.7%) and Linyphiidae (19.5%) were the most abundant families.

Comparisons of the Shannon Diversity Index showed a statistically significant difference between the two grasslands overall (p=0.02). When the data for both
grasslands was pooled and the pre- and post-treatment was compared there was no
significant difference detected (p=0.88). Additionally, comparing each grassland
individually for the pre- and post-treatment there was no significant difference in the
Shannon Diversity Index (p=0.12 for the both grasslands). Although not statistically
significant, it should be noted that there did appear to be an increase in the Shannon
diversity index for the BBS when comparing the pre- and the to the post-burn (H’ of 1.69
and 1.95 respectively), and the PP showed the opposite trend, with a decrease in the
Shannon diversity index between the two sampling periods (H’ of 1.71 and 1.49
respectively) (Figure 5.2).

MRPP analysis at both the family and species level did not demonstrate any
statistically significant differences between the two grasslands (p= 0.08 for both family
and species-level analyses), but comparing the pre-burn to the post –burn overall was
significant (p=0.001) (Table 5.2). Further analysis, comparing the pre- and post- burn of
each individual grassland showed a significant difference for both grassland (p=0.014
family level BBS, p=0.013 species level BBS, p = 0.009 family level PP, p=0.005 species
level PP.) Indicator species analysis suggests that *Varacosa avara* (Lycosidae) was
associated with the BBS, and *Neoantistea agilis* (Hahniidae) was associated with the PP.
There were 3 indicators of the Pre-burn and 1 indicator of the post-burn sampling periods
when data from both grasslands were pooled. BBS-Pre had 1 indicator species, BBS-post
had 4 indicator species, PP-Pre had 2 indicator species, and there were no indicators for
the PP-Post (Table 5.3).
The nMDS ordination (Figure 5.3) resulted in a 2 dimension solution with a final stress of 0.153 and shows some overlap of the spider communities of the 2 grasslands prior to the burn, and shifts after October 25. The resulting location of the post burn plots demonstrates a greater similarity in the BBS post-burn site to the pre-treatment sites, whereas the PP shows less similarity to either the pre-burn plots or the BBS post-burn.

Discussion

Most studies have shown a decrease in spider richness and/or abundance in the time post-burn when compared to pre-burn and/or control sites (Rice 1932, Dunwiddie 1991, Zelhart and Robertson 2009, Riechert and Reeder 1972, Pascoe 2003). Although it should be noted that these studies (except Riechert and Reeder (1972) that used hand collection and litter sorting) utilized sweep netting sampling exclusively. Sweep-netting is a technique that is most often utilized to sample arthropods dwelling on low vegetation (Ozannne 2005, New 1998). Therefore, in the timeframe immediately following a fire, sweep netting would yield minimal results, as there would be limited vegetation for sweeping to occur on. Ground spiders, on the other hand, have been shown to benefit or have no short-term impacts from burning in two studies that utilized pitfall trapping (Hore and Uniyal 2008, Jansen et al. 2013). Understanding sampling techniques is an important aspect to arthropod research as there is potential for biases and errors (Leather and Watt 2005). In comparing pitfall traps, sweep nets, and visual searches Churchill and Arthur (1999) found that 94% of families were captured in pitfalls, 25% with sweep nets
and 41% by visual sampling. Therefore, when trying to determine short-term effects, when nearly all the vegetation and litter are presumed to be consumed in the prescribed burn, pitfall trapping seems to be the most logical sampling technique to examine the immediate and short term impacts of prescribed burning on spider communities.

We did not find evidence to support the hypothesis that there would be a reduction in diversity and abundance in the time frame immediately following burning. In fact we observed an increasing trend in the Shannon Diversity Index in the burned grassland post burning, although it was not statistically significant. This leads to the conclusion that spiders are either surviving the fire in situ, or are able to recolonize the area very quickly. In the mop-up phase of the prescribed burn numerous spiders were observed on the burned surface (Figure 5.4). In addition, a Varacosa avara (Lycosidae) male was captured in the trapping period of 23Nov2015-07Dec2015 with obvious burn injuries to his extremities (Figure 5.5). As the burn occurred on the October 25, one explanation is that he suffered the injuries in the prescribed burn and survived until he was captured in the pitfall trap several weeks later. Additionally, as there are multiple grassland habitats in close proximity to the burned grassland at the Gwynne Conservation Area, and ballooning spiders were observed on sampling days after the prescribed burn, it is likely that recolonization was also occurring. Other studies have stated the importance of maintaining refuge habitat and varying the spatiotemporal variation (i.e. burning on a rotational basis) among sites in these types of ecosystems (Swengel 2001) in order to provide source populations for recolonization. Thus a combination of survival and recolonization may be responsible for the lack of a decline in diversity and abundance.
Although shifts in community composition were detected they seem more pronounced for the companion unburned grassland then for the grassland subjected to the prescribed burn. As this study took place in the fall it is possible that these shifts are just part of the phenological changes in spider community that occur naturally each year. As the 2 grasslands utilized for the study were significantly different in the pre-burn time frame it is not possible to use the unburned as a control, therefore we are not able to conclude if any of the changes were specifically due to the burn. Further studies would need to be completed to evaluate this in more detail, with greater sampling size and better replication. It is clear that we still are lacking in our knowledge of the impact of prescribed burning on the spider community and further studies are warranted in order for land managers and restoration ecologists to gain the insights needed for proper care of these ecosystems.

Acknowledgements

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this project, including advising on pitfall trap construction, study design, and tremendous assistance with spider identification. We would also like to thank Timothy Rose for his assistance in the field, and John and Elizabeth Rose for their assistance in constructing the pitfall traps. Finally, we wish to thank the two anonymous reviewers who provided useful editorial suggestions.
Figure 5.1: Grasslands at the Gwynne Conservation Center, London, Ohio. (A) Big Bluestem September 2014 (pre-burn) (B) Prairie Planting September 2014 (C) Big Bluestem November 2014 (post-burn) (D) Prairie Planting November 2014
Figure 5.2: Comparison of the spider Shannon Diversity Index (H) of the two grasslands (BBS=Big Bluestem, and PP=Prairie Planting) at the Gwynne Conservation Center, London Ohio. Only the comparison of the two grasslands (BBS and PP) was significant (p-value 0.02). Although not significant (p-value 0.12) there appears to be an increase in H when comparing the BBS pre to the BBS Post.
Figure 5.3: Non-metric multidimensional scaling of the spider communities of the grasslands of the Gwynne Conservation Center, London, Ohio. BBS=Big Bluestem, PP=Prairie Planting. Pre=prior to prescribed burn, Post=after prescribed burn (Stress of 0.1532.).
Figure 5.4: Lycosidae (wolf spider) observed on the burnt substrate of the Big Bluestem during the mop-up phase of the prescribed burn at the Gwynne Conservation Center, London, Ohio.

Figure 5.5: *Varacosa avara* caught in the Big Bluestem grassland of the Gwynne Conservation Center, trapping period 23Nov2014-07Dec2014, with visible burn injuries to legs and pedipalps.
Table 5.1: Spiders species collected at the Gwynne Conservation Center, London, Ohio, by grassland and sampling period.

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<tr>
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<td>Oct 26-Dec 7</td>
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</tr>
<tr>
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<td>(abbreviation)</td>
<td>Author</td>
</tr>
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<td>Marpissa lineata</td>
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</tr>
<tr>
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<tr>
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<th>Oct 26-Dec 7</th>
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<tr>
<td>(abbreviation)</td>
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<td></td>
</tr>
<tr>
<td>(Thsp)</td>
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<td></td>
</tr>
<tr>
<td><strong>Trachelidae</strong></td>
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<td></td>
</tr>
<tr>
<td><em>Meriola decepta</em></td>
<td>Banks 1895</td>
<td>1</td>
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<td>(Mede)</td>
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Table 5.2: MRPP Comparisons of the spider community at the Gwynne Conservation Center, London, Ohio, by grassland and sampling period.

<table>
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<tr>
<th>Comparison</th>
<th>Species</th>
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<th>Delta 2</th>
<th>Delta 3</th>
<th>Delta 4</th>
<th>A</th>
<th>Obs delta</th>
<th>Exp Delta</th>
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<td>na</td>
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<tr>
<td>BBS vs PP</td>
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<tr>
<td>Pre vs Post</td>
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<tr>
<td>BBS Pre vs Post</td>
<td>Family</td>
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<td>2.24</td>
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<td>na</td>
<td>0.654</td>
<td>2.307</td>
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<tr>
<td>BBS Pre vs Post</td>
<td>Species</td>
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<td>2.308</td>
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<td>na</td>
<td>0.639</td>
<td>2.414</td>
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<td>PP Pre vs Post</td>
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<td>0.659</td>
<td>2.253</td>
<td>6.604</td>
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Table 5.3: Spider indicator species analysis by grassland and sampling period for the Gwynne Conservation Center, London, Ohio. Species abbreviation (Indicator value, p-value).

<table>
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<tr>
<th>Habitat Type</th>
<th>BBS</th>
<th>PP</th>
<th>Pre</th>
<th>Post</th>
<th>BBS-Pre</th>
<th>BBS-Post</th>
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<th>PP-Post</th>
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<td>0.03)</td>
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<td>&lt;0.01)</td>
<td>0.04)</td>
<td>0.03)</td>
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</tr>
<tr>
<td>Vaav</td>
<td>Neag</td>
<td>Pasa</td>
<td>Agpr</td>
<td>Pasa</td>
<td>Erau</td>
<td>LinUnkl</td>
<td>Vaav</td>
<td>Pimi</td>
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<td></td>
<td>(60.0,</td>
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<td>(70.0,</td>
<td>(83.3,</td>
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<tr>
<td></td>
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<td>0.01)</td>
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<td>&lt;0.01)</td>
<td>0.03)</td>
<td>&lt;0.01)</td>
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References


Chapter 6: Changes to the spider community after an EF-2 tornado impacted a North-Central Ohio forest.

Abstract

In the Central Hardwood Forest region, catastrophic winds, such as thunderstorms and tornadoes, are important natural disturbances that affect ecosystem structure and function. Few studies, however, have evaluated the natural succession of forests impacted by catastrophic winds. In 2010, an EF-2 tornado impacted the forests of the Secrest Arboretum on the Wooster campus of The Ohio State University, providing an opportunity to quantify the impact and recovery of a relatively undisturbed natural forest ecosystem. Following the tornado, a network of geo-referenced sample plots were established in the tornado-impacted stand and an adjacent unimpacted reference stand for comparisons of forest composition and structure. In 2013, spiders were sampled visually, with vegetation beating, leaf litter extraction, and pitfall traps. A total of 3,316 spiders from 24 families were collected; with 21 families present in the reference stand, and all 24 families present in the tornado-impacted stand. Using the unimpacted stand as a reference I observed a shift in the spider community composition related to the catastrophic canopy disturbance associated with the tornado-impacted (e.g. higher densities of Lycosidae and Linyphiidae, and lower densities of Dictynidae in the tornado.
stand when compared to the reference stand). Both Shannon Diversity Index and overall spider abundance were greater in the tornado impacted stand when compared to the reference stand (P = 0.04). This study provides important baseline information on the role that natural disturbances processes, and their legacies, play in regulating the structure and composition of spider communities at a family level. As we continue to study these communities, we will develop a better understanding of role that natural disturbances, and the legacies of these disturbances, play in regulating the structure and composition of spider communities following wind disturbance. Such information is important as we develop restoration strategies that emulate natural models of ecosystem development.

Introduction:

Catastrophic winds, including gales, windstorms, cyclonic storms, and tornadoes (Everham and Brokaw 1996), play an important role in the successional dynamics of many forests (Bouget and Duelli 2004, Long 2009). Tornadoes, specifically, are estimated to impact an average of 600km² annually in the United States (Peterson 2000). Although tornadoes are a short lived phenomena they can have long lasting effects, especially on forest communities (Peterson 2000). In the Central Hardwoods region of the Midwestern United States, forests have an estimated rotation period of 1200-1300 years for catastrophic wind disturbance (Whitney 1994), and in response to global climate change, there may be an increase in the number and intensity of tornadic storms (Foster et al. 1998).
In general, weather events, such as catastrophic wind, increase the patchiness and heterogeneity of forest ecosystems (Gandhi et al. 2007). Wind disturbance, by altering the forest structure, influences the temperature regime, light availability, as well as forage quality and quantity for wildlife (Wolff et al. 2009). Changes to forest structure and the lasting legacies of the storm are a result of the particular storm characteristics and the pre-storm plant community (Everham and Brokaw 1996). For example, the intensity and storm size are thought to mainly be driven by meteorological and atmospheric conditions (Foster et al. 1998), whereas the pre-storm vegetation characteristics and physiography may influence the localized effect of the storm (Peterson 2000). Tornadoes create unique damage due to the spiral and lift of the wind, which can uproot trees, twist and shatter the trunks, and scatter debris and stumps in all directions (Oliver and Larson 1996). In addition, falling trees may influence the microtopography via the creation of pits and mounds (Brewer and Merritt 1978) that persist for long periods of time (Gandhi et al. 2007). These pit and mound structures open up habitat to new plant species, and the reduction of the canopy can create additional growing space (Oliver and Larson 1996). New growth can originate from the previous vegetation community (i.e. seedlings and sprouting from existing trees, and seeds maintained in the seedbank) or from newly dispersed seeds (Peterson 2000). This, in turn, could make the site susceptible to the introduction of exotic and invasive plant species.

While there is some information on the successional dynamics of forests impacted by catastrophic winds, less is known about animal responses (McGlinn et al. 2010). Even less is known about major taxa (such as Arachnida), as these organisms have generally
been overlooked in studies of catastrophic wind (Gandhi et al. 2007). Of all the taxa that have been examined, the impacts of wind on bird populations have been studied most frequently (Prather and Smith 2003, McClure 1945, McGlinn et al. 2010), and a few mammal studies (Pauli et al. 2006, Wolff et al. 2009). In terms of invertebrates, Skłodowski and Garbalińska (2011) explored the response of Ground Beetles (family: Carabidae) to tornado damage in a forested habitat, and found a significant decline in forest specialists following the tornado, an increase in species richness, and an overall reduction in abundance due to the impacts of the tornado. Little is known about other invertebrate species, especially spider community response to catastrophic wind disturbance. Those studies that have explored these relationships have focused on wind damage from hurricanes, including Spiller et al. (1998) that examined the response of spider communities to Hurricane Lili on 19 islands in the Bahamas. They found an immediate decline in the abundance of spiders with some localized extinctions, but noted that the populations recovered within one year. In contrast, the only tornado related spider study we found in the literature evaluated the fluctuating asymmetry of Schizocosa ocreata (brush-legged wolf spider) in a post tornado stand (Uetz et al. 2009), demonstrating that individuals in a tornado impacted area had a greater fluctuating asymmetry, and thus, the authors concluded, were exposed to greater environmental stress than those in an area not impacted by the tornado.

There are a variety of reasons to focus on changes in spider communities following disturbance, in part because spiders are a highly diverse group of animals (Beccaloni 2009, Wise 1993) that are sensitive and respond quickly to environmental
conditions (Marc et al. 1999). Bultman and Uetz (1982) stated that an understanding of the ecology of spider communities provides valuable insights into the nutrient and energy dynamics of forest ecosystems. Langellotto and Denno (2004) hypothesized that arthropod predators respond to five major changes with increased in habitat complexity; 1) Increased prey abundance; 2) Refuge from predations; 3) Increased ability to locate and capture prey; 4) Greater access to preferred microclimate conditions; 4) Access to additional alternative resources, such as pollen and nectar. In this chapter I explore the changes in the spider community (diversity, abundance, and community composition) in response to catastrophic wind disturbance in a Central Hardwoods forest ecosystem. My hypotheses are: 1) the tornado-impacted stand will have higher diversity due to the heterogeneous structure created by the tornado; 2) There will be differences in the spider communities due a higher abundance of open habitat specialists in the impacted stand and a higher abundance of forest specialists in the reference stand.

Methods:

On September 16, 2010, the natural forest stands of the Secrest Arboretum, located on the Wooster campus of the Ohio State University and Ohio Agricultural Research and Development Center (Wooster, Ohio), were impacted by an EF-2 tornado, with winds up to 217 kph. This event provided us with a unique opportunity to examine the changes in both the plant and animal communities following a tornado, especially as a nearby Secrest Arboretum stands showed very little impact from the tornado (providing a
reference stand to compare the tornado-impacted stand). Additionally, the Secrest Arboretum agreed to allow natural succession to occur, with little to no human intervention (i.e. no salvage harvesting or planting). In the spring and summer of 2011, the impacts of the tornado on forest plant communities were measured using a network of geo-referenced sampling plots within a 0.6-ha tornado-impacted stand and a nearby undisturbed reference or control stand of similar size (24 plots per stand for a total of 48 sample plots).

Within each stand every tree greater than 10 cm diameter at breast height (DBH) was tagged, identified, and DBH was measured in 2011. The relative density (RDi), absolute density (Di), coverage (Ci), relative coverage (RCi) and an importance value (IVi) were calculated for each tree species (Brower et al. 1997). Within the impacted stand all overstory trees were rated from 1 to 6, where 1 was undamaged and 6 was broken between the ground and crown base. An average damage rating was then calculated for each species. Additionally, all downed wood (greater than 10cm DBH) was also inventoried within the impacted stand by species and size. No downed wood was observed in the reference site in response to the tornado.

In 2013, using the same network of geo-referenced sample plots four spider sampling techniques were utilized. These included:

1. *Pitfall traps*: At each trap location a hole was dug such that a one gallon flower pot fit snuggly into the hole with the top rim of the pot level with the natural ground. Following the design by Bradley (2004) a 16 oz. deli food container with ~2” of propylene glycol/dish soap solution was placed in the flower pot. Propylene glycol was
selected as it helps to kill and preserve the specimens in the trap and is less harmful to other wildlife than the alternatives (specifically ethylene glycol). The dish soap reduces surface tension on the solution, causing the caught invertebrates to sink into the solution. The trap was placed securely over the catch container and flower pot. The roof and base were constructed using ¼” plywood. The base had a 3” hole cut into the center in which a solo cup with the bottom removed was inserted to serve as a funnel, guiding the invertebrates to the catch container. A 2’ x 2’ piece of chicken wire was secured of the top of the trap with landscape pins. This was done to reduce the chance of mammalian disturbance to the traps. Samples were collected at regular intervals, and spiders and other invertebrates separated and stored in 70% ethanol until identification.

2. **Visual Sampling**: An area of 1-m² within in each sample plot was search visually for 15 minutes. Any spiders found were collected in 70% ethanol, and stored for identification.

3. **Vegetation Beating**: A tarp was placed over the ground and vegetation in the same 1-m² used for visuals sampling was struck with a wooden pole for 60 seconds. Any spiders that fell to the tarp were collected and stored in 70% ethanol for identification.

4. **Leaf Litter Extraction**: The leaf litter of ¼ of the 1-m² area in each plot was collected in Ziploc bags and returned to the lab. At time of collection the volume of each bag was estimated, and the mass of the litter was recorded. At the lab the litter was placed in a Berlese funnel for three days. After three days the samples were sorted and spiders stored in 70% ethanol for identification.
Pitfall trapping occurred from January 19th, 2013 to May 19th, 2013; visual, vegetation beating, and leaf litter extraction occurred in October of 2013. After collection in the field spiders were identified using a Nikon SMZ 1270 microscope and resources including Ubick et al. (2005) and the World Spider Catalog (2017).

At the time of visual, beating, and leaf litter sampling a variety of local habitat data was collected in both the tornado impacted and reference stands. A Kestrel 3500 weather meter was used to determine temperature, relative humidity, wind speed, barometric pressure, and leaf litter temperature. Vegetation structure was characterized by using a modified vegetation sampling method from Kearns and Rodewald (2013), with a 3-m pole placed at each corner of a 1-m² sampling quadrat centered at each sampling plot. Along this 3-m pole the number of vegetation hits was recorded at 0.5-m intervals starting at the ground. Ground cover at each of these four points was categorized as live vegetation, litter, soil, log, moss, rock, or other. Canopy cover was estimated by the researcher using an ocular tube.

Statistical Analyses

As the network of sample plots associated with the study were established on a 12-m x 12-m grid, I treated sampling plot as independent. Several studies have treated sample plots as independent if sufficient spacing is present beyond typical organism movement (Woodcock 2005, Moore et al. 2002, Moretti et al. 2002, Obrist and Duelli
1996), and a research study by Perry et al. (2017) in similar forest types suggests that the majority of daily spider movements (>95%) are restricted to distances smaller than 12 m.

Family richness, evenness (J), and Shannon Diversity Index (H’), and total spider abundance were calculated for each quadrat using BiodiveristyR (Kindt and Coe 2005). Comparisons between the impacted and reference stands was analyzed using a t-test (all data were normally distributed). Habitat structure variables were compared using a t-test (for normally distributed data) and Mann-Whitney tests (for non-normally distributed data). These analyses were completed using R (R Core Team 2013).

The overall differences in the spider community composition between the tornado-impacted and reference stands were determined using Multi-response Permutation Procedures (MRPP). Finally, to further explore the patterns in spider community a non-metric multidimensional scaling (nMDS) ordination plot was performed with Bray-Curtis distance matrix calculated and ENVFit was applied to determined environmental drivers of the changes in the spider community. These analyses were completed in R (R Core Team 2013)

Results

There were dramatic differences in the vegetative structure between the two sites following the tornado (Figure 6.1). Less than 4% of the trees in the impacted stand surviving unscathed and 127 trees, ranging in DBH from 10-109 cm, were blown down or had broken tops. After the tornado the reference stand was dominated by Carya
*tomentosa* (mockernut hickory), *Quercus veluntina* (black oak), *Acer rubrum* (red maple), *Acer Saccharum* (sugar maple), and *Prunus serotina* (black cherry), while the tornado-impacted stand was dominated by *Quercus rubra* (red oak), *Pinus strobus* (white pine), *Q. veluntina* (black oak), and *Quercus alba* (white oak) (Table 6.1). The reference stand had higher canopy closure (P<0.001), and higher understory densities of *Prunus serotina* (P<0.001). The impacted stand had significantly higher leaf litter mass (P=0.004), total understory vegetation density (P<0.001), shrub density and *rubus* sp. density (P<0.001). *Juniperus virginiana* was only recorded in the impacted stand. Standing dead vegetation density (P=0.739) and percent of bare soil (P=0.739) were not significantly different between the stands (Table 6.2).

I collected 3,316 spiders from 24 families (Table 6.3). The most common families were Dictynidae (25.9%), Linyphiidae (13.3%), and Lycosidae (10.8%), and Agelenidae (10.1%), which compose over 60% of the total number spiders collected. All 24 families were collected in the impacted stand, and only 21 families were collected in the reference stand. The three families collected in only the impacted stand were Oxyopidae (6 individuals collected), Theridiosomatidae (2 individuals collected) and Trachelidae (2 individuals collected).

The impacted stand had a significantly higher overall spider abundance (P=0.030)(Figure 6.2d), with 73.96±3.07 spiders collected per m² in the impacted stand, compared to 64.21±3.49 spiders collected per m² in the reference stand. This trend, however, differed for individual families; there was a higher abundance of Dictynidae in the reference stand (P =0.002), a higher abundance of Linyphiidae (P =0.007), and
Lycosidae (P <0.001) in the impacted stand (P =0.007), and Agelenidae showed no significant difference (P =0.730) between the stands (Figure 6.3). There was no significant difference in the family evenness (P =0.078)(Figure 6.2b) nor the family richness (P =0.259)(Figure 6.2a). The impacted stand had a mean evenness of 0.85±0.01, and the reference stand had a mean evenness of 0.83±0.01. The impacted stand had a mean richness of 12.75±0.38, compared to the reference stand which had a mean richness of 12.17±0.34. The tornado-impacted stand had a significantly higher Shannon Diversity Index (H’) than the reference stand (P=0.039) (Figure 6.2c), with the mean H’ in the impacted stand 2.16±0.03, compared to a mean H’ in the reference stand of 2.06±0.03.

Non-metric multidimensional scaling (nMDS) demonstrated some overlap in the spider community (stress 0.266) (Figure 6.4). The x-axis represents the change from the early successional habitat of the tornado-impacted stand on the right to the later successional stages in the reference-stand on the left. This seems to be driven by the higher abundance of Dictynidae, Thomisidae, Philodromidae, and Antrodiaetidae in the reference stand and higher abundances of Linyphiidae, Lycosidae, and Oxyopidae in the tornado-impacted stand. ENVFit environmental factors provide additional evidence of this, as bare soil and canopy closure are associated with the left side of the ordination, and understory vegetation density and leaf litter mass are associated with the right side of the ordination (Figure 6.4, Table 6.2). Multiple Response Permutation procedures (MRPP) also supported the conclusion that the communities differed between the two stands (P =0.001).
Discussion

Tornadoes are isolated and not easily studied due to the limited areas that they impact and their unpredictable nature, but are still an importance disturbance of forest ecosystems (Peterson 2000). In the United States 90% of recorded tornadoes are EF-0 or EF-1, and only 9.4% are EF-2 or EF-3 (Peterson 2000). These varying levels of intensity add a layer of complexity to studying tornadoes. While few studies have explored shifts in plant communities following tornadoes, there is almost no research that has examined changes in animal communities due to tornado damage, and I was unable to find any published studies on the shifts in spider communities in response to tornadoes.

Not surprisingly, there were drastic changes in the vegetation structure between impacted and reference stands. The loss of most of the canopy in the impacted stand by means of blow down, bent trees, and defoliation increased light levels and promoted understory plants to grow, including some invasive species. The amount of leaf litter in the impacted stand was greater than the reference stand; this may be due to the amount of down wood from the storm, as well as the high influx of plant material from herbaceous and shrubby plants. One of the striking differences between tornadoes and other major forest disturbances (i.e. fire) is the fact that tornadoes leave most of the vegetation and wood within the site (Pauli et al. 2006). Larger trees are more vulnerable to damage, which causes shifts in the plant structure from larger to smaller trees, as well as community compositional shifts to more early-successional species (Peterson 2000).
Studies on ground beetle (family: Carabidae) have shown that tornado disturbance reduces abundance but increases richness (Skłodowski and Garbalińska 2011). Therefore, I hypothesized that the impacted stand would have higher spider diversity, and this was shown to be the case for H’. I also found a significant increase in overall spider abundance, and this trend was likely due to the dramatic shifts in understory and canopy vegetation creating a much more heterogeneous habitat in the impacted stand compared to the reference stand.

Assigning habitat affiliations as a family level for spiders is difficult, as there is a great deal of diversity within each family. In general, Oxyopidae are a grassland/open habitat family (Brady and Santos 2005), while Amaurobiidae (Ubick 2005), Dictynidae (Bennett 2005), Liocranidae (Ubick and Richman 2005), and Philodromidae (Dondale 2005) are considered forest specialist families. A high percentage of Lycosidae and Linyphiidae are also associated with open/grassland habitats (Jocqué and Dippenaar-Schoeman 2006). I hypothesized that more open habitat spiders would be found in the impacted stand, and more forest specialists would be found in the reference stand. This hypothesis was somewhat supported. Oxyopidae (grassland/open habitat specialists) were only found in the impacted stand, although at low numbers. No Liocranidae species were collected, and there was no significant difference in the presence of the Amaurobiidae (but only seven specimens were collected), but both Dictynidae and Philodromidae were significantly more abundant in the reference compared to the impacted stand. Lycosidae and Linyphiidae were found in significantly higher abundances in the impacted stand,
which is consistent with the higher proportion of these species being associated with open habitat.

The five main drivers of changes to invertebrate community post-disturbance have been hypothesized to be: 1) changes in prey abundance 2) changes in areas that can serve as refuge from predation 3) changes in the ability to locate and capture prey 4) changes in microhabitat conditions 5) Changes in availability of alternative resources (i.e. nectar, pollen, etc.) (Langellotto and Denno 2004). Wind damage, in general, adds complexity to the forest floor with the addition of coarse woody debris and early successional vegetation (Bouget and Duelli 2004). This added complexity could serve as refuge from predation, may attract additional prey insects (especially those that feed on dead plant matter), provide the opportunity for additional early successional plants that provide alternative food resources, and alter the microhabitat conditions. I found higher masses of leaf litter in the impacted stand, and increased litter depth has been correlated to an increase in prey richness (Uetz 1979). Additionally, although spiders are usually considered obligate predators, there are many reported cases of use of alternative resources, such as nectar and pollen (Pollard and Beck 1995; Jackson et al. 2001; Taylor & Pfannenstiel 2008; Taylor & Bradley 2009; Chen et al. 2010), which may be more readily available in the impacted stand due to the shift to an early-successional community. This study provides important baseline information on the role that tornadoes, and their legacies, play in regulating the structure and composition of spider communities.
Acknowledgements

Salaries and research support for this research was provided by state and federal funds appropriated to the Ohio Agricultural Research and Development Center (OARDC) at The Ohio State University, and the “Linking watershed research and GK-12 education within an ecosystem context” project funded by NSF. I especially thank the support of the Secrest Arboretum for allowing us access to the study sites. I are very grateful to Dr. Richard A. Bradley for his assistance throughout this project, including tremendous assistance with spider identification. I would also like to thank Linnea Rowse, Charles Goebel, John Rose, and Ellie Monarch for their assistance in the field.
Figure 6.2: Comparison of means ±SE of a) Richness spider richness (P =0.259) b) spider evenness (P=0.078) c) spider shannon diversity index (P=0.0390) and d) overall spider abundance (P=0.042) comparing the Tornado impacted stand (grey) and reference stand (white) at the Secrest Arboretum, Wooster, Ohio.
Figure 6.3: Comparisons of mean abundance per m² ± SE for the ten most abundant families. Dictynidae (P= 0.002), Linyphiidae (P= 0.007), Lycosidae (p-value <0.001), Agelenidae (P= 0.731), Tetragnathidae (P =0.198), Anyphaenidae (P= 0.611), Theridiidae (P= 0.530), Thomisidae (P= 0.790), Salticidae (P= 0.592), and Araneidae (P= 0.085) in the tornado impacted stand (grey) and reference stand (white) at the Secrest Arboretum, Wooster, Ohio.
Figure 6.4: Non-metric multidimensional scaling (nMDS) of the spider community in the tornado-impacted (grey) and adjacent non-impacted reference (white) mixed-hardwood forest stand of north-central Ohio (stress=0.266) with ENVFit variables (see table 6.2 for p-values of habitat variables).
Table 6.1: Importance values, number of downed trees, and damage ratings for overstory species in the tornado-impacted and adjacent non-impacted reference stands of the Secrest Arboretum, Wooster, Ohio.

<table>
<thead>
<tr>
<th>Tornado-impacted Species</th>
<th>IVi</th>
<th># Down</th>
<th>Avg Damage</th>
<th>Reference Species</th>
<th>IVi</th>
</tr>
</thead>
<tbody>
<tr>
<td>Quercus rubra</td>
<td>0.55</td>
<td>29</td>
<td>5.4</td>
<td>Carya tomentosa</td>
<td>0.40</td>
</tr>
<tr>
<td>Pinus strobus</td>
<td>0.39</td>
<td>45</td>
<td>5.5</td>
<td>Quercus velutina</td>
<td>0.31</td>
</tr>
<tr>
<td>Quercus velutina</td>
<td>0.35</td>
<td>9</td>
<td>5.9</td>
<td>Acer rubrum</td>
<td>0.30</td>
</tr>
<tr>
<td>Quercus alba</td>
<td>0.18</td>
<td>4</td>
<td>3.4</td>
<td>Acer saccharum</td>
<td>0.29</td>
</tr>
<tr>
<td>Acer rubrum</td>
<td>0.11</td>
<td>4</td>
<td>3.6</td>
<td>Prunus serotina</td>
<td>0.23</td>
</tr>
<tr>
<td>Taxus spp.</td>
<td>0.10</td>
<td>13</td>
<td>5.5</td>
<td>Quercus rubra</td>
<td>0.18</td>
</tr>
<tr>
<td>Tilia americana</td>
<td>0.08</td>
<td>0</td>
<td>6</td>
<td>Ostrya virginiana</td>
<td>0.15</td>
</tr>
<tr>
<td>Sassafras albidum</td>
<td>0.06</td>
<td>8</td>
<td>3.1</td>
<td>Fagus grandifolia</td>
<td>0.08</td>
</tr>
<tr>
<td>Prunus serotina</td>
<td>0.05</td>
<td>3</td>
<td>4.2</td>
<td>Juglans nigra</td>
<td>0.03</td>
</tr>
<tr>
<td>Acer saccharum</td>
<td>0.04</td>
<td>1</td>
<td>4.4</td>
<td>Fraxinus americana</td>
<td>0.02</td>
</tr>
<tr>
<td>Tsuga canadensis</td>
<td>0.04</td>
<td>5</td>
<td>6</td>
<td>Quercus alba</td>
<td>0.01</td>
</tr>
<tr>
<td>Ulmus americana</td>
<td>0.02</td>
<td>1</td>
<td>1.7</td>
<td>Carya cordiformis</td>
<td>0.01</td>
</tr>
<tr>
<td>Populus grandidentata</td>
<td>0.01</td>
<td>2</td>
<td>6</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ailanthus altissima</td>
<td>0.01</td>
<td>2</td>
<td>5</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fraxinus americana</td>
<td>0.01</td>
<td>0</td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ostrya virginiana</td>
<td>0.01</td>
<td>0</td>
<td>5</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 6.2: Comparison of habitat structure variables between the tornado-impacted and adjacent non-impacted reference mixed-hardwood forest stands of north-central Ohio (for data with normal distribution comparisons made with a t-test, for non-normal data comparison were made with a Mann-Whitney test). Additionally, the ENV Fit p-values are listed.

<table>
<thead>
<tr>
<th></th>
<th>Impacted Mean</th>
<th>Impacted SD</th>
<th>Reference Mean</th>
<th>Reference SD</th>
<th>Comparisons t</th>
<th>Comparisons P</th>
<th>ENV Fit P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total Understory vegetation (Veg pole hits)</td>
<td>65.2</td>
<td>20</td>
<td>24.9</td>
<td>9.5</td>
<td>8.9042</td>
<td>&lt;0.001</td>
<td>0.001</td>
</tr>
<tr>
<td>Litter Mass (g)</td>
<td>223.6</td>
<td>80.8</td>
<td>163</td>
<td>54.6</td>
<td>3.0465</td>
<td>0.004</td>
<td>0.027</td>
</tr>
<tr>
<td>Canopy Closure (%)</td>
<td>0.5</td>
<td>80</td>
<td>75</td>
<td>90</td>
<td>33.5</td>
<td>&lt;0.001</td>
<td>0.001</td>
</tr>
<tr>
<td>Percent Bare Soil</td>
<td>0</td>
<td>25</td>
<td>0</td>
<td>50</td>
<td>275</td>
<td>0.739</td>
<td>0.017</td>
</tr>
<tr>
<td>Prunus serotina (Veg pole hits)</td>
<td>0</td>
<td>40</td>
<td>3.5</td>
<td>15</td>
<td>124.5</td>
<td>&lt;0.001</td>
<td>0.054</td>
</tr>
<tr>
<td>Juniperus virginiana (Veg pole hits)</td>
<td>0</td>
<td>4</td>
<td>0</td>
<td>0</td>
<td>300</td>
<td>0.999</td>
<td>0.001</td>
</tr>
<tr>
<td>Standing Dead Vegetation (Veg pole hits)</td>
<td>0</td>
<td>30</td>
<td>0</td>
<td>3</td>
<td>290</td>
<td>0.739</td>
<td>0.034</td>
</tr>
<tr>
<td>Shrubs (Veg pole hits)</td>
<td>49</td>
<td>38.75</td>
<td>8</td>
<td>11.25</td>
<td>485</td>
<td>&lt;0.001</td>
<td>0.001</td>
</tr>
<tr>
<td>Rubus spp. (Veg pole hits)</td>
<td>29.5</td>
<td>93</td>
<td>0</td>
<td>19</td>
<td>494</td>
<td>&lt;0.001</td>
<td>0.001</td>
</tr>
</tbody>
</table>
Table 6.3: Total number of spiders collected by family in the tornado-impacted and adjacent non-impacted reference mixed-hardwood forest stands of north-central Ohio.

<table>
<thead>
<tr>
<th>Family</th>
<th>Reference</th>
<th>Impacted</th>
</tr>
</thead>
<tbody>
<tr>
<td>Agelenidae</td>
<td>171</td>
<td>163</td>
</tr>
<tr>
<td>Amaurobiidae</td>
<td>3</td>
<td>4</td>
</tr>
<tr>
<td>Antrodiaetidae</td>
<td>5</td>
<td>1</td>
</tr>
<tr>
<td>Anyphaenidae</td>
<td>123</td>
<td>113</td>
</tr>
<tr>
<td>Araneidae</td>
<td>44</td>
<td>68</td>
</tr>
<tr>
<td>Clubionidae</td>
<td>2</td>
<td>4</td>
</tr>
<tr>
<td>Corinnidae</td>
<td>28</td>
<td>8</td>
</tr>
<tr>
<td>Dictynidae</td>
<td>503</td>
<td>357</td>
</tr>
<tr>
<td>Gnaphosidae</td>
<td>1</td>
<td>4</td>
</tr>
<tr>
<td>Hahniidae</td>
<td>12</td>
<td>11</td>
</tr>
<tr>
<td>Linyphiidae</td>
<td>169</td>
<td>272</td>
</tr>
<tr>
<td>Lycosidae</td>
<td>54</td>
<td>304</td>
</tr>
<tr>
<td>Mimetidae</td>
<td>1</td>
<td>6</td>
</tr>
<tr>
<td>Oxyopidae</td>
<td>0</td>
<td>6</td>
</tr>
<tr>
<td>Philodromidae</td>
<td>37</td>
<td>4</td>
</tr>
<tr>
<td>Phrurolithidae</td>
<td>14</td>
<td>8</td>
</tr>
<tr>
<td>Pisauridae</td>
<td>24</td>
<td>18</td>
</tr>
<tr>
<td>Salticidae</td>
<td>65</td>
<td>72</td>
</tr>
<tr>
<td>Tetragnathidae</td>
<td>127</td>
<td>161</td>
</tr>
<tr>
<td>Theridiidae</td>
<td>78</td>
<td>91</td>
</tr>
<tr>
<td>Theridiosomatidae</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td>Thomisidae</td>
<td>76</td>
<td>81</td>
</tr>
<tr>
<td>Trachelidae</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td>Uloboridae</td>
<td>4</td>
<td>15</td>
</tr>
</tbody>
</table>
References


Chapter 7: Spider communities’ response to disturbance, overall conclusions

From a restoration ecology standpoint, studying the changes in spider communities, including species, diversity, and abundance, can provide insights into the natural development of areas impacted by disturbances, as well as insights into many aspects of the habitat structure. Overall, habitat heterogeneity has been shown to be influential across many taxa (Tews et al. 2004; Barbaro 2005). Langellotto and Denno (2004) hypothesized that there are five primary factors that are altered by increasing habitat heterogeneity that would be influential to arthropod predators, including spiders: 1) increased the abundance of prey resources 2) increased ability to find refuge from predation 3) differences in the ability to locate and capture prey 4) altered access to microclimates and 5) changes to the availability of alternative resources (i.e. nectar).

Herbivorous arthropod prey have been shown to increase with greater vegetation diversity (Ziesch and Roth 2013), although, one should note that herbivorous invertebrates do not constitute the entire prey base for spiders (Langellotto and Denno 2004) as spiders are known to not only feed on small vertebrate prey (McCormick and Polis 1982) but often will feed on other arthropod predators (Beccaloni 2009). Therefore, an increase is herbivorous prey may not only directly influence the prey abundance for spider, but also indirectly as it may attract other predators that they feed on. Additionally,
prey richness has been observed to increase with increased litter depth (Uetz 1979). Some disturbances may increase the litter habitat and its complexity, as I found in the tornado impacted mixed-hardwood stand (Chapter 6), and other disturbances may reduce the litter habitat, as seen in young post-wildfire jack pine stands of northern Lower Michigan (Chapters 3 and 4).

The increase in habitat complexity may also influence predation on spider communities. Interspecific predation among spiders is considered an important mortality factor (Gunnarsson 1985). Complex litter habitat was shown to reduce interspecific predation within spiders (Uetz 1979), although intraspecific cannibalism was not found to be influenced by habitat complexity in Schizocosa ocreata spiderlings (Wagner and Wise 1996). Predation from insectivorous birds is considered to exert major influences on spider communities (Askenmo et al. 1977), and it was noted that to avoid predations one strategy is to remain unseen to predators (Gunnarsson and Wiklander 2015), which may be more easily accomplished in complex habitats.

Habitat complexity not only influences the prey abundance, but may also alter the ability of the spiders to locate and capture the prey (Langellotto and Denno 2004). Areas higher in prey abundance may offer greater choices, allowing for a variety of foraging techniques utilized by a variety of spiders (Uetz 1979). Web building spiders, although select web sites based on vegetation characteristics, only maintain fidelity to those sites only if sufficient prey is captured (McNett and Rypstra 2000). Lycosidae are known to visually orient to prey (Foelix 2011), which may be why they seem to prefer the more open habitat of recently disturbed sites.
Spider communities have been shown to be associated with and respond to microhabitat conditions (Greenstone 1984, Barton et al. 2017). Spiders are sensitive to moisture gradients (Entling et al. 2007), and temperature (Ziesch and Roth 2013). Buddle et al. (2000) specifically noted that CWD increases micro-habitat heterogeneity, and causes shifts in spiders communities. Deadwood provides critical microhabitat conditions suitable for spiders, especially in sites with limited overstory (Work et al. 2014). Although, it has been hypothesized that some spiders may be able to tolerate wider ecological conditions than previously thought (Buchholz 2010).

Although spiders are usually considered obligate predators, there are many cases of alternative resource use, such as feeding on nectar and pollen (Pollard and Beck 1995; Jackson et al. 2001; Taylor and Pfannenstiel 2008; Taylor and Bradley 2009; Chen et al. 2010). Recently disturbed sites may see an increase in flowering forbs and fruit bearing plants, similar to what was documented in the post-tornado site (Chapter 6). This may provide additional resources to spiders. When I was rearing species of Cheiracanthium in the lab they refused all live insect prey they were offered, but I found that they would readily feed on black currant jam (personal observation). Additionally, these alternate resources may attract large fruit eating species, which indirectly could attract a higher prey density as many arthropods are attracted to animal dung (Janetos 1986) that would be left behind.

My studies did find changes to the habit structural heterogeneity due to disturbance. Both the early successional post-wildfire jack pine stands and tornado-impacted stands had lower canopy closure and higher understory vegetation densities
This understory vegetation may provide hiding places for spider to avoid predation, access to alternative food resources, and attract prey for the spiders. Regardless of ecosystem examined, I found shifts in spider diversity, community composition, and guild structure associated with disturbances, and post-disturbance succession. For example, I found higher spider diversity in mature jack pine stands, compared to young stands, following-wildfire (Chapters 3 and 4). In contrast, I found that in the short term after prescribed burning in a restored grassland that there was a trend of higher spider diversity immediately post-fire, with some species showing an increase in abundance in the post-fire system (e.g., *Erigone aletris*, *Varacosa avara*) (Chapter 5). Similarly, I found that a forest impacted by catastrophic wind had higher spider diversity when compared with an unimpacted reference stand (Chapter 6); however, this study system is still recovering from the disturbance, and the goal is to continue to monitor the changes over many years.

Indicator species were identified for most of the disturbances I examined, and there appears to be some overarching trends. Lycosidae (wolf spiders), for example, were indicators of the recently disturbed ecosystems, including the five year old post-wildfire jack pine stands in northern Lower Michigan (Chapter 3), and, stands impacted by an EF-2 tornado in north-central Ohio (Chapter 6), while another Lycosidae (*Varacosa avara*) was shown to increase in abundance following the prescribed grassland burn (Chapter 5). Lycosidae are generally thought of as open habitat specialists (Jocqué and Dippenaar-Schoeman, 2006), and therefore they may find the habitat created by disturbances more suitable. In comparison, Dictynidae (Mesh web weavers), were found to be indicators of
the more mature wildfire-regenerated jack pine stands (Chapter 3), and the reference stand that was paired with the tornado-impacted stand (Chapter 6), however, when examined on the species level I found that the ground hunting Dictynidae were indicators in both young and mature jack pine stands (Chapter 4). The members of the family Dictynidae collected as part of this research are from two subfamilies, Cicurininae and Dictyninae. Cicurininae are known to act as ground spiders, whereas Dictyninae occur in a variety of habitats ranging from branch tips to leaf litter (Bennett 2005). Both of these subfamilies need the appropriate understory structure, which is more consistently found in later successional stages associated with forest development.

I also observed other spider species that were associated with habitats associated with successional seres. Anyphaenidae (ghost spiders) were indicators of young post-wildfire jack pine stands in northern Lower Michigan sites (Chapter 4). Anyphaenidae are known for utilizing understory vegetation and create a curled leaf retreat (Kaston 1981), and this dependence on understory vegetation would explain their affinity for young stands.

Philodromidae (running crab spiders) were found to be indicators of the reference mature mixed-hardwood stands of north-central Ohio (Chapter 6). Although, they were an indicator of the five year post-wildfire jack pine stands (Chapter 3). Philodromidae are known for their ambush hunting style on vegetation (Dondale 2005). They can be found on vertical tree trunks where the stalk and chase their prey and hide in bark crevices (Dondale and Redner 1978). I hypothesize that in these early successional post-wildfire jack pine stands that this family is utilizing the standing dead trees as hunting grounds,
whereas in the tornado-impacted stands of north-central Ohio stand most of the trees were blown over or broken, reducing vertical tree trunk habitat for this family.

Finally, I observed that Corinnidae (ant runner spiders) were also an indicator of these mature mixed-hardwood stands (*Chapter 6*), but surprisingly were associated the youngest and oldest post-wildfire jack pine stands (*Chapter 4*). Many of these families are diverse, so it is not surprising that species specific responses are different than family and guild level responses. Further work is needed to understand the species-level responses to disturbance for Corinnidae.

Secondly, I set out to evaluate what the changes in spider community composition and structure reveal about habitat structure and changes in post-disturbance ecosystem development. We did find some overarching themes. Lycosidae seem to prefer open habitat, Philodromidae like standing trees, Dictynidae need a well-developed understory, and Anyphaenidae need understory vegetation suitable for building web retreats. While I observed that there are many consistent trends across disturbance types, there are also important differences. Much more investigation into these differences is needed as spiders are a very diverse group, with over 46,000 species known worldwide (World Spider Catalog 2017). It is through the ecosystem-level comparisons that have been the focus of this dissertation that we will begin to untangle the species-environment interactions associated with spiders, helping us to better understand the important functional role spiders play in ecosystem development across the world.

Lastly, I set out to see if spiders that are disturbance specialists share similar life traits that I can use to classify all spiders on a spectrum from disturbance specialist to
disturbance avoiders. My studies focused on disturbances that altered the habitat structure. Stand replacing wildfire (Chapter 3 and 4), stand altering catastrophic wind (Chapter 6), and the reduction of the aboveground plant material in a prescribed grassland burn (Chapter 5). These studies show an increase in open habitat spiders in early succession development, and those relying on an increased structure in the understory in the later stages. Although we can make generalizations, it is clear that this is an oversimplification, as seen when I focused on a single guild of spiders (Chapter 4), and looked at species specific responses.

Overall, I found that there were changes in the spider communities in these study systems in response to the disturbances. This could be seen at the broadest (guild analysis) to the finest level (species specific responses). My worked started with the idea that one possible downfall or limitation in evaluating the success of restoration practices is the tendency to evaluate only the plant community. That by focusing on the plant community exclusively is an example of the “Field of Dreams Myth” (Hilderbrand et al. 2005, McAlpine et al. 2016), the idea that if we build the appropriate structure (plants) that the animal community will self-assemble (Bradshaw 1983). In many cases of ecological restoration the professionals intentionally establish the plant community, so using the plant community as the primary or single source of evaluating success could likely lead to obtaining measures of positive success in error. Therefore, in order to obtain a more holistic view of ecological restoration there needs to be an integration of plant and animal metrics to evaluate success of restoration practices (McAlpine et al. 2016). And to do that, we need to understand the species-environment relationships
among diverse taxa, including spiders. Therefore, I advocate, based on the results of this research, that spiders are a good choice of organism to bridge this gap.
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