

**GROUND-FLORA COMPOSITION AND DIVERSITY OF YOUNG AND
MATURE WILDFIRE-REGENERATED JACK PINE FORESTS**

THESIS

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Abstract

Ecological forestry has become an increasingly important tool as forest management and restoration efforts look to incorporate into management practices the types of vegetative structures, functions, and spatial patterns created by natural disturbances. One of the major factors leading forest managers to consider implementing ecological forestry practices is that many current management practices do not recreate the complexity and diversity created by natural disturbance regimes. This is currently the case for jack pine (*Pinus banksiana* Lamb.) forests in northern Lower Michigan where many jack pine forests are managed as plantations to increase habitat for the endangered Kirtland's Warbler (*Dendroica kirtlandii* Baird, KW). Jack pine plantation management has come under scrutiny for creating homogenized stand structures, reducing natural regeneration of jack pine, and having a single-species restoration goal (the KW). Less is known about how stand-replacing wildfires affect the development of jack pine forests, particularly the effects of wildfire on the composition and structure of the ground flora. Ground flora, and the factors (e.g., stand structure, fuel loadings) that drive the ecological processes that shape the ground-flora vegetation, can provide vital information on how natural disturbances and biological legacies impact ecosystem structure. If principles of ecological forestry are to be incorporated into current and future management plans, it is

important to understand the impacts of disturbances and how their biological legacies shape plant communities.

To further our knowledge of the role wildfires have on the composition, structure, and function of plant communities, and provide information that could be used to support the implementation of ecological forestry practices, we studied the composition, structure, diversity, and spatial heterogeneity of ground-flora communities associated with wildfire-regenerated jack pine forest ecosystems in northern Lower Michigan. Specifically, we examined the ground flora at 12 sites that were either < 8 years post-wildfire (young) or > 22 years post-wildfire (mature). Percent cover of all woody and herbaceous vegetation < 1 m tall was collected within a nested 1-m² quadrat using a modified Braun-Blanquet cover class system. Data analyses included comparisons (using t-tests) of species diversity and dominance (as expressed by percent cover) of individual species and functional lifeform guilds, Canonical Correspondence Analysis (CCA) to examine the relationships among ground-flora vegetation, stand structures and fuels, and semivariograms to measure spatial heterogeneity in ground-flora diversity among stands.

Overall, we found the ground flora of young post-wildfire stands to be dominated by blueberry (*Vaccinium* spp.) and sedges (*Carex* spp.), while eastern teaberry (*Gaultheria procumbens*) and various mosses and lichens characterized the ground flora of the mature stands. On average (± 1 SD), the mature stands had significantly higher species richness, with a total of 13.4 ± 3.3 species per m² in the young wildfire-regenerated stands and 17.4 ± 4.8 species per m² in the mature wildfire-regenerated

stands ($P < 0.01$). Gradient analyses suggest the composition of ground-flora vegetation shifts as these stands develop over time, and these changes are related to shifts in the overstory and fuel structures. For example, the young stands have a strong positive correlation with seedling density and a negative correlation with overstory basal area, while the mature stands have a positive correlation to overstory basal area. The mature stands also appear to cluster into three groups along the first canonical axis, presumably along a productivity gradient (as indicated by the strong, positive relationship with live herbaceous cover). This suggests that even with relatively homogenous soils and physiography, the composition and structure of the ground-flora community is variable. Spatial analyses suggest that this variability of species richness and diversity is expressed at relatively small spatial scales as the sill and range values were low for most of the sites. The sill value for species richness of the mature sites was between 2.8 - 3.9 (no.m²)² and the range value was mostly 0 m. Species diversity for mature sites had similar variability. The results from this study suggest that the ground flora developing following wildfires in jack pine forests can be variable and shift in terms of the dominance of species and species functional groups over time. These changes appear to be driven by changes in the stand structure and fuel loadings, factors that influence light availability and forest floor conditions. When compared with other studies of the ground flora that develops in jack pine plantations, restoration and management practices that emulate these patterns in managed stands could enhance plant species diversity and composition, as well as promoting other ecosystem services such as habitat for additional threatened grassland and openland bird species.

Dedicate to my Mom, to my family, and to my friends who were sources of strength.

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Fields of Study

Major Field: Environment and Natural Resources

Specialization: Ecological Restoration

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Chapter 1: Introduction

As forest managers explore options to manage forest ecosystems for multiple ecosystem services, there has been an increased interest in new approaches that focus on emulating the complexity in stand structure and function that often follow natural disturbances and stand development processes. One such approach, ecological forestry, has received considerable interest over the past decade (Franklin et al. 2002; Franklin et al. 2007). This approach is based upon understanding the outcomes of natural disturbances (e.g., plant structure and patterns) and emulating those outcomes with forest management practices (Mitchell and Beese 2002; Franklin et al. 2007; Franklin and Johnson 2012). Ecological forestry accomplishes this by focusing on biological legacy retention, intermediate treatments to incorporate stand heterogeneity, and recovery periods between harvests (Franklin et al. 2007). Successful implementation, however, requires an understanding of how disturbances affect the structural development of forest ecosystems before silvicultural practices can be adapted to guide forest management activities (Franklin et al. 2002).

As a major goal of ecosystem restoration is to return an ecosystem to a natural developmental trajectory (SER 2004), understanding forest ecosystem development patterns following natural disturbances is an important factor that will help improve restoration treatments, such is the case with jack pine (*Pinus banksiana* Lamb.) forest

ecosystems in northern Lower Michigan. Prior to EuroAmerican settlement and shifts in land use, stand-replacing wildfires occurred on average every 59 years (Byelich et al. 1985; Cleland et al. 2004). These fire-prone forests were well adapted to this dominant disturbance type, as jack pine typically has shorter life spans and are able to produce serotinous cones a decade after germination (Cleland et al. 2004). Due to increases in fire suppression activities and changes in the fire regime, jack pine forest ecosystems have been altered considerably with total jack pine forest land cover decreasing from 53.4% to 36.8% across northern Lower Michigan since the 1800s (Cleland et al. 2004; USFWS 2012).

Across this landscape, most jack pine forest ecosystems are now managed as plantations with a rotation age of 40-50 years old. Jack pine plantation management has been a critical component of increasing populations of the endangered Kirtland's Warbler (*Dendroica kirtlandii*, KW); however, the impacts of these plantations on other important ecosystem services have been debated (Corace and Goebel 2010). While plantations can promote biodiversity and other ecosystem services when developed on abandoned agricultural fields, they often have lower levels of biodiversity when compared with natural forests (Paquette and Messier 2013). Applying ecological forestry concepts to forest ecosystems that are historically wildfire-dependent, such as jack pine forest ecosystems of northern Lower Michigan, has the potential to improve the ecosystem services provided by these forests (Corace and Goebel 2010; Corace et al. 2012).

Current research and restoration efforts in these once dominant forest ecosystems types focuses primarily on how managed jack pine plantations differ from 'natural' forest

structure and fuels (Spaulding and Rothstein 2009; Kashian et al. 2012; USFWS 2012). This is driven, in part, by the focus on restoring habitat for KW. It has been suggested that this single-species restoration can result in the landscape becoming homogenized and other important ecosystem functions may be reduced or lost (Corace and Goebel 2010). The single-species focus of these management and species restoration efforts can lead to simplified forest structures (Spaulding and Rothstein 2009) and may not provide other important ecosystem services such as biodiversity, animal and plant species habitat, and carbon and nutrient cycling. Research in boreal and temperate forests has demonstrated that as species richness and biodiversity increase so do the services provided by these forests (Gamfeldt et al. 2013). Further more, research has shown that mixed-species forests have higher productivity compared to monocultures (Gamfeldt et al. 2013). While these studies focused on different forest ecosystems, it could be related to the differences between the monoculture jack pine plantations and the wildfire-regenerated jack pine forests which are associated with other tree species such as oak (*Quercus* spp.), aspen (*Populus* spp.), and red pine (*Pinus resinosa* Aiton) (Carey 1993).

As a habitat specialist, KW, a neotropical migratory bird, nests in jack pine stands that are between 5 and 23 years in northern Lower Michigan (USFWS 2012). The decrease in jack pine habitat associated with EuroAmerican settlement severely impacted KW populations. In 1951, a census of singing males indicated an estimated population of 1,000 birds; later, a 1971 census showed a 60% decrease in singing males in northern Lower Michigan (Byelich et al. 1985). In response to this dramatic decline, active forest management in the 1970s focused on planting dense stands of jack pine in an opposing

weave pattern (Figure 1) to increase suitable for KW populations (Byelich et al. 1985). These efforts have been very successful as KW population levels have risen from 100 singing males in 1970 to 1,828 singing males in 2011 (Byelich et al. 1985, USFWS 2012). In response to this successful effort to restore populations of KW, there is the possibility that KW will be ‘delisted’ as an endangered species, and other options for maintaining current KW populations considered including those that are based upon ecological forestry principles. To support this effort, more information is needed on the natural development of wildfire-regenerated forest ecosystems in order to take a more holistic approach to management and restoration of these ecosystems (Corace and Goebel 2010).

In 2011, a study comparing the effects of natural wildfire on the structural heterogeneity of jack pine forests both before and after KW occupancy was initiated in northern Lower Michigan. While this previous work focused on differences in woody species composition, structure, and fuel loadings, the **purpose of this project was to extend that comparison by focusing on ground-flora vegetation between young, pre-KW and mature, post-KW occupancy wildfire-regenerated jack pine stands.** The results provide additional knowledge on ground-flora composition and diversity that can guide management for a more diverse array of ecosystem services and functions, including restoration efforts that look to integrate either prescribed burning or wildfire (Environment Canada 2006; Corace et al. 2010a).

The primary questions my thesis research addresses are: 1) how does wildfire influence the composition, structure, and diversity of the ground-flora vegetation between

pre- and post-occupancy KW jack pine stands; and 2) how spatially heterogeneous is the ground-flora vegetation in these pre- and post-KW occupancy stands? To answer these questions, this thesis includes a brief review of the relevant literature related to KW and jack pine forests (Chapter 2), the results of a field-based study examining ground-flora dynamics in jack pine forests following natural wildfires (Chapter 3), and a discussion of the implications of these patterns in ground-flora composition and structure to forest management and restoration (Chapter 3).

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Figure 1. Aerial photo contrasting the difference in stand structure between a stand regenerated following a prescribed fire (left) and a clearcut stand planted with the opposing weave pattern typical of managed Kirtland's Warbler jack pine habitat (Photo courtesy Greg Corace, Seney National Wildlife Refuge).

Chapter 2: Review of Relevant Research on Kirtland's Warbler and Jack Pine Forest Ecosystems

In the jack pine (*Pinus banksiana* Lamb.) forests of northern Michigan, fire suppression and fire return intervals outside of the natural range of variation have resulted in shifts in species composition and structure, leading to degraded conditions relative to the historical pre-EuroAmerican condition (Schulte et al. 2007). These changes led to a loss of habitat and a dramatic decline in the populations of Kirtland's Warbler (*Dendroica kirtlandii* Baird; KW) (Probst et al. 2005). In response, federal and state land managers have implemented a very successful effort that involves clearcutting mature jack pine and planting jack pine seedlings in dense stands in an "opposing weave" pattern. This approach has been successful, and as a result, some wildlife and forest managers are examining new approaches to jack pine forest management that will better emulate the outcomes of natural disturbances such as wildfire. The objective of this chapter is to provide a context for the ground-flora analysis provided in chapter 3, including information on KW and jack pine forest stand development.

Kirtland's Warbler

KW is an endangered neotropical migrant that overwinters in the Bahamas and migrates to jack pine forests of the northern Lake States in the summer to nest and

reproduce. While initial documented searches began in 1977 and indicated that KW were found primarily in northern Lower Michigan, recent censuses have found the populations of KW to be expanding into the Upper Peninsula of Michigan (1996), Wisconsin, and Ontario (2007) (USFWS 2012). Historical records indicate that prior to organized census, KW were observed in these locations (Ontario since 1990 and Wisconsin since the 1840s), which could indicate previous nesting grounds before the decline in population (Byelich et al. 1985; USFWS 2012).

KW are habitat specialists and evolved with wildfire-regenerated jack pine stands that are between 5 and 23 years post-fire with a canopy cover greater than 20% (USFWS 2012). KW will nest at the base of jack pine once it reaches 1.4 – 3.8 m in height and use the jack pine's low branches to act as shade and cover (Probst and Weinrich 1993; Kashian et al. 2001). KW is a ground-nesting species, and lines their nests with various ground-flora vegetation found in the stands including Pennsylvania sedge (*Carex pensylvanica* Lam.) and low-bush blueberry twigs (*Vaccinium angustifolium* Aiton), and will have various grasses (e.g., *Andropogon* spp.), sedges and other ground flora at 10-30 cm high surrounding the nest (USFWS 2012). Once jack pine reaches 3.8 m in height and the lower branches die, the bases of the trees start to become unsuitable due to the lack of shade and camouflage (Probst and Weinrich 1993). KW are mainly insectivores, but in a fecal analysis 42% of samples contained blueberries (Deloria-Sheffield et al. 2001), suggesting that the ground-flora composition and structure may also regulate the presence of KW through providing habitat for its preferred food source. It has been suggested that KW might choose stands based upon prey abundance, in which case younger jack pine

stands may provide better habitat as that age class has a higher arthropod population totals (Fussman 1997), although it has been argued that total insect populations do not indicate total prey available for KW (Deloria-Sheffield et al 2001). KW may not utilize older stands that have a decreased insect density in the lower vegetation of trees (Fussman 1997).

Jack Pine Forest Ecosystems

Jack pine-dominated ecosystems have a wide distribution in the north-central and northeastern United States and Canada (Carey 1993). Typically, these ecosystems occur on glacial outwash, fluvial, or lacustrine gently rolling coarse-textured sand plains (Whitney 1986; Carey 1993). Seed production, mostly serotinous, begins between 5-10 years of age producing some seed yearly and the seeds have a delayed release after fire (Carey 1993). Jack pine is well-adapted to wildfire disturbances due to fast growth, delayed seed release, and reproductive maturation at an early age (Carey 1993).

Jack pine ecosystems are typically classified into one of two types: forests and savannas. Jack pine forests tend to have a closed canopy and are densely spaced (1,000 stems ha⁻¹) (Weber 1987). The ground flora tends to be composed of cherry (*Prunus* spp.), low-bush blueberry, bracken fern (*Pteridium aquilinum* [L.] Kuhn), and trailing arbutus (*Epigaea repens* L.) (Cornett 1997). Conversely, jack pine savannas have < 10% canopy cover and a dense understory composed mainly of grasses with few shrubs (Cornett 1997). Jack pine savannas, also referred to as pine barrens, typically are found on xeric sites, especially sandy soils on glacial outwash (Whitney 1986).

Jack pine forest ecosystems are fire-dependent ecosystems that historically experienced stand-replacing fire return intervals (the time between two successive fires) approximately every 59 years prior to EuroAmerican settlement (Dickmann and Cleland 2002; Cleland et al. 2004). Following the widespread logging activities of the 1880s and 1890s, large wildfires increased in frequency due to fuels left following logging, which in turn likely lead to an increase in KW populations (USFWS 2012). In the 1950s, as agricultural efforts and fire suppression increased in northern Lower Michigan, the fire rotations (the time it takes for the entire study area to be completely burned) for jack pine forests increased dramatically from ~60 years to an estimated 775 years in 2011 (Cleland et al. 2004; Dickmann and Cleland 2004). As a result, jack pine forests that once composed over half of the total land area of northern Lower Michigan (53.4%) have declined to almost a third of the total land area (36.8%) (Cleland et al. 2004; USFWS 2012). These changes in forest structure, the impact on jack pine regeneration and establishment, and the extent of change in land use altered nesting habitats and are considered to have been major contributing factors to KW population decline.

Ground Flora and Relation to Environment

There is considerable evidence, including studies from jack pine forests, that stand structure, composition, and natural disturbances can heavily influence the environmental conditions (e.g., light, soil nutrients, and moisture) of an ecosystem and in turn impact the composition and structure of the ground flora (Rowe 1956; Kashian and Barnes 2001; Brown 2004; LaPaix et al. 2009). For example, several studies have

demonstrated the association between ground flora and canopy cover (Rowe 1956; Berger and Puettmann 2000). Canopy cover density impacts the amount of light and moisture that reaches the understory, and as coverage increases, the amount of light and soil moisture decrease (Rowe 1956). This has an impact upon the ground flora as demonstrated by the difference between the higher light levels in poplar (*Populus* spp.) canopies that encourages shrub growth versus dense spruce (*Picea* spp.) canopies with low light and few shrubs (Rowe 1956). Natural disturbance events also influence the ground-flora composition and diversity. Stand-replacing wildfire will often reduce aboveground vegetation by 80% or more (Brown and Smith 2000). Various species have adaptations to this severe disturbance type, such as jack pine's serotinous cones that allows the species to regenerate and influence the composition of the post-fire stand (Brown and Smith 2000). Due to this interaction with environmental variables and stressors, ground-flora species can be indicators of disturbance or stress (LaPaix et al. 2009), and abundance or distribution of certain species can indicate environmental stressors (Pykälä 2004; LaPaix et al. 2009).

Restoration Efforts

The first active restoration efforts associated with jack pine forests for KW began in 1957 with a program to set aside KW breeding grounds. These areas were planted with jack pine in an opposing weave pattern (Figure 1) to emulate the openings created by wildfire, and then once the stands reached maturity (~40 years), the stands were clearcut and replanted with jack pine (Byelich et al 1985; USFWS 2012). In the 1960s, the United

States Forest Service increasingly focused on management plans that favored jack pine habitat resulting in additional land targeted for KW nesting habitat. When the Federal Endangered Species Act passed in 1973, restoration efforts for KW increased dramatically and the Kirtland's Recovery Plan was developed and implemented to actively promote jack pine habitat for KW breeding grounds (Byelich et al. 1985; USFWS 2012).

There is increasing evidence, however, that these methods create over-simplified stand structures at young and intermediate ages (Spaulding and Rothstein 2009). For example, early successional development in clearcut jack pine stands have shown that, over a period of three growing seasons, the ground-flora vegetation of these clearcuts developed into monocultures of sedges (Abrams et al. 1985), creating a homogenized structure that could have unintended consequences upon the overall landscape and the reestablishment of KW. In some instances researchers and managers have looked to integrate deliberate burning into jack pine management efforts to remove logging slash, however, these attempts have not been particularly productive in promoting adequate jack pine regeneration. While natural wildfire often sears the serotinous cones and releases jack pine seeds, the controlled burns following clearcutting often incinerate the cones in the slash (Abrams et al. 1985).

In terms of ecosystem restoration, the majority of the research focuses on the impacts of KW restoration treatments upon woody vegetation (Spaulding and Rothstein 2009; Kashian et al. 2012). Two studies documented the early changes of deliberate burning and clearcutting upon ground-flora vegetation; however, these studies only

examined the initial response of the ground flora following treatment (e.g., initial six years after treatment) (Abrams and Dickmann 1982; Abrams and Dickmann 1984). As KW is a ground-nesting bird that will only reside in stands between 5 and 23 years post-disturbance, there is a significant gap in knowledge related to the impact of wildfire on ground-flora communities associated with jack pine forest ecosystems. Research has also been conducted that focused on the composition of ground flora following wildfire, mainly the first three years post-fire (Abrams et al. 1984; Abrams et al. 1985). Additionally, Kashian and Barnes (2001) examined the role of soils and glacial geology in regulating the ground-flora composition of naturally regenerated jack pine stands that were either occupied by KW or past the KW occupancy period following wildfire. Little is known, however, about the spatial patterns of these ground-flora communities following wildfire, or how stand development processes influence other threatened and rare species. Jack pine forest ecosystems also have several rare plants and wildlife that are at various levels of state and federal concern. For example, species such as pale agoseris (*Agoseris glauca* Pursh), Hill's thistle (*Cirsium hillii* Canby), and prairie chicken (*Tympanuchus cupido*) are several rare species that share the same habitat as KW (Kost et al. 2007).

Knowledge Gaps and Implications

KW management has focused primarily on KW habitat requirements while largely ignoring to some degree the impacts of clearcutting and planting jack pine in high densities at the landscape scale the landscape scale (Corace and Goebel 2010). This

singular focus can homogenize forest structure and result in unintended consequences (Spalding and Rothstein 2009). Expanding jack pine management plans to consider and include ground-flora vegetation and functional guilds can also improve KW management plans. The diversity and density of ground-flora vegetation have often been used as potential indicators of ecosystem health and integrity (Brown 2004; Gray and Azuma 2004; LaPaix et al. 2009). Determining levels of ground-flora diversity and composition in wildfire-regenerated jack pine stands provide a reference or benchmark with which to compare managed stands.

While there is no doubt that current management of jack pine habitat has successfully increased KW populations, some are critical of the single-species focus, which mostly ignores other birds and animals that could benefit from more holistic restoration efforts that center on restoring the outcomes of wildfire. Several birds listed as United States Fish and Wildlife Service Regional Conservation Priority species were recorded in 90% of the KW jack pine stands sampled (Corace et al. 2010a). These species included Black-billed Cuckoo (*Coccyzus erythrophthalmus* Wilson), Field Sparrow (*Spizella pusilla* Wilson), Northern Flicker (*Colaptes auratus* L.), and Upland Sandpiper (*Bartramia longicauda* Bechstein). These species were found to live in the KW habitat and age classes in jack pine plantations, while Northern Flicker had a wider habitat range (Cleland et al. 2010a). With these and other species inhabiting jack pine plantations, increasing habitat for other species should become a priority in jack pine management plans. Expanding KW management so that it emphasizes the role that wildfire plays in regulating ecosystem structure and function may continue to increase

KW populations while at the same time promoting other important ecosystem services and the species that rely on those services.

Finally, by furthering our understanding of jack pine forest ecosystems, we will be increasing our knowledge of the effects of wildfire on ground-flora composition and diversity, which should in turn, improve restoration efforts of wildfire-regenerated ecosystems. The focus of this research is to continue increasing the information and knowledge of ground flora by focusing on composition, and also diversity and structure (guilds and spatial heterogeneity). By examining other ecosystem components, restoration efforts can be improved and expanded to include other ecosystem services. In trying to include other ecosystem services, we can take a broader approach toward single species restoration rather than focusing solely on one element.

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Chapter 3: Ground-Flora Dynamics in Jack Pine Forests of Northern Lower Michigan Following Natural Wildfires

Abstract

Fire suppression efforts and land-use practices have resulted in significant changes to the natural fire regimes of jack pine (*Pinus banksiana* Lamb.) forests of northern Lower Michigan. Recently there is increased interest in restoring these forest ecosystems in a manner that emulates natural disturbance regimes. In the current study, we expand on efforts to quantify the effects of wildfire on forest structure and fuel loadings in jack pine forests by focusing on the composition, structure, and spatial heterogeneity of the ground flora at 12 sites that were either < 7 years post-wildfire (young) and > 23 years post-wildfire (mature). Overall, we found the ground flora of the young stands are dominated by low-bush blueberry (*Vaccinium angustifolium* Aiton), jack pine, and Pennsylvania sedge (*Carex pensylvanica* Lam.), while *Cladina* spp., *Cladonia* spp., and eastern teaberry (*Gaultheria procumbens* L.) characterize the mature stands. Functional guild cover was significantly different between young and mature stands, with graminoids, woody seedlings, woody shrubs and vines ($P < 0.01$), and pteridophytes ($P < 0.05$) cover higher in young stands and mosses/lichen ($P < 0.01$) cover higher in mature stands. Ground-flora species diversity (H'), evenness (E), and richness (S) were higher in the mature post-wildfire stands than in the young post-wildfire stands,

supported by an increase in spatial heterogeneity as the stands develop over time. The results from this study suggest that the ground flora of these stands regenerated from wildfire are different from those of plantations, and restoration practices designed to emulate the fine-scale spatial heterogeneity in ground flora diversity could promote overall diversity and other ecosystem services in managed jack pine forests. As KW populations recover, these results provide a framework to develop restoration practices that emulate the outcomes of natural disturbances, and enhance habitat for other rare species found in jack pine ecosystems of northern Lower Michigan.

Introduction

Since the middle of the 19th century, there have been dramatic changes in natural fire-dependent jack pine forest ecosystems of northern Lower Michigan (Byelich et al. 1985; USFWS 2012). Prior to EuroAmerican settlement, jack pine forests ranging from open barrens to dense even-aged forests dominated the landscape of northern Lower Michigan, especially on glacial outwash plains characterized by coarse, sandy soils (Voss and Crow 1976; Whitney 1986). During the 1880s and 1890s, widespread harvesting of the original forests followed by severe wildfires (originating from unnaturally high accumulations of residual fuels) shifted the successional dynamics of these forests (Byelich et al. 1985; Pregitzer and Saunders 1999). Later attempts to convert these forests to agricultural uses, in conjunction with active fire suppression activities over the past 80 years, have led to significant changes in the structure and function of these forest ecosystems, as well as in the disturbance regimes (Byelich et al. 1985). For example,

Cleland et al. (2004) estimate that these changes in land use have increased the fire rotation (i.e., the amount of time for an area of interest to be completely burned; Dickmann and Cleland 2002) in jack pine forests from 50 years to 775 years. As a result of this increase, the jack pine forest cover has declined from 53.4% to 36.8% across northern Lower Michigan since the 1800s (Cleland et al. 2004; USFWS 2012).

Historically, the stand-replacing wildfires characteristic of jack pine forests created spatially heterogeneous stand structures that influenced the composition and structure of both the woody and the herbaceous plant communities (Houseman and Anderson 2002; Kashian et al. 2007). These forests supported a variety of species (Corace et al. 2012), including KW, a neotropical migrant bird species that nests in young, dense jack pine forests in northern Lower Michigan (Probst 1988; USFWS 2012). In 1973, KW was listed as a federally endangered species leading to extensive habitat management for KW that focuses primarily on densely stocked jack pine plantations using an opposing-weave pattern to provide both nesting and foraging habitat for KW (Byelich et al 1985; Huber et al. 2001; USFWS 2012). Due in large part to the large-scale conversion of natural jack pine forests to densely stocked jack pine stands, KW has recovered to a point where recommendations have been made to consider removing the species from the Endangered Species List (USFWS 2012).

Despite the increase in KW populations, the majority of current jack pine forests in northern Lower Michigan, especially those occurring on state or federal lands, will likely continue to be managed primarily for KW habitat. Most of these forests are managed as pure plantations that are clearcut on a 50-year rotation followed by a suite of

site preparation and planting techniques that foster the development of dense jack pine stands utilized by KW (Houseman and Anderson 2002, USFWS 2012). Jack pine plantations are typically planted at a density of 4,510 trees/ha with jack pine seedlings planted in “1.2 m intervals in rows that are 1.8 m apart” (Houseman and Anderson 2002). KW occupy these stands between 8-23 years after planting, with stem densities of 1,272-4,296 trees/ha (Probst and Weinrich 1993; USFWS 2012). Not all jack pine plantations, however, support high populations of KW. Upland ecosystem types with warm temperatures during seasonal breeding periods characterized by level or rolling terrain, Grayling, Greycalm, Montcalm or Rubicon soils, and a dense, patchy jack pine overstory canopy have been shown to provide the most suitable and preferred habitat for KW (Zou et al. 1992).

While this type of plantation forest management has been successful for increasing numbers of KW, research has shown that these forests are different in terms of forest composition and structure from their naturally regenerated counterparts. For example, there is evidence that when compared to naturally regenerated jack pine stands, managed plantations tend to have more homogenized stand structures (Abrams and Dickmann 1984; Abrams et al. 1985, Spaulding and Rothstein 2009). Site preparation methods following clearcutting also can negatively impact jack pine forest development as the deliberate burning of logging debris limits the regeneration and establishment of jack pine (Abrams et al. 1985). Site preparation methods also result in low snag densities, and even if snags are created as part of the post-harvest management, created snags in jack pine plantations decay rapidly (Corace et al. 2010*b*). This suggests that the stand

structural features in managed jack pine forests do not completely replicate the biological legacies of wildfire, a trend also observed in other forest ecosystems (Franklin et al. 2007). The single-species focus of these restoration efforts has been called into question as other rare and endangered species of plants and birds have been observed in the jack pine plantations (Kost et al. 2007; Corace et al. 2010a). At the same time, some forest and wildlife ecologists are calling for a more holistic approach to jack pine forest management for KW, including the restoration of natural processes such as fire or the application of silvicultural practices that foster structural complexity in managed forests (Corace et al. 2012). In this way, important ecosystem services such as increased habitat and nutrient cycling (including carbon sequestration), can be provided through enhanced structural and functional complexity (Corace et al. 2010a; Puettmann et al. 2013).

Currently, most research and restoration efforts in jack pine forests focus on the differences between plantations managed for KW and naturally regenerated jack pine stands (Spaulding and Rothstein 2009; Kashian et al. 2012). Less is known about how natural wildfires affect the composition and structure of jack pine forests over time, especially with respect to the ground-flora vegetation (woody and herbaceous plants < 1 m tall). Ground-flora species and functional guilds can be reflective of soil nutrient availability, pH, light availability, and other environmental conditions that influence their composition and distribution and can be used as an indicator of ecosystem health (Rowe 1956; Kashian and Barnes 2001; Brown 2004; LaPaix et al. 2009). Furthermore, individual species that are stress-sensitive can be used as indicators of disturbance or stress that an ecosystem has undergone or is undergoing (LaPaix et al. 2009), and

changes in abundance or distribution of those species can indicate the environmental stressors the ecosystem is undergoing (Pykälä 2004; LaPaix et al. 2009). Thus, information on how ground-flora vegetation develops following natural disturbances, such as wildfires, is critical to design effective practices that restore the composition and structure of jack pine forests. In particular, elucidating how overstory structure and fuel loadings (factors that may be surrogates for light availability) influence ground-flora dynamics is an important first-step and these factors are often the focus of restoration efforts in fire-dependent forests. To address this need, we quantified the composition, structure, diversity, and spatial heterogeneity of ground-flora communities associated with jack pine forests regenerating following wildfire in northern Lower Michigan. This effort was in conjunction with a larger study led by scientists with the U.S. Fish and Wildlife Service, Seney National Wildlife Refuge, Wayne State University, and The Ohio State University funded by the Joint Fire Science Program (an interagency program of federal land management organizations focused on fire science research and outreach). The focus of the study is on quantifying the temporal and spatial variability in overstory structure and fuel loadings of naturally regenerated jack pine forests following wildfire

Methods

Study Locations

Study sites were located in the Grayling Outwash Plain (Sub-Subsection VII.2.2; Albert 1995) at wildfire sites in Oscoda, Crawford, Ogemaw, Iosco, Roscommon, and

Otsego counties of northern Lower Michigan. All locations were sites of stand-replacing wildfires 3-42 years ago with little evidence of recent human disturbance and dominance by jack pine. Landform-level ecosystems including the Grayling Outwash Plain are highly variable and include a variety of landforms (Kashian et al. 2003). The Grayling Outwash Plain, which contained the study sites, has similar environmental characteristics and is characterized by sandy, excessively drained soils found in glaciofluvial deposits associated with outwash plains, deltas, kames, moraines, and Wisconsinan lake plains (Bvelich et al. 1985; Host and Pregitzer 1992; Albert 1995).

Using data provided by the Michigan Department of Natural Resources and United States Department of Agriculture Forest Service, we reviewed the wildfire records of over 50 wildfires that occurred across northern Lower Michigan since 1970. From these wildfires, we identified 20 wildfires $> 800,000\text{-m}^2$ (~ 200 ac) in size (range 80 to 2,428 ha) and which were not currently occupied by Kirtland's Warbler (KW). A field reconnaissance was conducted of each wildfire site to ensure active forest management did not impact it, including evidence of supplemental jack pine planting, recent harvesting, or other anthropogenic disturbance (e.g., roads and trails, gas exploration, etc.). Locations of these activities were noted on field maps and geo-referenced using Garmin® Oregon450 GPS unit. Of the 20 wildfires visited, we identified nine wildfires that met our sampling conditions (Table 1). Wildfires were categorized as either pre-KW occupancy (< 8 years) or post-KW occupancy (> 22 years), with three classified as pre-KW and six classified as post-KW (Table 1). We were not able to successfully locate more than three recent (< 8 years) wildfires where forest management activities had not

affected fuels and vegetation (i.e., in many recent wildfires patches with inadequate jack pine regeneration were supplemented with planted seedlings).

Following the field reconnaissance of each wildfire, information from field maps was transferred to an ArcGIS (version 9.0) layer and a $\sim 405,000\text{-m}^2$ (100 ac) sample area (or window) placed within areas of each wildfire that met our sampling conditions.

Sample windows were square in shape with dimensions of ~ 636 m by 636 m. In three wildfire sites, the areas that met our sampling conditions were large enough that we were able to establish two independent sample windows (Table 1).

In order to examine differences in the composition and structure of the ground-flora vegetation associated with these wildfires, as well as the spatial relationships of the ground flora, we established a random sample of study points that was based upon the distances between randomly generated points located within each wildfire sample window. Our procedure was as follows:

- 1) Using ArcGIS, we established 25 random points within each sample window and measured the distances between all 25 random points.
- 2) A histogram was made of distances between all 25 random points and was examined to determine a unique transect length for each sample window (all were found to represent a normal distribution).
- 3) Using the histogram of distances between all 25 points, we selected the distance associated with the 15% percentile of each distribution of distances as the unique transect length for each sample window.

After completing this process for each sample window, we selected randomly six of the 25 points used in the analysis to determine a unique transect length (see above). The location of these points was noted and entered in a Garmin® Oregon450 GPS unit, and was the basis of our sampling transects within each window. Prior to field sampling, a random cardinal direction was selected for each transect (N, E, S, or W). In cases where the selected random direction either overlapped another transect or would have been outside of the sample window, we moved the direction of the transect in a clockwise fashion to the next suitable cardinal direction.

Field Methods

In the field, we located each sample point using the coordinates entered in a Garmin® Oregon450 GPS unit. Once the location was determined, we established a sample transect in the pre-assigned cardinal direction. Along this transect, we established sample plots at distances of 0, 10%, 25% and 50% of the total transect length (Figure 2). These distances were different for each sample window and were determined by the total unique transect length. A second transect and corresponding sample plots were established 20 m from the first transect in a clockwise direction, for a total of eight sample plots for each random sample point in each sample window (Figure 2). In total, we established a total of 575 sample plots (8 sample plots per location; 6 sample locations per window; 12 total sample windows; note at one sampling location a single sample plot was not sampled).

During the summer of 2011 and 2012, fuel and stand structure data were collected for each plot. Overstory (stems > 10.0 cm dbh and > 2.0 m tall) trees were sampled on a 50.2-m^2 plot (4-m radius circular plot). We identified each tree to species and measured the dbh (cm) and height (m) using a height pole, both live and dead trees (snags) were recorded. We also sampled the saplings (live stems < 10.0 cm dbh and > 2.0 m tall) and seedlings (stems < 2.0 m tall) on a nested 12.6-m^2 plot (2-m radius circular plot). We identified each sapling to species and measured the dbh (cm) and height (m) using a height pole. Seedlings were also identified to species and then categorized into one of four height classes: 1 (≤ 0.50 m tall); 2 (0.51-1.00 m tall); 3 (1.01-1.50 m tall); and 4 (1.51-2.00 m tall).

Fuels were sampled using a modified US Forest Service Forest Inventory and Analysis (FIA) approach (Woodall and Monleon 2008). From each sample plot center, we established three 7.31-m (24 ft) transects arrayed at 30° , 150° , and 270° . Along each transect we measured down and live fuels using the following:

1,000-hr fuels - Along the length of each 7.31-m transect, we measured all down wood that was ≥ 8 cm in diameter where it intersected the transect. For each down wood piece, we identified the species, and measured the diameter of the piece at the intersection (D_X ; cm), diameter of the piece at the small end (D_S ; cm); diameter of the piece at the large end (D_L ; cm), total length (L ; m) and decay class (classes 1-5 following the FIREMON CWD decay class descriptions).

100-hr fuels – Along a 3.05-m (10 ft) section of each transect beginning at 4.26 m (14 ft) from the sample plot center, we counted all pieces intersecting the transect that were between 2.51-8.00 cm in diameter.

10-hr fuels – Along a 1.82-m (6 ft) section of each transect beginning at 5.49 m (18 ft) from the sample plot center, we counted all pieces intersecting the transect that were between 0.61-2.50 cm in diameter.

1-hr fuels – Along a 1.82-m (6 ft) section of each transect beginning at 5.49 m (18 ft) from the sample plot center, we counted all pieces intersecting the transect that were between < 0.61 cm in diameter.

Duff/litter – At 7.31 m (24 ft) from the beginning of each transect the duff and litter depth was measured (cm) and the percentage of litter in the duff estimated.

Live vegetation – Live fuels were measured in a 2-m² (1 m by 2 m) quadrat placed 90° and 3.66 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).

In the summer of 2013, this network of sample sites was used to examine differences in the ground-flora vegetation. At the center of each 50.2-m² plot used to characterize the overstory, we established a nested 1-m² quadrat. Within this quadrat, we measured the percent cover of all woody and herbaceous plants \leq 1-m tall using the following cover classes: <1%, 1-5%, 6-20%, 21-40%, 41-70%, and 71-100%. Ground-flora species were grouped into lifeform functional guilds (graminoids, forbs, lichens and mosses, pteridophytes, woody shrubs and vines, and woody seedlings). Nomenclature and lifeform categories follow the Plants Database (U.S.D.A. 2014).

Data Analysis

Prior to analysis, the ground-flora cover data were summarized as the mean percent cover per plot for each species to minimize pseudoreplication (Hurlbert 1984). Individuals that could not be identified to genus were not included in the data analyses. Overall, this resulted in 30 sample plots located in the young stands and 42 sample plots in the mature stands.

A multi-response permutation procedure (MRPP) was used to test the hypothesis that the overall ground-flora composition (as expressed by mean percent cover) is different between the young and mature stands using a natural weighing factor and Sorenson distance (Mielke 1984; McCune and Mefford 1995). To test for indicator species associated with either the young and mature wildfire-regenerated stands, we used Dufrene and Legendre's (1997) Indicator Analysis within PC-ORD (McCune and Mefford 1995) software. The significance of each species as an indicator species was

assessed using a Monte Carlo permutation procedure to test the association of each species with each age class, and generate a p-value that is the proportion of randomized trials in the permutation procedure with an indicator value equal to or exceeding the observed indicator value (Dufrene and Legendre 1997).

We also summarized canopy and ground-flora diversity using a variety of measures, including: (1) species richness (S), or the number of species present within a 1 m² plot; (2) Shannon's Diversity Index (H'); $H = -\sum (p_i \ln(p_i))$ where p_i is the relative importance (based on relative abundance determined by cover class) of the i th species; Ludwig and Reynolds 1988); and (3) an evenness ratio (E; $E = H / \ln(S)$; Ludwig and Reynolds 1988). Finally, Mann-Whitney tests were used to determine if there were differences in species richness, species diversity (H'), and evenness of the ground-flora vegetation between the young and mature wildfire-regenerated stands. We also used a series of Mann-Whitney tests to test for differences between age class with respect to the different compositional and structural characteristics (e.g., mean cover by species, mean cover by functional guild) of the ground-flora vegetation described above.

The relationships among the mean cover of plant species and environmental factors of stand structural and fuel loading were examined using canonical correspondence analysis (CCA). CCA is a direct gradient analysis restricted by multiple regression of the explanatory factors (ter Braak and Šmilauer 1997). Seventeen explanatory factors measured as part of the larger study on temporal and spatial variability of stand structure and fuel loadings were summarized and used in the CCA as explanatory variables that may regulate the distribution of ground-flora species (Table 2).

The explanatory factors were standardized by the maximum value to avoid error from different units of measurement prior to analysis.

The spatial variation of ground-flora species richness and diversity (H') was described using a series of spatial statistical analysis techniques. First, spatial autocorrelation analysis was used to construct semivariograms for species richness and diversity to determine the scale at which semivariance and distance has autocorrelation. We then compared these scales by variable and then by sample window to evaluate if patterns in species richness and diversity are constant across windows and between age classes. Spatial analysis was performed using the 'geoR' spatial package (Ribeiro and Diggle 2001) in R statistical computing software. A spherical model was used to describe the theoretical variograms for each variable, and the weight applied to each of the semi-variance estimates was proportional to the number of couples of data involved in that estimate (Cressie 1985).

Results

Differences in Stand Structure and Fuel Loadings

While mean (± 1 SD) total fuel loadings was not significantly different between the young and mature stands (3.17 ± 1.89 kg m⁻² and 3.30 ± 1.09 kg m⁻², respectively; $P = 0.65$), we did observe differences in the various fuel components between young and mature stands (Table 2). While young stands had significantly higher loadings of dead herbaceous material ($P < 0.01$) and live woody fuels ($P < 0.05$), mature stands had significantly higher loadings of 1-hour fuels, duff, and litter ($P < 0.01$) (Table 2). There

were no differences in the 10-hour, 100-hour, or 1,000-hour fuel loadings between the young and mature stands.

Most measured variables of stand structure were significantly higher in mature stands as compared to young stands ($P < 0.01$), with the exception of snag density, which was not significantly different between the two age classes ($P = 0.89$) (Table 2). These differences in stand structure were related to successional status, as young stands had on average $15,790 \pm 15,898$ seedlings ha^{-1} as compared to $3,232 \pm 3135$ seedlings ha^{-1} for the mature stands (Table 2). Total density was significantly higher in young stands than mature stands ($17,218.82 \pm 17,749.91$ stems ha^{-1} and $6,818.21 \pm 4,893.64$ stems ha^{-1} , respectively). Similarly, mature stands had on average more than twice the number of overstory stems than young stands ($3,586 \pm 2,776$ stems ha^{-1} and $1,428 \pm 2,498$ stems ha^{-1} , respectively), and nearly three times the total overstory basal area (5.68 ± 5.73 m^2 ha^{-1} and 1.46 ± 2.70 m^2 ha^{-1} , respectively) (Table 2).

Ground-flora Composition and Indicator Species

The overall ground-flora composition is different between young and mature stands (MRPP; $T = -21.39$, $P < 0.01$). Of the 41 species that occurred on at least 5% of the sample plots, Pennsylvania sedge, jack pine, and low-bush blueberry were significant indicators of the young stands while *Cladina* spp., *Cladonia* spp., and eastern teaberry (*Gaultheria procumbens* L.) were all significant indicators of the mature wildfire-regenerated jack pine stands (Table 3). Additionally, we found that the mean cover of white oak (*Quercus alba* L.), northern pin oak (*Q. ellipsoidalis* E.J. Hill), and black oak

(*Q. velutina* Lam.) were greater in the young stands while kinnikinnick (*Arctostaphylos uva-ursi* [L.] Spreng), rattlesnakeweed (*Hieracium venosum* L.), narrowleaf cowwheat (*Melampyrum lineare* Desr.), and hairy goldenrod (*Solidago hispida* Muhl. Ex. Willd.) were greater in the mature stands (Mann-Whitney test; $P < 0.05$; Table 3).

Ground-flora Structure

Corresponding to differences in the composition of the ground-flora between the young and mature jack pine stands, we observed differences in the structure of the ground flora (as represented by total cover of functional lifeform guilds) (Table 4). Mean total cover was significantly higher ($P < 0.01$) in young stands than in mature stands (104.6 ± 26.54 and 77.3 ± 24.17 , respectively), as was the mean cover of pteridophytes ($P < 0.05$), graminoids, woody shrubs and vines, and woody seedlings ($P < 0.01$). Conversely, lichen and moss cover ($P < 0.01$) was higher in mature stands than in the young stands (Table 4). No significant differences were detected in forb cover between young and mature stands ($P = 0.11$).

Relationship of ground-flora composition with fuel loadings and stand structure

CCA revealed significant relationships ($P < 0.01$) between ground-flora composition and stand structure and fuel loading factors (Figure 3). The first two canonical axes of the CCA explain 26.3% of the total variation in ground-flora species composition (Table 5), and show the strong relationships among ground-flora composition, stand structure, and fuel loadings. Specifically, live herbaceous cover,

overstory basal area, and overstory height were positively correlated with the first canonical axis ($r = 0.8, 0.4,$ and $0.4,$ respectively), while stand age and overstory basal area were positively correlated with the second axis ($r = 0.7$ and $0.6,$ respectively). Seedling density and dead herbaceous fuels were negatively correlated with the second canonical axis ($r = -0.5$ and $-0.4,$ respectively).

The first CCA axis had the strongest correlation with live herbaceous cover (kg/m^2), which represents the total amount of live biomass (kg m^{-2}) and is a proxy for ground-flora productivity. On the far left of the CCA first axis were plant species such as *Cladina* spp., *Cladonia* spp., and sand cherry (*Prunus pumila* L.), all species that are commonly found on xeric sites and indicate poor soil nutrients and low soil moisture. On the far right of the CCA first axis species such as Virginia strawberry, eastern teaberry, and black cherry were more abundant. These species are typically found in upland mixed-pine forests or wetlands with closed canopies and are indicative of more productive sites. Towards the center of the first CCA axis, there also appears to be a third group of species that are typically associated with jack pine forests (i.e., xeric to dry-mesic), including bracken fern, rattlesnakeweed, hairy goldenrod, poverty oatgrass (*Danthonia spicata* [L.] P. Beauv. ex. Roem. & Schult), and narrowleaf cowwheat (Figure 3).

Based upon the relationships of the CCA, the ground-flora of the young stands (located in the lower left-hand quadrant of the CCA) were dominated by jack pine and various grasses that are typically associated with open areas (as indicated by the negative correlation with increasing overstory basal area) (Figure 3). The CCA also revealed that the mature stands appear more variable in terms of ground-flora composition than the

young stands, as indicated by the spread of the sample plots representing the young and mature stands (Figure 3).

Ground-flora Diversity

Mean species richness, evenness, and Shannon's Diversity Index of the ground flora were significantly different between the young and mature stands ($P < 0.01$) (Figure 4). On average, the mature stands had significantly higher species richness, with a total of 13.4 ± 3.3 species per m^2 in the young wildfire regenerated stands and 17.4 ± 4.8 species per m^2 in the mature wildfire regenerated stands (Figure 4). Similar patterns were observed between young and mature stands with evenness (0.55 ± 0.07 and 0.62 ± 0.08 , respectively), and Shannon's Diversity Index (1.41 ± 0.21 and 1.74 ± 0.22), suggesting that the mature stands are more diverse and more equitable in terms of abundance of individual species per m^2 .

Spatial Heterogeneity of Ground-flora Diversity

Semivariograms of ground-flora species richness and diversity illustrate the spatial complexity of ground-flora diversity metrics in both young and mature wildfire regenerated jack pine stands. In terms of species richness, semivariograms appear to suggest that the ground-flora richness is highly variable across most sample windows regardless of stand age excluding Howes Lake W2, Hughes Lake W1, and Ostego (Figure 5). Those three sites have semivariograms where the spherical model did not fit the empirical semivariograms well and indicated that the patch sizes of species richness

are more evenly distributed. Additionally, the range of the sill statistic ((number species m^{-2})²) may suggest that ground-flora species richness is more spatially variable in the young jack pine stands than the mature jack pine stands (Tables 6). Nugget values ((number species m^{-2})²) tended to be low (near zero) for both the young and mature stands, suggesting that there is little additional information to be provided by these statistics and that there is full dispersion in species richness at scales above the minimum distance between sample 1- m^2 quadrats (~ 5 m). Finally, range values (m) for species richness were highly variable for the young stands, but are more reflective of the lack of a distance-semivariance relationship than by some spatial autocorrelation level (Table 6). All but one of the mature sample windows (Ostego) had range values equal to zero (Table 6), suggesting that the patch size for ground-flora species richness was not evenly distributed and there was no autocorrelation in the species richness of the ground-flora of these sampled stands.

We also observed high variability in Shannon's Diversity Index (H') as based upon the semivariogram statistics for each sample window (Figure 6). All but two of the sample windows (Howes Lake W1 and Ostego) showed a poor distance-semivariance relationship with respect to H' (Table 7). Sill ($(H' m^{-2})^2$) statistics suggest that both the young and mature stands were variable in terms of the semivariance of H' , and the range (m) statistics tend to suggest that the ground-flora diversity is spatially heterogeneous (Tables 7). As with the nugget values for species richness, these statistics were near zero suggesting there was no error or autocorrelation below the measured scale (Table 7).

Discussion

The current approaches to jack pine plantation management for KW have recently come under scrutiny for creating monocultures of jack pine, limiting regeneration, and focusing solely on one species (KW) when other rare and threatened species have been recorded in jack pine forests (Abrams and Dickmann 1984; Abrams et al. 1985; Kost et al. 2007; Spaulding and Rothstein 2009; Corace et al. 2010*a*). As KW is considered for removal from the federal Endangered Species List, it is important to take into consideration how a broader focus of jack pine forest management, particularly one that focuses on fostering complexity in forests and emulating the legacies of natural disturbance, will support other important ecosystem functions such as promoting biodiversity and carbon sequestration and cycling (SER 2004; Corace and Goebel 2010; USFWS 2012). Such a focus is important as levels of biodiversity are linked to the services and functions provided by an ecosystem (Gamfeldt et al. 2013).

Historically, jack pine forest ecosystems experienced stand-replacing wildfire with return intervals ranging from 26 - 69 years with biological legacies such as snags, mineral seedbeds, and very little to no immediate post-burn overstory canopy (Byelich et al. 1985; Cleland et al. 2004; Corace et al. 2012). For example, Abrams and Dickmann (1984) observed that post management, 2-year old burned jack pine stands had a greater variability in early successional species that was not found in 5-year old grass-dominated clearcut sites. As demonstrated in other forest ecosystems, biological legacies following

stand-replacing disturbances influence the succession, composition and diversity, and function of ecosystems (Franklin et al. 2002; Franklin et al. 2007). By analyzing the ground-flora species as point of reference for future restoration, and as ecological indicators of biological legacies and ecosystem health and function (Gray and Azuma 2004; Brown 2004; Franklin et al. 2007; LaPaix et al. 2009), forest management and restoration projects can be designed to increase complexity. The scope of single species restoration projects can be broadened to include a focus on other important ecosystem services such as ecosystem functions and other species (LaPaix et al. 2009).

The wildfire-regenerated jack pine forests examined in this study are all located in the Grayling Outwash Plain ecoregion characterized by glacial landforms that tend to have similar environmental characteristics (Host and Pregitzer 1992). This similarity in glacial landforms and soil types suggests that differences we observed in the ground flora between the young and mature stands can be attributed to the successional development following wildfire. As demonstrated by the CCA ordination, however, there is some variability in ground-flora species composition, and this variation may be due to small-scale differences in soil nutrients and moisture (Host and Pregitzer 1992; Kashian and Barnes 2001), as well as the effects of the stand conditions that may have influenced wildfire behavior. These legacies of the pre-disturbance condition have been shown to be important factors that shape the composition, structure, and function of future post-disturbance ecosystems (Franklin et al. 2007).

Similar relationships have been observed in other forest ecosystem types that experience stand-replacing wildfires where overstory composition and stand structure

have been found to influence ground flora diversity. For example, Berger and Puettmann (2000) found that increases in canopy cover were negatively correlated with a decrease in shrub height and an increase in foliage height diversity in balsam fir forests. In the jack pine forests we examined, we also observed that as canopy cover increased the density of blueberry cover decreased. Additionally, it is likely that as jack pine stands develop over time and canopies close, changes to the environmental conditions (e.g., light availability) result in a shift of the ground-flora composition and structure from one dominated by graminoids and pteridophytes to a community dominated by mixture of grasses, perennial forbs, and woody species. This relationship, however, is a complex one, as there appears to be considerable variability within individual wildfire-regenerated stands. This variability is most likely related to legacies that remain following the stand-replacing wildfires, as factors that regulate the ground flora (e.g. soil moisture, light availability, and nutrient availability) are influenced by the biological legacies (Rowe 1956; Franklin et al. 2007). Consequently, ground flora can be used as an indicator of ecosystem type, function, and structure (Rowe 1956; Berger and Puettmann 2000; Kashian et al. 2000; Kashian and Walker 2003; Gray and Azuma 2005).

Following wildfire, young jack pine stands had high densities of jack pine and oak seedlings, low-bush blueberry, and graminoids (such as Pennsylvania sedges) which were negatively correlated with total overstory basal area. This pattern is consistent with other studies examining the legacies of stand-replacing wildfires. Stand-replacing events, such as wildfires, in general have the tendency to create homogeneous conditions in the post-disturbance ecosystem (Franklin et al. 2007). Stand-replacing fire regimes in pre-

EuroAmerican jack pine forests decreased the amount of competition from overstory and shade-tolerant species, allowing for the establishment of a ground flora dominated by grasses and jack pine seedlings following the release of seeds from serotinous cones (Brown and Smith 2000). A similar pattern was observed in the wildfire-regenerated stands in the current study. While wildfire creates this pattern, site preparation methods including prescribed burning of slash may create a different trajectory of stand development. There is evidence that jack pine stands managed with these techniques either developed into meadows (*Carex* spp. in particular) or stratified into early successional woody seedlings and shrubs (Abrams et al. 1985). This suggests that burning slash following a clearcut may not be an adequate technique to emulate the outcomes of natural wildfires in these forests. Additional comparisons including the use of experimental studies comparing the successional development of jack pine forests managed with prescribed burning regimes and natural wildfires are needed to help disentangle these relationships.

While the ground-flora composition and structure seemed to be more consistent in the young wildfire-regenerated stands included in this study, the mature stands appeared to be clustered into three groups. While these different species groups may be related to small-scale environmental differences within each stand, it is also possible that these different ground-flora communities are the result of potentially different legacies of wildfire. One group of stands, characterized by species such as black cherry, Virginia strawberry, and eastern teaberry are characteristic of upland mixed-pine forests and embedded wetlands. The second group of mature stands was characterized by species

such as lichens, sand cherry, and greater overstory basal area, while a third group was characterized by bracken fern, rattlesnakeweed, hairy goldenrod, poverty oatgrass, and narrowleaf cowwheat. While all these species are common to jack pine ecosystems, the results suggest that there is likely a gradient of conditions in the mature wildfire-regenerated stands that grade from more savanna-like to more forest-like conditions. These different ground-flora communities could also be related to “crown tree streets” or “stringers” that are unburned areas within stand-replacing wildfires (Kashian et al. 2012). Stringers introduce spatial heterogeneity (Kashian et al. 2007) and based upon field observation had a high canopy with very little understory or ground-flora development. The distribution of plant species among these three mature groups was consistent with previous studies that examined the relationship between ground flora and landforms (Rowe 1956; Kashian et al. 2003), further supporting the use of ground flora as an indicator of ecosystem development (Gray and Azuma 2004; Brown 2004; LaPaix et al. 2009).

While the results of our spatial analyses of ground-flora diversity were not consistent between all sampled windows, our results suggest that these legacies of the pre-disturbance ecosystem not only result in spatial heterogeneity of the canopy layer as suggested by Kashian et al. (2012), they may also influence ground-flora diversity and structure. Spatial heterogeneity is a common legacy of stand-replacing wildfires, which is found at all spatial scales, and is a function of the varying intensities and behavior of wildfire (Houseman and Anderson 2002; Franklin et al. 2007). Stringers, which are created by high intensity fires on areas typically greater than 80 ha, are one example of

the spatial heterogeneity in stand structure that results from a stand-replacing wildfire (Kashian et al. 2012). The zero range values for the species richness and diversity from our semivariogram analysis suggest that there is no spatial autocorrelation in either species richness or Shannon's Diversity Index at the scales measured in the current study. This can be interpreted as an indicator that the ground flora is highly variable at even small spatial scales (i.e., < 5-10 m) as the result of high spatial heterogeneity created by the high severity fires. More research into these patterns, however, is needed before the specific influence and scale at which these legacies of disturbance regulate the ground flora of wildfire-regenerated jack pine forests, as well as how these spatial relationships differ with managed jack pine forests.

Limitations of this Study

Differences in topography have been shown to impact the rate of succession in wildfire-regenerated jack pine forests (Kashian and Barnes 2001). The impact of microclimate associated with different jack pine ecosystem types and elevations was not considered in this study and could be a potential area for further research. Microclimate plays an important role in the development of ecosystem structure and function, and has been shown to regulate ground-flora community composition and structure (Kashian and Barnes 2000). These differences, in turn, result in variable plant communities and successional trajectories following wildfire (Kashian et al. 2003).

The wildfire-regenerated jack pine forests examined in this study have spatially heterogeneous canopies, and as a result have conditions that may emulate those

conditions associated with both savanna and forest (Weber 1987; Cornett 1997). It is possible that the ground flora is responding to these small-scale differences in microclimate and future studies should examine the possible effects, and at what scale, these factors regulate the ground-flora community.

Future Management Recommendations

Our results support past research on the complexity, structure, and function of jack pine forests that experienced historical stand-replacing wildfires, and the importance of biological legacies in regulating these characteristics (Kashian et al. 2003; Franklin et al. 2007). Using past research as reference points for this comparison, we can infer that there are likely differences in the ground-flora community between wildfire-regenerated stands and managed jack pine plantations (Abrams et al. 1984; Abrams et al. 1985; Spaulding and Rothstein 2009). As awareness of an ecological forestry approach becomes more prevalent among forest managers, management and restoration plans will change to reflect the main concepts of this approach (Franklin et al. 2007).

As it is highly unlikely a natural fire regime will be reintroduced to jack pine forests in northern Lower Michigan, an alternative approach would be to explore how the legacies of wildfires can be incorporated into current management practices. By considering the landowners' goals and plans for the stand and harvested trees, management plans can be customized to interweave management goals and ecological forestry (SER 2004; Franklin et al. 2007).

There is considerable evidence that clearcutting is not effective in emulating historical biological legacies and tend to create oversimplified stand structures and inhibit jack pine regeneration (Abrams et al. 1984; Abrams et al. 1985; Spaulding and Rothstein 2009; Corace et al. 2012). The historical legacies of stand-replacing wildfires in young jack pine stands include a dominance of graminoids and woody seedlings (especially jack pine); however, the distribution of these ground-flora guilds is spatially heterogeneous. Additionally, there are high numbers of snags in both young and mature wildfire-regenerated jack pine stands (890 ± 741 stems ha^{-1} and $920 \pm 1,035$ stems ha^{-1} , respectively) compared to young and mature plantations (3 stems ha^{-1} and 252 stems ha^{-1} , respectively) (Spaulding and Rothstein 2009). Harvest methods can be modified to leave snags and woody debris and can include planting of various species of woody seedlings and grass seeding to avoid creating the monocultures common in clearcuts (Abrams and Dickmann 1982; Abrams et al. 1984; Franklin et al. 2007). While it would be difficult, and potentially troublesome for forest managers to incorporate snags at the density levels found in this study, a potential management plan would be to create small clusters of snags throughout the site, thereby increasing spatial heterogeneity and habitat.

As wildfire-regenerated jack pine stands develop over time, canopies close and the ground-flora community diversifies in plant lifeform functional guilds. Stand replacing disturbances such as stand-replacing wildfires appear to create large heterogeneous stands (Franklin et al. 2007). Although KW plantations use an opposing-weave pattern that creates a dichotomy of closed and open habitat conditions and have successfully increased KW populations (Figure 1), they do not emulate the patchiness

and heterogeneity caused by a high-intensity wildfire (Byelich et al. 1985, USFWS 2012). Other species that utilize the jack pine plantations may benefit from management plans that incorporate a broader variability in patch size, openings, and other structural and functional environmental characteristics. Intermediate treatments, including the use of prescribed burning, could be used to create spatial heterogeneity through thinning treatments implemented when the KW nesting season is over (Franklin et al. 2007).

As jack pine stands mature and move beyond the KW occupancy stage, our results suggest there are potential different successional trajectories based upon either microclimatic differences or the legacies associated with the pre-disturbance forest (Weber 1987; Cornett 1997; Kashian et al. 2012). Current jack pine plantations are managed to create a relatively homogenous forest structure of dense jack pine with opposing-weave openings that is harvested and replanted with jack pine when the stands reaches ~40 years old (Byelich et al. 1985; USFWS 2012). Forest management plans should begin to incorporate other silvicultural prescriptions to be able to use these different trajectories and increase the spatial heterogeneity and stand structure.

Finally, restoration efforts can be improved by incorporating the results of the current study into restoration plans. Specifically, the results of this study provide reference conditions for both early successional and later-successional conditions of wildfire-regenerated jack pine forests. Such information is critical to help guide active restoration and management (Kashian and Barnes 2001; Brown 2004; Gray and Azuma 2004; SER 2004; LaPaix et al. 2009). By incorporating research on ground flora and the

principles of ecological forestry, jack pine forests can be managed to create more complex and diverse structures and thus support a greater array of ecosystem services.

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Table 1. Characteristics of sampled wildfires in northern Lower Michigan including year of fire, age class, area burned, and ownership. Sampled area (window) was ~40.5 ha (100 ac). * Two sample windows in wildfire-regenerated site; see text for more information.

Wildfire	Fire Year	Age	Area Burned (ha)	Ownership
Four Mile	2008	Pre-KW	544	Michigan DNR
Howes Lake*	2011	Pre-KW	331	Michigan DNR
Hughes Lake*	2006	Pre-KW	2428	USDA Forest Service
Luzerne	1992	Post-KW	277	USDA Forest Service
Perry Holt	1988	Post-KW	572	Michigan DNR
Ostego 018	1987	Post-KW	91	Michigan DNR
St. Helen	1987	Post-KW	166	Michigan DNR
Stephan Bridge*	1990	Post-KW	2394	Michigan DNR
Rollways	1972	Post-KW	189	USDA Forest Service

Table 2. Mean (\pm SD) of environmental variables of young and mature jack pine stands in northern Lower Michigan. Asterisk indicates level of significant difference between the two age classes (Mann-Whitney test; * $P < 0.05$, ** $P < 0.01$).

Variable	Age		
	Young (n=30)	Mature (n=42)	
<i>Fuels (kg m⁻²)</i>			
1-hr	0.04 (0.03)	0.07 (0.03)	**
10-hr	0.19 (0.15)	0.19 (0.21)	
100-hr	0.31 (0.24)	0.23 (0.23)	
1000-hr	0.59 (0.8)	0.31 (0.41)	
Duff	1.05 (0.57)	1.52 (0.57)	**
Litter	0.48 (0.26)	0.69 (0.21)	**
Dead Herbaceous	0.03 (0.02)	0.01 (0.01)	**
Live Herbaceous	0.17 (0.1)	0.13 (0.18)	
Live Woody	0.32 (0.32)	0.18 (0.13)	*
Total	3.17 (1.89)	3.34 (1.09)	
<i>Stand Structure</i>			
Overstory Density (stems ha ⁻¹)	1428.33 (2498.34)	3585.71 (2776.05)	**
Seedling Density (stems ha ⁻¹)	15790.49 (15897.92)	3232.49 (3134.94)	**
Snag Density (stems ha ⁻¹)	890.83 (741.90)	920.833 (1035.03)	
Total Density (stems ha ⁻¹)	17218.82 (17749.91)	6818.21 (4893.64)	**
Overstory Basal Area (m ² ha ⁻¹)	1.45 (2.7)	13.71 (5.68)	**
Overstory Height (m)	1.56 (1.48)	5.72548 (1.9)	**
Overstory Diameter (cm)	2.04 (2.89)	7.93 (2.24)	**

Table 3. Mean (\pm SD) cover (%) of ground-flora species of young and mature jack pine stands in northern Lower Michigan. Asterisk indicates level of significant difference between the two age classes (Mann-Whitney test; * $P < 0.05$, ** $P < 0.01$).

Species	Age	
	Young (n=30)	Mature (n=42)
<i>Acer rubrum</i>	0.02 (0.08)	0.01 (0.03)
<i>Arctostaphylos uva-ursi</i>	0.28 (1.27)	1.01 (1.89) *
<i>Amelanchier</i> spp.	0.02 (0.07)	0.05 (0.26)
<i>Apocynum androsaemifolium</i>	0.03 (0.06)	0.03 (0.08)
<i>Campanula rotundifolia</i>	0.02 (0.04)	0.0 (0.1)
<i>Carex pensylvanica</i>	36.21 (12.51)	14.70 (12.15) **
<i>Cladina</i> spp.	0.0 (0.0)	8.72 (9.00)**
<i>Cladonia</i> spp.	0.01 (0.03)	1.97 (4.70)**
<i>Comptonia peregrina</i>	3.68 (5.95)	2.45 (3.21)
<i>Convolvulus arvensis</i>	0.02 (0.08)	0.01 (0.02)
<i>Danthonia spicata</i>	0.61 (1.61)	0.87 (2.24)
<i>Dichanthelium</i> spp.	0.21 (0.49)	0.36 (0.93)
<i>Epigaea repens</i>	0.0 (0.02)	0.01 (0.06)
<i>Fescue</i> spp.	0.29 (1.05)	0.0 (0.0)
<i>Fescue</i> spp.	0.10 (0.39)	0.0 (0.0)
<i>Fragaria virginiana</i>	0.0 (0.0)	0.03 (0.11)
<i>Gaultheria procumbens</i>	0.35 (0.84)	3.36 (6.70)**
<i>Gaylussacia baccata</i>	0.02 (0.07)	0.17(0.87)
<i>Hieracium floribundum</i>	0.0 (0.0)	0.06 (0.27)
<i>Hieracium venosum</i>	0.0 (0.1)	0.03 (0.10)*
<i>Maianthemum canadense</i>	0.02 (0.04)	0.03 (0.07)
<i>Melampyrum lineare</i>	0.01 (0.03)	0.03 (0.05)**
<i>Pinus banksiana</i>	0.64 (1.19)	0.02 (0.07)**
<i>Pinus resinosa</i>	0.12 (0.47)	0.01 (0.03)
<i>Populus grandidentata</i>	0.04 (0.11)	0.0 (0.0)
<i>Poa</i> spp.	0.07 (0.32)	0.0 (0.01)
<i>Prunus pumila</i>	2.66 (4.40)	1.54 (2.67)
<i>Prunus serotina</i>	0.30 (0.85)	0.61 (1.80)
<i>Pteridium aquilinum</i>	15.72 (15.74)	8.27 (12.06)*
<i>Quercus alba</i>	2.62 (5.89)	0.01 (0.06)*
<i>Quercus ellipsoidalis</i>	0.77 (1.45)	0.09 (0.27)*

Continued

Table 3 Continued

<i>Quercus velutina</i>	1.06 (2.24)	0.08 (0.33)*
<i>Rubus flagellaris</i>	0.0 (0.0)	0.05 (0.28)
<i>Solidago hispida</i>	0.0 (0.02)	0.03 (0.06)*
<i>Solidago simplex</i>	0.0 (0.0)	0.02 (0.07)
<i>Trientalis borealis</i>	0.0 (0.10)	0.03 (0.10)
<i>Vaccinium angustifolium</i>	35.32 (16.32)	19.66 (16.07)**
<i>Vaccinium myrtilloides</i>	0.05 (0.3)	0.60 (2.18)
<i>Vaccinium</i> spp.	0.04 (0.14)	0.38 (1.58)
<i>Viola adunca</i>	0.0 (0.2)	0.01 (0.02)

Table 4. Mean (\pm SD) cover (%) of functional guilds in young and mature jack pine stands in northern Lower Michigan. Asterisk after a value indicates level of significant difference between the young and mature comparison (Mann-Whitney test; * $P < 0.05$, ** $P < 0.01$).

Lifeform	Age		
	Young (n=30)	Mature (n=42)	
Graminoids	39.73(12.46)	20.38(13.04)	**
Forbs	0.15(0.18)	0.53(1.5)	
Pteridophytes	15.72(15.74)	8.27(12.06)	*
Lichens and Mosses	0.01(0.03)	17.15(14.88)	**
Woody shrubs and vines	42.58(20.76)	29.9(17.87)	**
Woody seedlings	6.37(26.54)	1.07(2.12)	**
Total	104.6(26.54)	77.3(24.17)	**

Table 5. Canonical correspondence analysis (CCA) summary relating ground-flora species and sample sites to environmental characteristics (stand structure and fuel loadings) for young and mature stands in northern Lower Michigan. Explanatory values (structure and fuels) were standardized by the maximum value.

	Axes			
	1	2	3	4
Eigenvalues	0.296	0.213	0.071	0.054
Species-environment correlations	0.878	0.834	0.822	0.617
Cumulative percentage variance of species data	15.3	26.3	30	32.8
Cumulative percentage variance of species-environment relation	37.3	64.1	73.1	79.9

Table 6. Semivariogram statistics for species richness of all 12 study windows in northern Lower Michigan. Sampled area (window) was ~40.5 ha (100 ac).

Window	Species Richness		
	Nugget (no.m ⁻²) ²	Sill (no.m ⁻²) ²	Range (m)
<i>Young</i>			
Four Mile	1.86	1374.10	331523.09
Howes Lake W1	0.00	1.56	0.00
Howes Lake W2	2.12	2370.77	533450.73
Hughes Lake W1	1.86	1565.93	291716.51
Hughes Lake W2	0.00	2.44	0.00
<i>Mature</i>			
Luzerne	0.68	3.38	0.00
Ostego	4.38	17.23	958.37
Perry Holt	0.48	3.60	0.00
Rollways	0.85	3.82	0.00
Stephan Bridge W1	0.00	2.89	0.00
Stephen Bridge W2	0.85	3.72	0.00
St. Helen	0.00	3.06	0.00

Table 7. Semivariogram statistics for Species Diversity (H') of all 12 study windows in northern Lower Michigan. Sampled area (window) was ~40.5 ha (100 ac).

<i>Young</i>	Species Diversity (H')		
	Nugget ($H'm^{-2}$) ²	Sill ($H'm^{-2}$) ²	Range (m)
Four Mile	0.00	0.09	0.00
Howes Lake W1	0.06	0.06	474.30
Howes Lake W2	0.02	0.10	0.00
Hughes Lake W1	0.02	0.09	0.00
Hughes Lake W2	0.02	0.09	0.00
<i>Mature</i>			
Luzerne	0.00	0.09	0.00
Ostego	0.08	1.36	35876.54
Perry Holt	0.00	0.12	0.00
Rollways	0.00	0.09	0.00
Stephan Bridge W1	0.02	0.10	0.00
Stephen Bridge W2	0.02	0.08	0.00
St. Helen	0.03	0.01	0.00

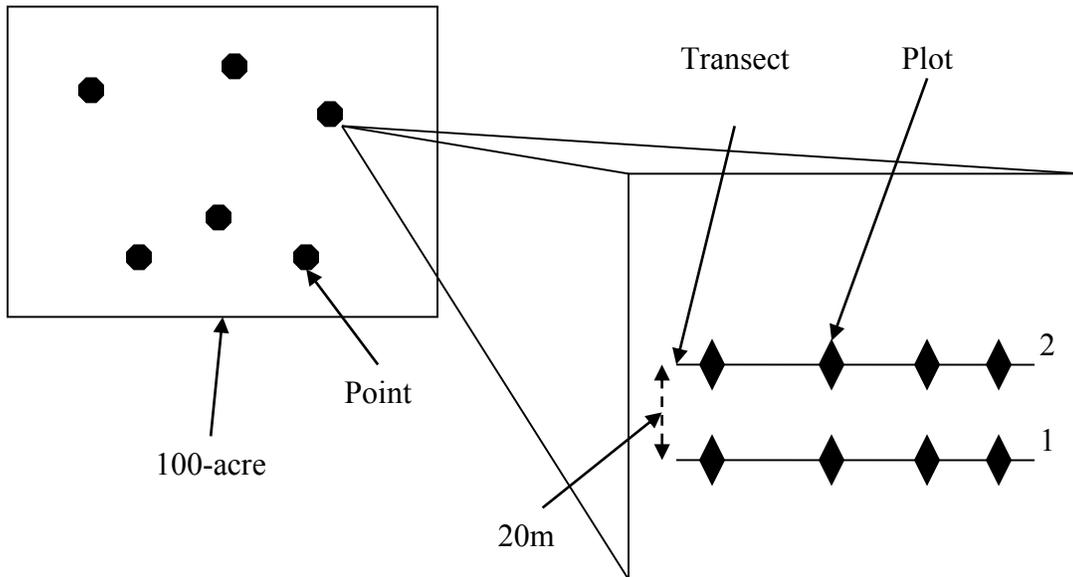


Figure 2. Sample plot layout for measuring the ground-flora vegetation in naturally wildfire-regenerated jack pine stands of northern Lower Michigan. Points were randomly selected. Transects were laid out in a random cardinal direction with the duplicate transect (2) established 20 m away in a clockwise direction.

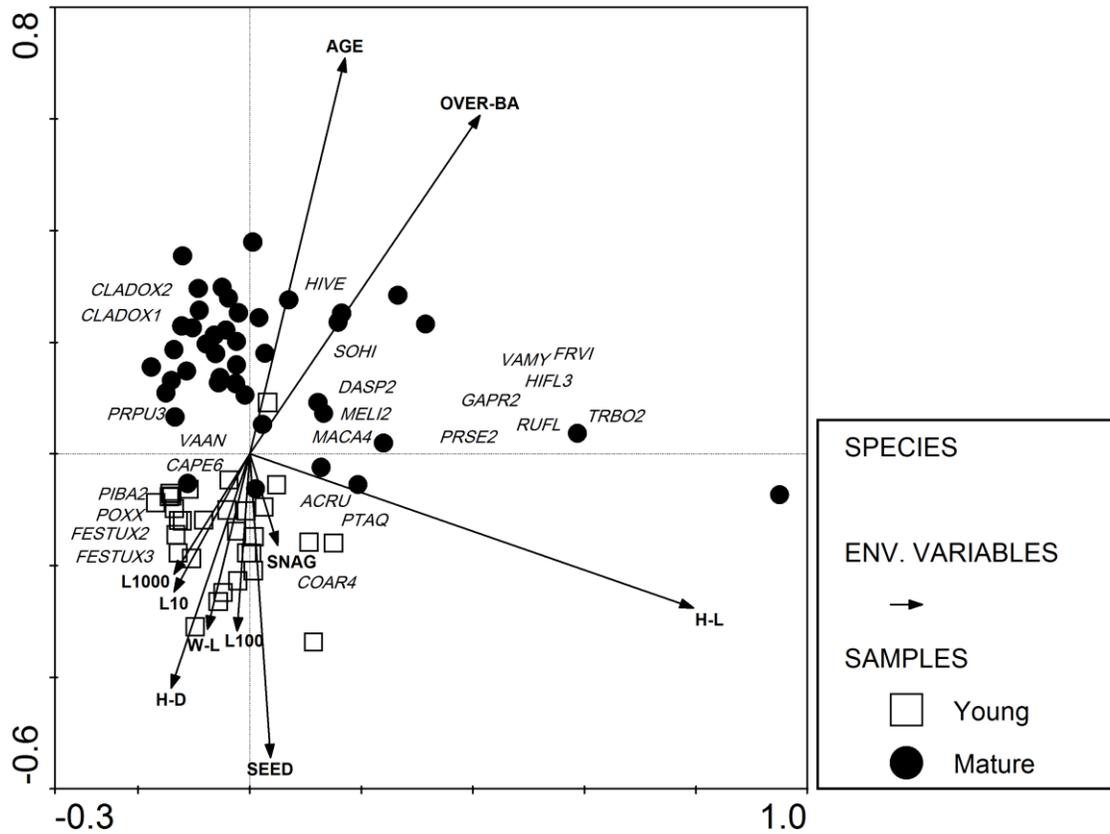


Figure 3. Canonical correspondence analysis (CCA) triplot relating species and sample sites to environmental characteristics (stand structures and fuel loadings) for young and mature jack pine stands in northern Lower Michigan. Variables displayed include age, overstory basal area (OVER-BA), seedling density (SEED), snag density (SNAG), live herbaceous cover (H-L), dead herbaceous cover (H-D), live woody cover (W-L), 10-hour fuels (L10), 100-hour fuels (L100), and 1000-hour fuels (L1000).

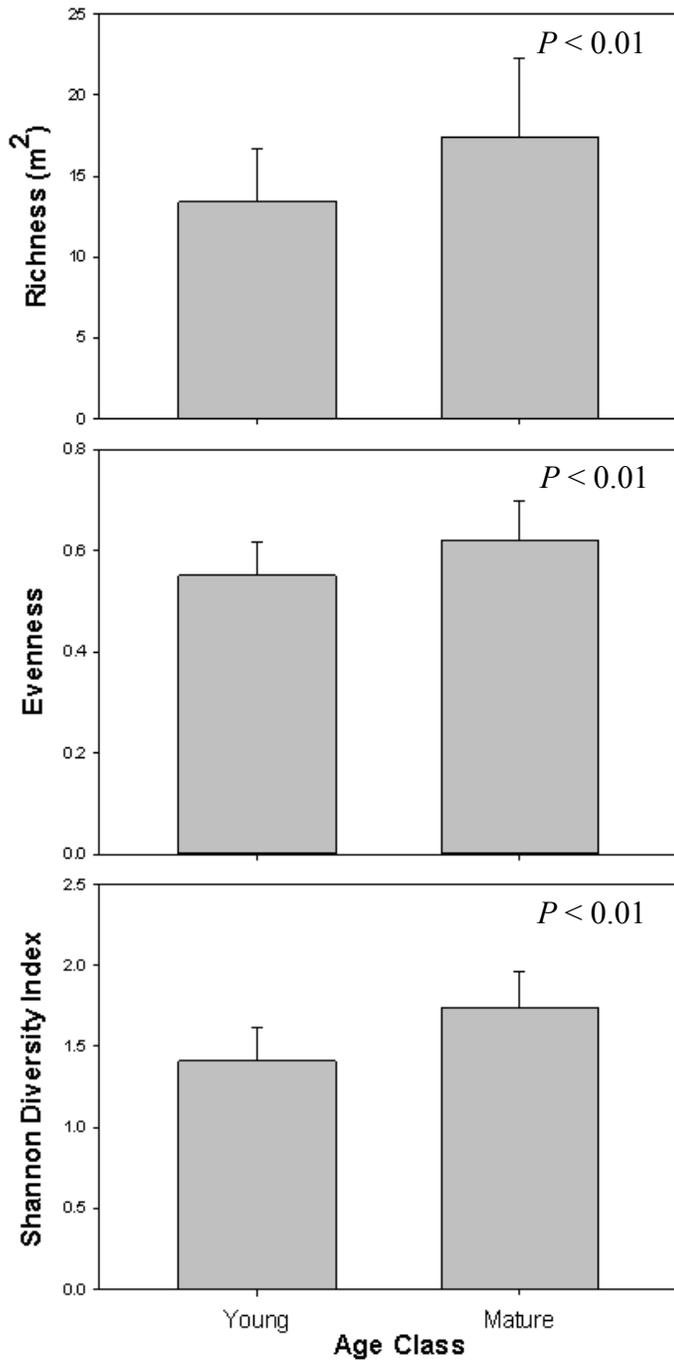
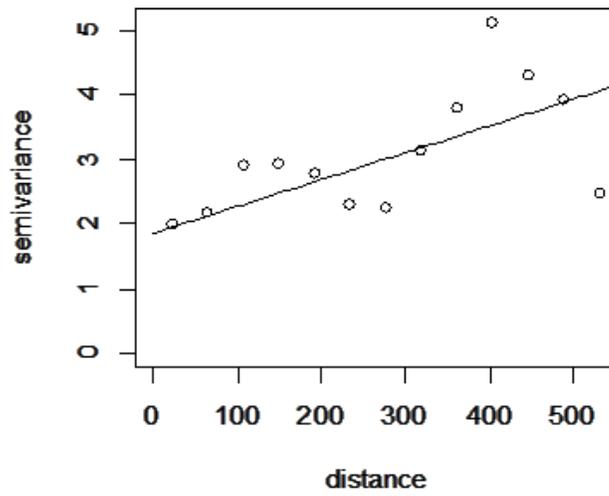
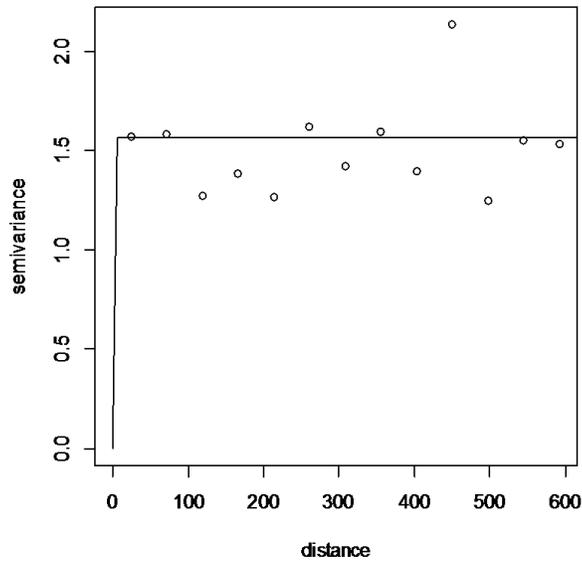


Figure 4. Mean (\pm 1 SD) of species richness, evenness, and Shannon's Diversity Index (H') of the ground flora in young and mature jack pine stands in northern Lower Michigan.

Four Mile



Howes Lake W1

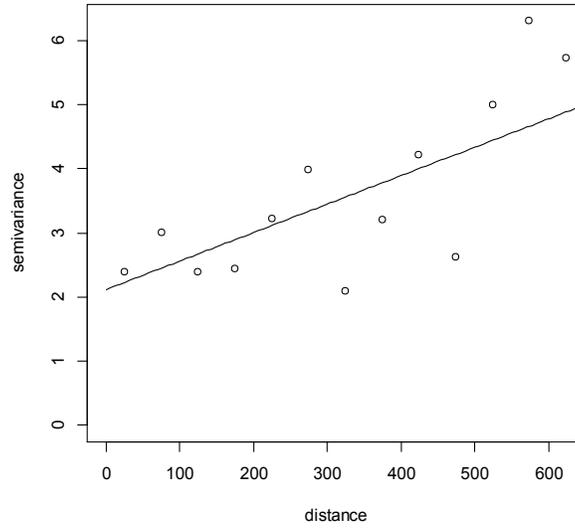


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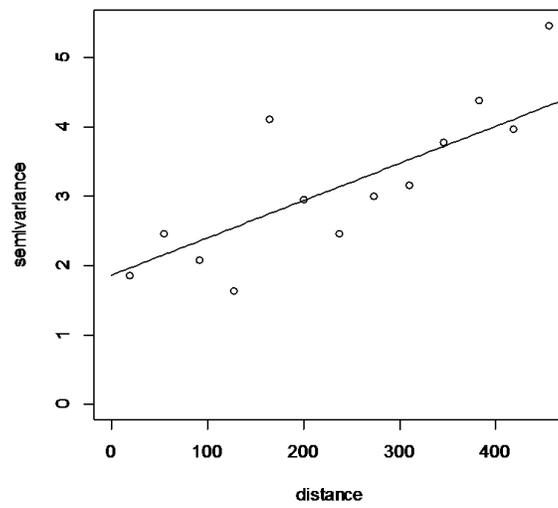
Figure 5. Semivariogram plots for spatial heterogeneity of species richness of the 12 windows in northern Lower Michigan. A spherical model was used for the spatial autocorrelation analysis. Sampled area (window) was ~40.5 ha (100ac).

Figure 5 Continued

Howes Lake W2



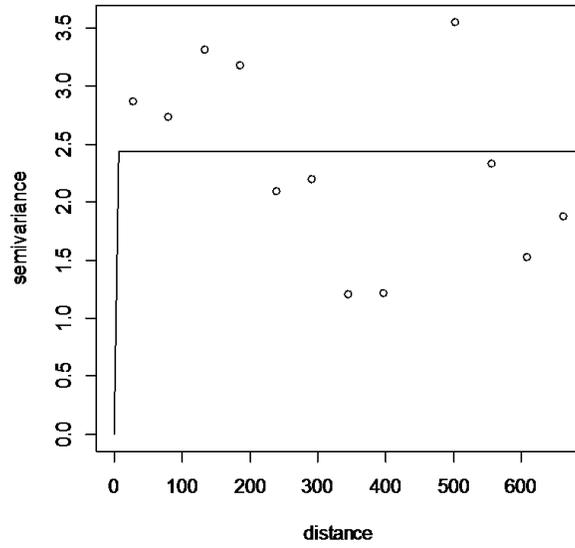
Hughes Lake W1



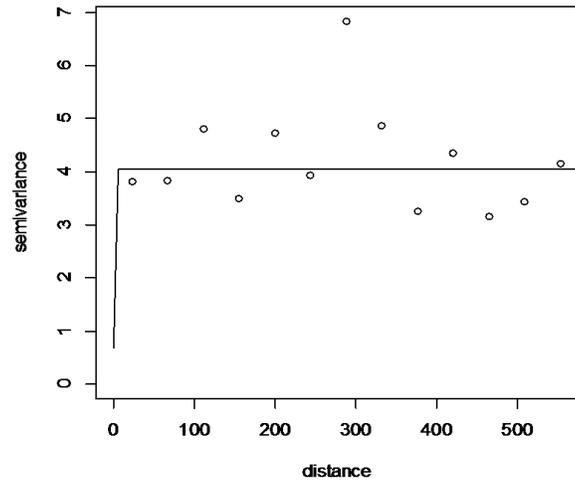
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Figure 5 Continued

Hughes Lake W2



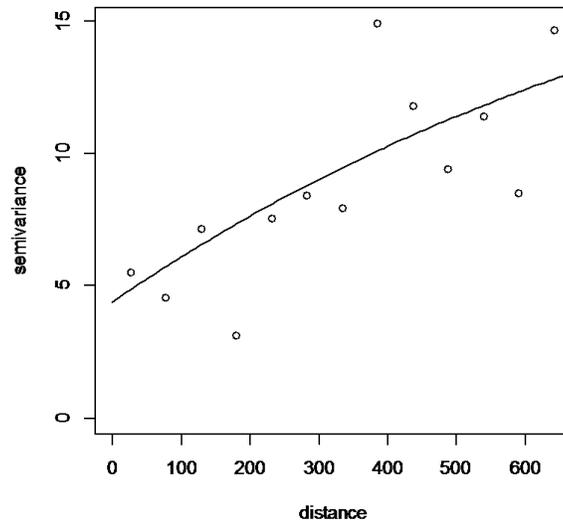
Luzerne



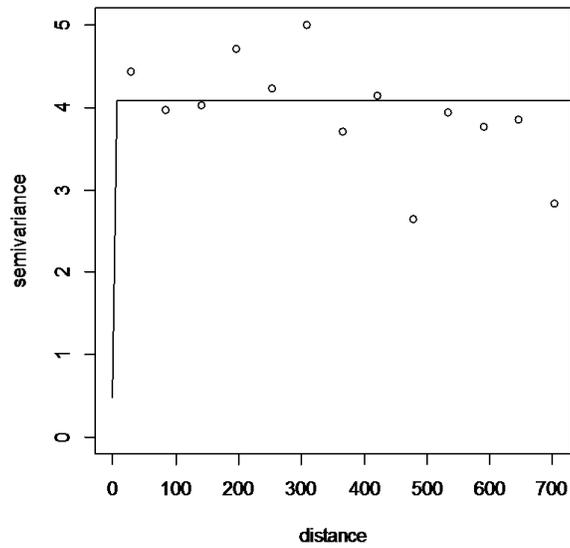
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Figure 5 Continued

Ostego



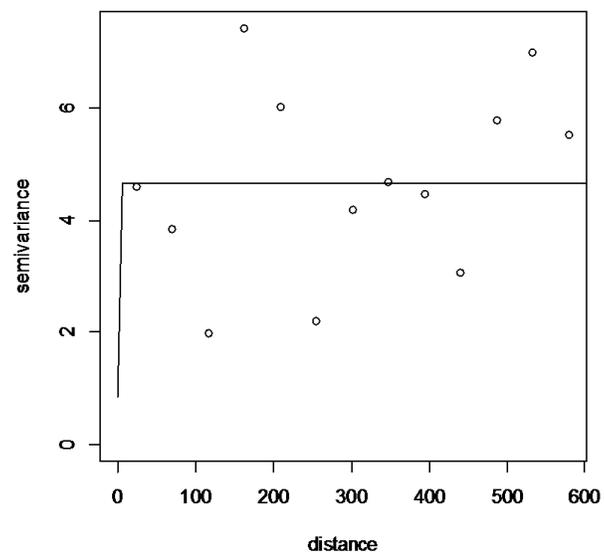
Perry Holt



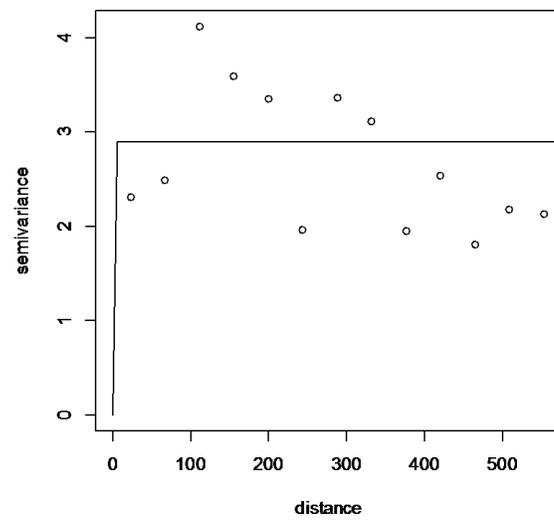
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Figure 5 Continued

Rollways



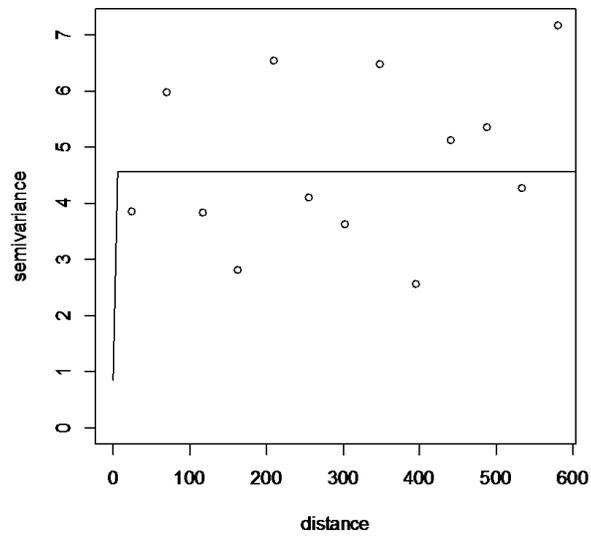
Stephen's Bridge W1



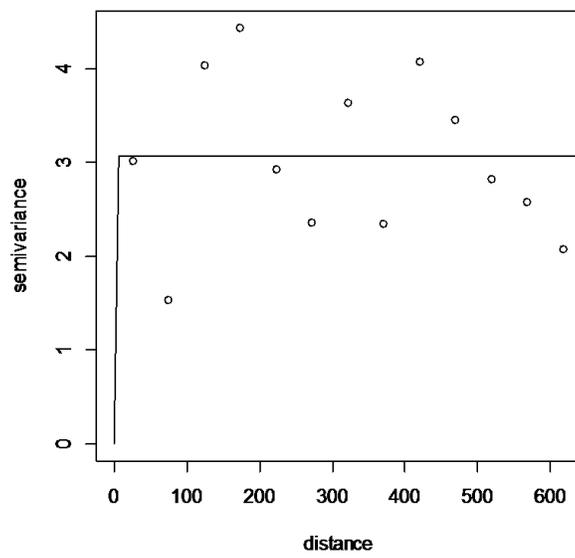
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Figure 5 Continued

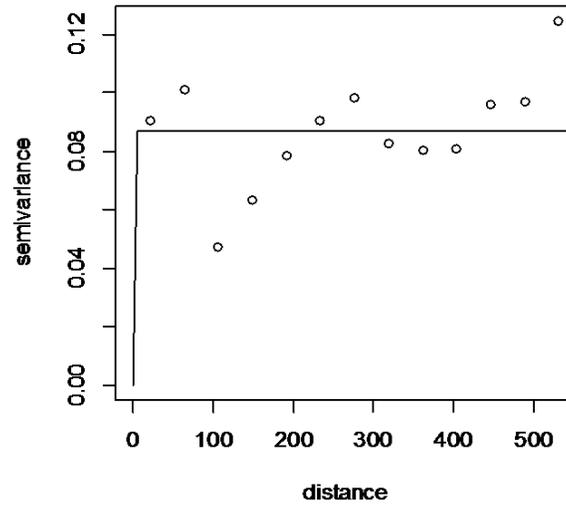
Stephen's Bridge W1



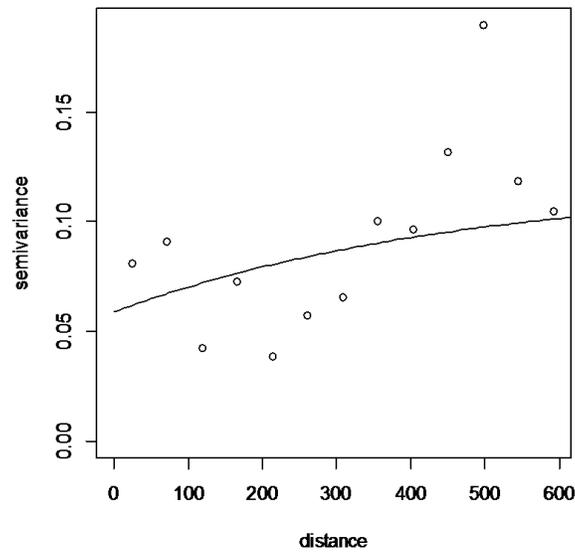
St. Helen



Four Mile



Howes Lake W1

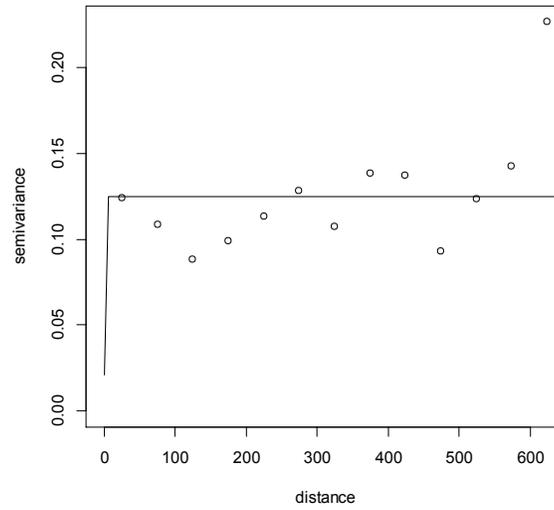


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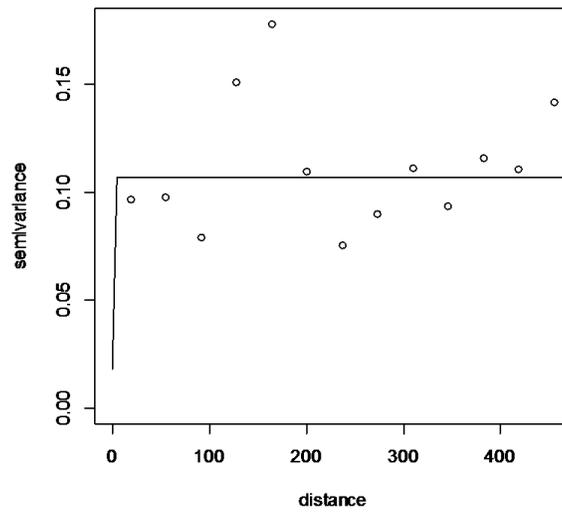
Figure 6. Semivariogram plot results for spatial heterogeneity of Shannon's Diversity (H') of the 12 windows located in northern Lower Michigan. A spherical model was used for the spatial autocorrelation analysis. Sampled area (window) was ~40.5 ha (100ac).

Figure 6 Continued

Howes Lake W2



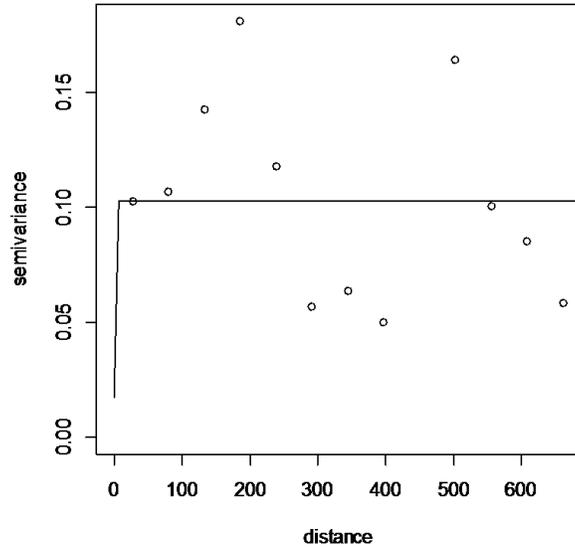
Hughes Lake W1



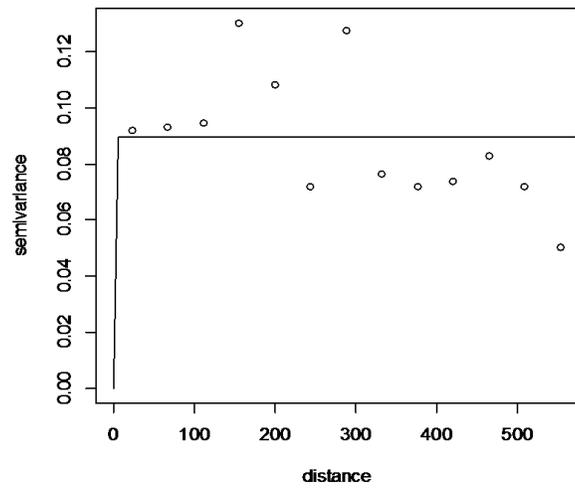
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Figure 6 Continued

Hughes Lake W2



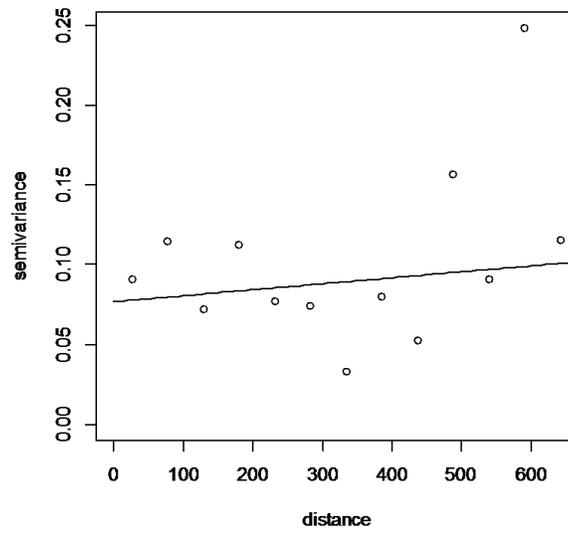
Luzerne



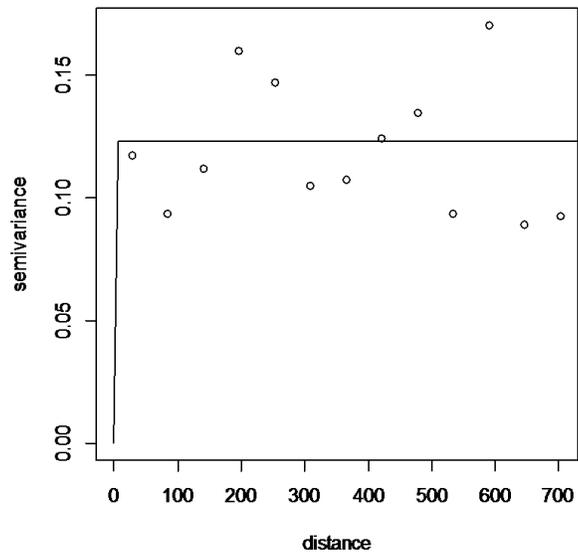
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Figure 6 Continued

Ostego



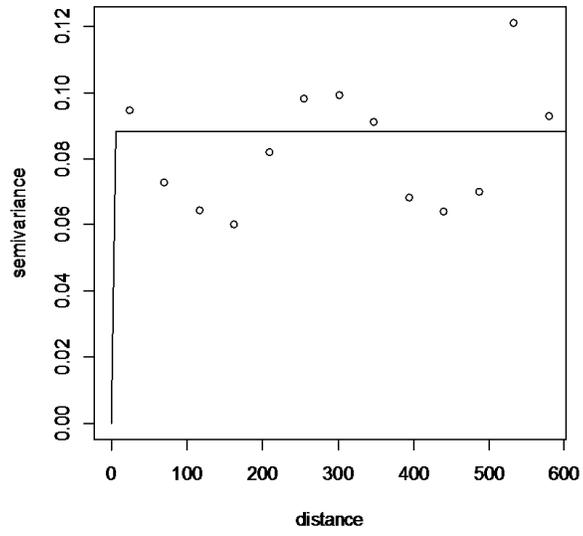
Perry Holt



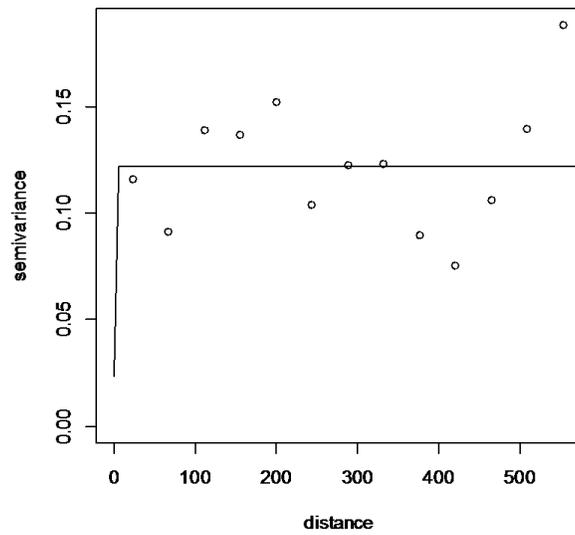
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Figure 6 Continued

Rollways



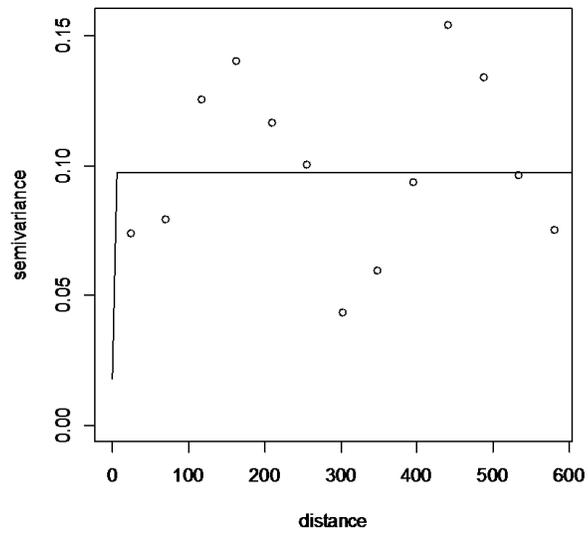
Stephen's Bridge W1



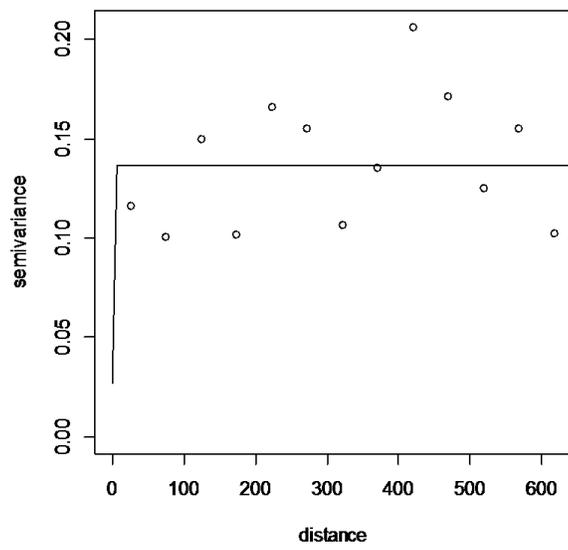
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Figure 6

Stephen's Bridge W2



St. Helen



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Appendix A: Field Results of Ground Flora

Table 8. Mean (\pm SD) of cover (%) for species collected in each study site located in northern Lower Michigan. Species identified to genus are indicated with XX in the code line. Codes with XXXX were unable to be identified to genus and were assigned to a functional guild if possible.

Species	Code	Functional Guild	Mean	Standard Deviation
<i>Acer rubrum</i>	ACRU	Woody Seedling	0.01	0.05
<i>Amelanchier</i> spp.	XXAM	Woody Shrub	0.04	0.2
<i>Anemone quinquefolia</i>	ANQU	Forb	0.00	0.02
<i>Apocynum androsaemifolium</i>	APAN2	Graminoid	0.03	0.07
<i>Arctostaphylos uva-ursi</i>	ARUV	Woody Shrub	0.71	1.69
<i>Aristida</i> spp.	XXAR	Graminoid	0.47	2.36
<i>Asclepias verticillata</i>	ASVE	Forb	0.00	0.02
<i>Betula</i> spp.	XXBETU L	Woody Seedling	0.06	0.47
<i>Campanula rotundifolia</i>	CARO2	Forb	0.01	0.03
<i>Carex pennsylvanica</i>	CAPE6	Graminoid	23.66	16.22
<i>Cladina</i> spp.	CLADOX X	Lichenous	5.09	8.09
<i>Cladonia</i> spp.	CLADOX X2	Lichenous	1.15	3.7

Continued

Table 8 Continued

<i>Clinopodium vulgare</i>	CLVU	Forb	0.01	0.06
<i>Comptonia peregrina</i>	COPE80	Woody Shrub	2.96	4.56
<i>Convolvulus arvensis</i>	COAR4	Forb	0.01	0.06
<i>Crataegus</i> spp.	XXCRATA	Woody Seedling	0.01	0.06
<i>Danthonia spicata</i>	DASP2	Graminoid	0.76	2
<i>Dendrolycopodium obscurum</i>	LYOB	Forb	0.00	0.01
<i>Dichanthelium clandestinum</i>	DICL	Graminoid	0.00	0.01
<i>Dichanthelium latifolium</i>	DILA8	Graminoid	0.01	0.06
<i>Dichanthelium sabulorum</i>	DISAT	Graminoid	0.03	0.24
<i>Dichanthelium</i> spp.	XXDICL	Graminoid	0.29	0.77
<i>Dichanthelium</i> spp.	XX2DICL	Graminoid	0.01	0.04
<i>Epigaea repens</i>	EPRE2	Woody Shrub	0.01	0.05
<i>Epipactis helleborine</i>	EPHE	Forb	0.08	0.66
<i>Festuca rubra</i>	FERU2	Graminoid	0.07	0.51
<i>Festuca</i> spp.	XX2FESTU	Graminoid	0.12	0.69
<i>Festuca</i> spp.	XX3FESTU	Graminoid	0.04	0.25
<i>Fragaria virginiana</i>	FRVI	Forb	0.02	0.08
<i>Fraxinus</i> spp.	XXFRAXI	Woody Seedling	0.01	0.05
<i>Gaultheria procumbens</i>	GAPR2	Woody Shrub	2.11	5.33

Continued

Table 8 continued

<i>Gaylussacia baccata</i>	GABA	Woody Shrub	0.11	0.67
<i>Hamamelis virginiana</i>	HAVI4	Woody Seedling	0.05	0.27
<i>Helianthemum canadense</i>	HECA3	Forb	0.00	0.02
<i>Helianthus divaricatus</i>	HEDI2	Forb	0.00	0.01
<i>Hieracium floribundum</i>	HIFL3	Forb	0.03	0.2
<i>Hieracium spp.</i>	XXHI	Forb	0.00	0.01
<i>Hieracium venosum</i>	HIVE	Forb	0.02	0.08
<i>Hypericum perforatum</i>	HYPE	Forb	0.00	0.02
<i>Juniperus horizontalis</i>	JUHO2	Woody Shrub	0.10	0.82
<i>Koeleria macrantha</i>	KOMA	Graminoid	0.00	0.01
<i>Maianthemum canadense</i>	MACA4	Forb	0.03	0.06
<i>Melampyrum lineare</i>	MELI2	Forb	0.02	0.04
<i>Monotropa hypopitys</i>	MOHY3	Forb	0.00	0.01
<i>Oryzopsis asperifolia</i>	ORAS	Graminoid	0.03	0.2
<i>Oryzopsis spp.</i>	XXOR	Graminoid	0.10	0.82
<i>Packera paupercula</i>	PAPA20	Forb	0.01	0.05
<i>Panicum implicatum</i>	DIACF	Graminoid	0.01	0.05
<i>Panicum spp.</i>	XXPAC	Graminoid	0.01	0.07
<i>Pinus banksiana</i>	PIBA2	Woody Seedling	0.28	0.82
<i>Pinus resinosa</i>	PIRE	Woody Seedling	0.06	0.31

Continued

Table 8 Continued

<i>Pinus strobus</i>	PIST	Woody Seedling	0.00	0.01
<i>Pinus sylvestris</i>	PISY	Woody Seedling	0.00	0.01
<i>Piptatheropsis pungens</i>	PIPU9	Graminoid	0.03	0.2
<i>Poa</i> spp.	XXPO	Graminoid	0.03	0.21
<i>Polygala polygama</i>	POPO	Forb	0.00	0.02
<i>Populus grandidentata</i>	POGR4	Woody Seedling	0.02	0.08
<i>Populus tremuloides</i>	POTR5	Woody Seedling	0.05	0.46
<i>Prunus pumila</i>	PRPU3	Woody Shrub	2.01	3.51
<i>Prunus serotina</i>	PRSE2	Woody Seedling	0.48	1.48
<i>Prunus virginiana</i>	PRVI	Woody Shrub	0.00	0.01
<i>Pteridium aquilinum</i>	PTAQ	Pteridophytes	11.37	14.1
<i>Pyrola asarifolia</i>	PYAS	Woody Shrub	0.00	0.01
<i>Quercus alba</i>	QUAL	Woody Seedling	1.10	3.98
<i>Quercus bicolor</i>	QUBI	Woody Seedling	0.22	1.876
<i>Quercus ellipsoidal</i>	QUEL	Woody Seedling	0.38	1.01
<i>Quercus</i> spp.	XXQU	Woody Seedling	0.08	0.36
<i>Quercus velutina</i>	QUVE	Woody Seedling	0.49	1.54
<i>Rubus flagellaris</i>	RUFL	Woody Shrub	0.03	0.21
<i>Rubus hispidus</i>	RUHI	Woody Shrub	0.01	0.05
<i>Rubus pensilvanicus</i>	RUPE3	Woody Shrub	0.05	0.45

Continued

Table 8 Continued

<i>Rubus</i> spp.	XXRU	Woody Shrub	0.00	0.04
<i>Salix discolor</i>	SADI	Woody Shrub	0.05	0.45
<i>Salix humilis</i>	SAHU2	Woody Shrub	0.00	0.01
<i>Schizachne purpurascens</i>	SCPU	Graminoid	0.18	1.55
<i>Schizachyrium scoparium</i>	SCSC	Graminoid	0.03	0.24
<i>Setaria pumila</i>	SEPU8	Graminoid	0.00	0.01
<i>Setaria</i> spp.	XXSE	Graminoid	0.00	0.01
<i>Sibbaldiopsis tridentata</i>	SITR3	Forb	0.01	0.04
<i>Solidago hispida</i>	SOHI	Forb	0.02	0.05
<i>Solidago simplex</i>	SOSIG2	Forb	0.01	0.06
<i>Solidago</i> spp.	XXSO	Forb	0.00	0.01
<i>Spiranthes lacera</i>	SPLA4	Forb	0.00	0.01
<i>Taraxacum officinale</i>	TAOF	Forb	0.00	0.01
<i>Toxicodendron radicans</i>	TORA2	Woody Shrub	0.03	0.21
<i>Trientalis borealis</i>	TRBO2	Forb	0.02	0.08
<i>Trillium</i> spp.	XXTRILL	Forb	0.00	0.01
<i>Vaccinium angustifolium</i>	VAAN	Woody Shrub	26.18	17.84
<i>Vaccinium myrtilloides</i>	VAMY	Woody Shrub	0.38	1.69
<i>Vaccinium</i> spp.	XXVA	Woody Shrub	0.24	1.22
<i>Viburnum acerifolium</i>	VIAC	Woody shrub	0.18	1.06
<i>Viola adunca</i>	VIAD	Forb	0.01	0.02
<i>Viola pedata</i>	VIPE	Forb	0.00	0.02
<i>Viola</i> spp.	XXVI	Forb	0.00	0.02

Continued

Table 8 Continued

XXXX1	Lichenous	3.14	9.02
XXXX2	Lichenous	0.63	1.72
XXXX3	Forb	0.00	0.01
XXXX4	Forb	0.01	0.03
XXXX5	Forb	0.00	0.01
XXXX6	Forb	0.00	0.01
XXXX7	Forb	0.00	0.02
XXXX8	Forb	0.00	0.03
XXXX9	Forb	0.00	0.01
XXXX16		0.10	0.82
XXXX17	Graminoid	0.65	2.85
XXXX18		0.00	0.01
XXXX19	Forb	0.01	0.05
XXXX20	Graminoid	0.69	3.74
XXXX21	Graminoid	0.11	0.7
XXXX22	Graminoid	0.06	0.5
XXXX23	Graminoid	0.03	0.19
XXXX25	Forb	0.01	0.04
XXXX26	Graminoid	0.25	1.36
XXXX27	Forb	0.00	0.01
XXXX28		0.02	0.07
XXXX29	Graminoid	0.00	0.01
XXXX30	Forb	0.00	0.02
XXXX31	Forb	0.01	0.04