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Effects Of Disturbance On Jack Pine- (pinus Banksiana Lamb.) Dominated Ecosystems In Northern Lower Michigan: Forest Management, Wildfires, And Climate Change

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EFFECTS OF DISTURBANCE ON JACK PINE (*Pinus banksiana* Lamb.) DOMINATED ECOSYSTEMS IN NORTHERN LOWER MICHIGAN: FOREST MANAGEMENT, WILDFIRES, AND CLIMATE CHANGE

by

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DISSERTATION

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DEDICATION

I dedicate this work to my wonderful family: Eddie, Julius, and Lorelei. You are my reason for everything. Ours is a crazy, busy, fun, stressful world - but it’s the only way I would ever want it to be. Thank you for always supporting my path, no matter how inconvenient. Thank you for picking me up when it’s all felt too overwhelming. Thank you for being the most wonderful distraction a person could hope for. I love you all more than you’ll ever know.

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As a student in Dan Kashian's lab, one must become resilient. Much as the forests we study, the students associated with Dan's lab are under constant onslaught from disturbances. We are trained to be a sturdy group - unafraid of dirty clothes, inclement weather, or complicated study designs. We further understand that any and every idea, method, or process must be able to withstand intense scrutiny and argumentative discourse. But in persevering through this difficult process, one is rewarded with confidence, collegiality, and trust, and the process of persistently defending oneself creates a steadfast will to succeed. Dan has treated me as a colleague even before I felt I deserved it, and I'll always be grateful for his patience and his confidence in my intellect and work.

My committee members have also provided valuable feedback and advice throughout this process. Dr. Donna Kashian has provided an example that has given me reason to hope that I'd ever be able to balance all of my commitments, and her success has been inspirational. She asks pragmatic, forward-looking questions that have helped me focus on the direction I want to take and the goals I am setting. Dr. Thomas Dowling has a unique perspective and has always pressed me to take a broader view at the context of my work. We have also had the opportunity to work together to improve teaching methods and coursework, and I've been inspired by his commitment and teaching philosophy. Dr. Brian Sturtevant's experience and expertise have been valuable assets, and have improved not only my projects, but also my process for logically investigating questions. I've also truly appreciated his flexibility and willingness to join my committee part-way through. My work has been improved by the feedback from my committee and I'm grateful for their input, but more so I'm grateful for their support throughout this process.

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On a personal note, I must recognize my MWA friends who are endlessly supportive, even when they don't know exactly what I do, and who give me a chance to get away from everything. I am blessed to have a village of smart, driven, compassionate, successful, fierce women around me, and I am so thankful for their companionship, comradery, and the occasional hand retrieving kids or delivering fresh clothes to school in a pinch.

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CHAPTER 1 – INTRODUCTION

Forested landscapes are composed of mosaics of stands with varying structural and compositional attributes, such as stand age, plant community diversity, and patterns of forest cover (Ahlgren 1960; Heinselman 1973; Turner et al. 2001). Interactions between these and other factors like climate, landforms, and biotic interactions combine to form the basis for the function of forest mosaics as broad, cohesive landscapes (Swanson 1988; Pastor et al. 1999). Therefore, within forested landscapes patches of various successional stages and community composition are distributed and interact at multiple spatial and temporal scales (Pickett et al. 1989; Kotliar and Weins 1990).

Nested within this overarching forest structure is an often finer-scaled, ever-shifting mosaic of disturbances. Defined as a relatively discrete event that alters ecosystem, community, or population structure, and changes either the physical environment or the resource availability within it (White and Pickett 1985), disturbances can affect landscapes across spatial scales and are major drivers of spatial and temporal heterogeneity. Disturbances themselves also act at multiple scales and with variable intensities resulting from interactions with vegetation, landforms, or other features (Turner et al. 1994). These disturbances can confer patterns of post-disturbance regeneration at multiple scales, such as gap dynamics from individual fallen trees or broad-scale reseeding following large forest fires. The overall landscape patch mosaic is a result of these and other processes interacting to form hierarchically-structured landscapes of varying patterns (Pickett et al. 1989; Turner et al. 1994; Albert 1995).

The restriction or elimination of disturbances on landscapes adapted to specific disturbance regimes can affect ecosystems in profound, unpredictable ways, such as compositional changes in species occurrence and abundance, or altered successional trajectories (Heinselman 1973; Romme

1982; Whitney 1986; Baker 1992). For instance, alterations to fire regimes due to fire suppression management have caused catastrophic consequences in ponderosa pine- (*Pinus ponderosa* Lawson & C. Lawson) dominated ecosystems where fuels accumulation creates uncharacteristically severe fires (Allen et al. 2002).

Patterns of forest regeneration following disturbances are functions of the disturbance type and intensity and are created through variable factors produced by natural disturbances (White and Pickett 1985; Turner 1989). For wildfires, wind speed and direction, fuel type and availability, weather and climate, and topography can all influence severity (Johnson 1992). This complex combination of factors results in a heterogeneous distribution of variably-disturbed stands, from severely damaged stands to islands of untouched, intact forests (Heinselman 1973; Hansen et al. 1991; Foster et al. 1998; Franklin et al. 2000). As succession proceeds and consecutive disturbances occur at variable spatial scales, these factors create the mosaic of ages and seral stages that typify many terrestrial landscapes. Large or severe disturbances may produce monotypic stands of even-aged regeneration, yet residual structures from the pre-disturbance landscape exist and may influence long-term patterns of the post-disturbance landscape (Foster et al. 1998; Franklin et al. 2000)

Landform position and composition can also affect the type and severity of disturbances on landscapes. Fire spread is faster and more intense uphill than it is downhill due to faster transfer of flame-front heat (Johnson1992), therefore creating variability of fire damage related to topography. Glacial landforms such as outwash plains and ice-contact features have coarse-textured soils and often support drought-tolerant, fire-prone vegetation, and such landforms may therefore drive disturbance regimes of entire regions (Whitney 1986). Extreme climatic conditions such as prolonged drought or extreme fire weather may override these mechanisms (Simard et al.

1983; Turner and Romme 1994), but landscapes often possess structures that can confer some resistance or a barrier to disturbance spread, such as streams, ridges, or terraced floodplains (Foster et al. 1998). In these ways, spatial patterns of species and age distributions are shaped by the landscape even as the landscape shapes the prevailing disturbances in an exquisitely coupled feedback.

As described, the spatial and temporal variability of disturbances and post-disturbance patterns create a range of conditions that persist over time and space. The historic range of variability (HRV) of an ecosystem describes the range of conditions found on the landscape, including vegetation distributions, burned area, structural stages, and other parameters (Morgan et al. 1994; Agee 2003; Tinker et al. 2003; Keane et al. 2009). The HRV concept encompasses naturally-created variation within forested landscapes and can be a useful benchmark for successful restoration management practices (White and Walker 1997; Landres et al. 1999; Agee 2003). Landscape management modeled after the restoration of historic fire regimes has many predicted ecological benefits from the re-implementation of HRV, such as increased mean patch size, lower patch density, and reduced edge density (Cissel et al. 1999; Tinker et al. 2003). Furthermore, restoration of disturbance regimes and structural heterogeneity within HRV may increase ecosystem resilience to novel disturbances such as climate change by incorporating a range of conditions that have variable sensitivities to perturbations and differing post-disturbance recovery rates and strategies (Holling and Meffe 1996; Churchill et al. 2013). Ambiguities relating to historic ecological integrity and uncertainty of historic records may complicate measures of HRV (Bourdo 1956; Schulte and Mladenoff 2001), but restoration of HRV may be instrumental for resilient, ecologically-focused landscape management in the future.

Historical structure and resilience may not be able to counteract effects of climate change however, and as such landscape-scale simulations of predicted conditions may provide insight for future management. When past is not prologue, predictive models may provide estimates and projections to influence management decisions or research directions toward fuller understanding of otherwise unpredictable challenges (Scheller and Mladenoff 2005; Gustafson 2013). Climate change is an overarching factor that confounds all previous calculations of disturbance, but that does not preclude the usefulness of ecologically-based management based upon empirical studies or HRV. In fact, restoration of HRV may mitigate effects of compounded or cascading disturbances as climate change continues, although such effects are difficult to predict (Buma 2015).

The following studies examine effects of disturbances across spatial and temporal scales. Chapter 2 describes effects of wildlife management on landscape age distributions using historical records to provide insight for future management. Chapter 3 examines post-wildfire living legacies and interactions between the pre-disturbance forest and the post-disturbance landscape. Finally, Chapter 4 uses a landscape model to predict effects of climate change on the fire regime and landscape structure. Taken together, these projects aim to provide insight for using forest and landscape ecology to inform relevant, ecologically-based forest management.

CHAPTER 2– LONG-TERM EFFECTS OF MANAGING FOR AN ENDANGERED SONGBIRD ON THE HETEROGENEITY OF A FIRE-PRONE LANDSCAPE[1]

Introduction

The 1973 Endangered Species Act (ESA) encourages protections and associated management priorities for imperiled species and has achieved varying levels of success at rehabilitating foundering populations (Stokstad 2005; Schwartz 2008). Explicit management practices focused on species of concern are often necessary to allow quick and decisive intervention (Simberloff 1998), and when successful may be replicated elsewhere to maintain at-risk populations. However, even recovered populations may be conservation-reliant in the long term, requiring considerable resources for habitat management or mitigation of population-limiting variables (Doremus and Pagel 2001; Scott et al. 2010). In many cases a narrowly-focused approach may emerge, resulting in landscape management that focuses mainly on a single imperiled species or population. As a result, management actions intended to accommodate species at risk may reduce the long-term variability of landscapes, concomitantly sacrificing other ecosystem properties such as biodiversity or resilience (Holling and Meffe 1996; Churchill et al. 2013), even while achieving or exceeding management objectives for the species or population of concern.

Forest management that produces heterogeneous landscapes has been proposed to support long-term viability of ecosystems and can sustainably manage both at-risk species and the landscapes they inhabit (Franklin 1993; Churchill et al. 2013). The historic range of variability (HRV) concept is increasingly used as a guiding principle of modern landscape management, where management objectives seek to identify and emulate the heterogeneity of naturally-

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[1] Reprinted by permission from Springer: Springer Nature, *Landscape Ecology* (2016) 31:2445-2458, with co-authors R. Gregory Corace III, David T. Cleland, Daniel M. Kashian

produced landscapes (Hessburg et al. 1999; Keane et al. 2009). Rather than a single, static condition, HRV has been used to sustainably manage ecosystems by encompassing a range of ecosystem characteristics that historically were often spatially and temporally variable, and resulted from interactions of disturbances with abiotic factors and vegetation processes (Landres et al. 1999). Given current, rapidly changing climate conditions, the utility of selecting historically relevant management objectives has been questioned (Millar et al. 2007). However, HRV can enhance overall ecosystem health and sustainability by incorporating heterogeneous conditions that differentially interact with future disturbances or climate extremes such as drought (Holling and Meffe 1996).

Site-specific measures of HRV have demonstrated marked changes to forests caused by management practices (Cyr et al. 2009). Determining the characteristics of historical landscapes is difficult, however, because data describing pre-anthropogenic conditions often do not exist, especially at broad scales (White and Walker 1997; Keane et al. 2009). The HRV of fire-adapted forests, in particular, may be especially difficult to determine from remnant stands due to widespread alteration of fire regimes and suppression (Baker 1992). Broad-scale documentation of pre-European settlement conditions may therefore be the best way to provide essential baseline data to determine reference conditions for comparison with modern managed landscapes (Schulte and Mladenoff 2001).

General Land Office (GLO) public land surveys have been widely used to describe landscapes prior to European settlement, particularly in the Great Lakes region (Whitney 1987; Schulte and Mladenoff 2001; Cleland et al. 2004). Originally conducted for township and property designation, the size and species of marker trees were recorded, and areas of recent disturbance such as wildfire or windthrow were documented (Liu et al. 2011). These data have been used as historic metrics of forest structure including species composition, stand density, tree size distributions, and landscape disturbance patterns (Schulte and Mladenoff 2001; Cleland et al. 2004; Williams and Baker 2011). To our knowledge GLO notes have not been previously used to determine the age of historic forests, yet historical stand age distributions determined from recorded tree size data may serve as a foundation for management within the HRV. This is especially true on landscapes managed for species that require specific successional stages for habitat, and where the age of the modern managed landscape is likely inconsistent with the historic age range.

Understanding landscape structure prior to European settlement is particularly relevant in northern Lower Michigan (U.S.A.; hereafter NLM) due to intensive and extensive management for breeding habitat for the federally endangered Kirtland's warbler (*Setophaga kirtlandii* Baird; KW). KWs are neotropical migratory songbirds that overwinter in the Bahamas and nest in NLM in large (> 32 ha) stands of young (< 20 years old) jack pine (*Pinus banksiana* Lamb.*;* Walkinshaw 1983). KW habitat historically was maintained by frequent (12-60 year fire return interval; Simard and Blank 1982), stand-replacing wildfires in the region that created a mosaic of dense jack pine stands interspersed with open barrens (Kashian et al. 2003a). This structure provided young trees with low branches to protect KW ground nests, along with foraging opportunities in the open areas. However, due to 20th century fire suppression, naturally regenerated, early-successional jack pine forests were reduced, and KW breeding habitat is currently maintained as large, young, dense jack pine plantations planted in an opposing-wave pattern to incorporate openings (Probst and Weinrich 1993). Further, brown-headed cowbirds (*Molothrus ater* Boddaert) have been observed in the region since the turn of the 20th century (Wood and Frothingham 1905; Strong 1919) and negative effects of brood parasitism by brown-headed cowbirds were observed when the KW population was low (Mayfield 1961). Although few data exist to determine current levels of parasitism and the number of cowbirds caught in traps has declined in recent years (C. Mensing USFWS, *pers. comm.*) trapping of cowbirds has been and continues to be a prevalent practice in the region. In combination with widespread habitat plantation management, these actions have successfully increased the population of the species to more than twice the original management objective, and delisting is likely in the next decade (MDNR et al. 2015).

Management of jack pine plantations by harvesting and reforesting on a 50-year rotation to maintain young stands has likely had a pronounced influence on the landscape pattern of the region, as more than 75,000 ha of public land are managed specifically for KW habitat in NLM (MDNR et al. 2015). Management protocols state that 3,830 ac (approx. 1,550 ha) of jack pine forests must be available annually as suitably-aged KW habitat, and although the region has been intensely managed in this way for more than 40 years, the potential impacts on landscape age heterogeneity have not been quantitatively assessed. Ecosystem-based management that incorporates ecosystem processes and diversity has recently been identified as central to KW breeding habitat management (Bocetti et al. 2012), thus baseline data that describe historical landscapes are critical for establishing best-practices for future, more holistic, management (Corace and Goebel 2010).

To determine the extent that breeding habitat management for KW has altered landscape-scale stand-age distributions in NLM, we described the pre-European settlement age distribution using nonlinear regression techniques that to our knowledge have previously not been used for pre-European survey data. We compared these historic data with the current landscape to answer the following questions:

1) How well does the current distribution of jack pine-dominated cover types compare with that prior to European settlement?
2) How does the current stand-age distribution compare to the historical landscape of this region? and;
3) How does the spatial distribution of stand ages compare between current and historical landscapes?

We predicted that the current, managed landscape would approximate the historical spatial location of jack pine cover types, but that the current landscape would be younger and have a more homogeneous stand-age distribution, as old, wildfire-produced jack pine stands have been replaced by younger, KW habitat plantations.

Methods

Study area

The study area lies mainly within the Grayling Outwash Plain (Sub-subsection VII.2.2) of the Highplains Subsection (VII.2) of the Northern Lacustrine-Influenced Lower Michigan Section (VII) of Region II (NLM; 44º30'N, 84º30'W). This sub-subsection is a broad outwash plain dominated by nutrient-poor, excessively drained sands (Albert 1995; Figure 1). The vegetation of the study area is dominated by jack pine with northern pin oak (*Quercus ellipsoidalis* E.J. Hill) and red pine (*P. resinosa* Sol ex. Aiton) as secondary species (Kashian et al. 2003a). The prevailing disturbance regime in the Highplains subsection was historically high-severity, stand-replacing wildfires with a 59-year rotation (Cleland et al. 2004) or a return interval from 12-60 years (Simard and Blank 1982). This disturbance regime created a mosaic of stand ages and forest structures (Leahy and Pregitzer 2003). Although the occurrence of fire has been reduced (Cleland et al. 2004), stand-replacing wildfire is still one of the dominant disturbances in the region

(Kashian et al. 2012). Serotinous cones in jack pine allow for rapid post-fire seed dispersal and germination, and facilitate establishment of nearly monotypic stands scattered with shrubby northern pin oak (Whitney 1987). Dense jack pine stands regenerated by fire are interspersed with large openings, or barrens, characterized by grasses and low, woody shrubs typical of dry prairies, such as blueberries (*Vaccinium* spp.) and sand cherry (*Prunus pumila*; Kashian et al. 2003a). Fire and the dry, acidic soils of the region effectively prevent encroachment of many species that could otherwise out-compete and displace jack pine under more productive conditions (Burns and Honkala 1990). We selected a study area of more than 450,000 ha based on the preponderance of jack pine coverage prior to European settlement (80% of all jack pine identified in the GLO notes for Lower Michigan; Figure 1). More than 64% of the study area falls within the Grayling Outwash Plain sub-subsection, and Kirtland's warbler management areas (KWMAs) comprise over 72,000 ha in the study area.

Historical vs. current jack pine spatial distribution

To determine the extent that modern KW breeding habitat management has changed the distribution of jack pine cover types in NLM, we compared the current reported cover type distribution for the Michigan Department of Natural Resources (MDNR) KWMAs (over 28,600 ha, or approximately 40%, of the KWMA's in the study area) with the pre-European distribution of jack pine-dominated cover types within those boundaries. Both plantations and wildfire-origin stands on the current landscape were used for the analyses. Pre-European jack pine coverage was determined using GLO survey data previously digitized and interpreted into cover type polygons by the Michigan Natural Features Inventory (Comer et al. 1995; Austin et al. 1999). Forest cover type categories common to both coverages included jack pine, red pine, and barrens.

Distribution of jack pine stand ages

We used GLO public land survey notes previously digitized into point coverages of surveyed line trees (Maclean and Cleland 2003) to model the pre-European distribution of jack pine stand ages in NLM. The extent of jack pine forests on the pre-European landscape was determined from the GLO point coverage using a two-step process. First, line trees were refined by species to select only jack pine across the study area. Second, to exclude forests where scattered jack pines were present but did not dominate the canopy, the pre-European data were extracted using overlaid mapped, historic land cover type polygons that were dominated by jack pine (Comer et al. 1995; Austin et al. 1999).

GLO survey notes include the species name and diameter at breast height (dbh) of trees, but not tree age. We estimated tree age from dbh using nonlinear regression analysis of data taken from living, naturally-regenerated jack pines (*n* = 1,790 trees) across the study area. We used residual plots to assess the assumption of equal variances, and histograms, skewness and kurtosis, and normal q-q plots to confirm normality of the randomly-sampled response variables (Whitlock and Schluter 2009) and found no violations of these assumptions. Tree age (determined from increment cores) and diameter data were fit to a Michaelis-Menten function, which was then applied to tree diameters in the GLO notes to determine the age of 6,847 surveyed trees from the historic landscape. While we did not explicitly characterize the relationship between dbh and density in jack pines, instead using a single model for predicting age from size regardless of density, we feel this is a valid method for a number of reasons. First, our use of the Michaelis-Menten function to model the relationship between age and dbh incorporated variability in stages, as the slope of the relationship varies with increasing dbh. Second, our large sample size of measured trees from which we based our regression model incorporated a variety of densities and therefore likely represents a relatively average relationship. Given the extended time period over which surveys were conducted in the region (1837-1858), tree ages were adjusted to the age they would have been in 1858, the latest year surveys were conducted in the region, to provide a standardized dataset. While this technique increased the age of the surveyed landscape, most of the data points (57%) required fewer than 10 years added to their age because most of the area was surveyed after 1848, and the standardized dataset could more accurately reflect the overall age distribution of the landscape. Additionally, areas noted by surveyors as "burned" or "recently burned" were delimited and added as young forest (Austin et al. 1999). These polygons were not associated with specific survey years in our data, therefore polygons were added to the pre-European surface as points arbitrarily assigned an age of 3 years in order to remove zero values from the data set.

To transform the grid of pre-European data points into polygons to map stand ages, areas between data points (average distance = 455 m) were interpolated using empirical Bayesian kriging (EBK) in ArcMap 10.2 (ESRI 2011). Kriging uses known spatial data to estimate unknown data through semivariogram analyses of the known values. EBK differs from traditional kriging methods in that it simulates a number of semivariograms to determine the best fit for the data, thus incorporating uncertainty of the estimated semivariogram model into the modeling process (Krivoruchko 2012). While spatial autocorrelation is necessary for the process of kriging, somewhat nonstationary data, such as individual tree data points, may be modeled robustly in EBK using local subsets of data during the process (Krivoruchko 2012). We confirmed the assumptions of spatial autocorrelation, moderate stationarity, and absence of directional trends using semivariogram clouds, Voronoi maps, and the trend analysis tool in ArcMap, respectively (Krivoruchko 2012), and found no violations of these assumptions. We then used EBK with 100 semivariogram simulations per subset, a subset size of 100 points, and a prediction output surface of polygons to model the pre-European landscape. This process provided a description of the age of the pre-European landscape across an approximately 450,000 ha region.

During the modeling process in ArcMap, validation points are created by the program by systematically removing individual points, modeling without the point, then determining the value at that point. After confirming the normality of the paired differences using a normal q-q plot and finding no violations of normality (Whitlock and Schluter 2009), we tested input survey data and the model-generated validation points for differences using a paired t-test. Accuracy of the kriged prediction surface was estimated using classification error matrices of omission and commission of the same points. The overall percent accuracy of each of the matrices was calculated, as well as the coefficient of agreement, kappa. Kappa is a measure of the similarity of matrices, and assumes independent, paired measurements organized into symmetric categorical matrices (Landis and Koch 1977). The statistic ranges between (-1) and (1), with (-1) having complete disagreement, and (1) having complete agreement; (0) indicates the amount of agreement expected due to pure chance (Landis and Koch 1977; Bonham-Carter 1994). While the assumption of independent samples is not strictly met in this case, as moderate spatial autocorrelation exists, these measures are still useful as investigations of the correlation between maps (Bonham-Carter 1994).

Current forest species and age distributions on public lands managed for KW were provided in the form of stand-age polygon maps by management agencies operating in NLM: MDNR, U.S. Forest Service, and U.S. Fish and Wildlife Service. We clipped regions overlaid by current KWMAs from the kriged pre-European coverage, allowing for comparison of discrete areas of historic and current land cover. We divided stand ages across both landscapes into three categories based on their role in the current management regime: stands < 20 years old (young, generally KW occupied), 21-50 years old (intermediate, abandoned by KW but remain within the management rotation), and > 50 years old (mature, stands awaiting harvesting and planting to produce new plantation habitat). The percent cover of each age class was determined for both coverages, and the mean ages of a subsample of 1,395 randomly-chosen points from each coverage were compared using the non-parametric Wilcoxon signed-rank test; the data display moderate non-normality (leptokurtosis), but lack skewness, thus making the Wilcoxon test appropriate (using R moments package; R Core Team 2014; Whitlock and Schluter 2009). All statistical analyses were performed with alpha = 0.05, and using R (v. 3.1.1; R Core Team 2014) and SPSS (v. 22; IBM corp. 2013).

Landscape patterns of stand ages

Age class- and landscape-level metrics for both the current and pre-European landscapes were calculated from raster maps exported at a resolution of 15.24 m (50 ft. using the State Plane projection) using FRAGSTATS v3.3 (McGarigal et al. 2002). We calculated the proportion of the landscape, number of patches, largest patch index (the percent of the landscape composed of the largest patch in that class), and Euclidean nearest neighbor distance for each age class on both landscapes. Landscape-scale metrics calculated for each landscape were: number of patches, mean patch size, patch contagion (a measure of patch connectedness), and interspersion and juxtaposition index (to describe the adjacency of patches of different types; McGarigal et al. 2002).

Results

Jack pine spatial distribution

The current distribution of Kirtland’s warbler management areas (KWMAs) in NLM is consistent with pre-European jack pine-dominated cover types. Greater than 99% of the area within KWMAs is located on landforms (glacial outwash plains) where jack pine-dominated ecosystems occurred prior to European settlement. On MDNR land, the proportion of jack pine-dominated cover types has increased by approximately 6%, from 27,203 ha on the pre-European settlement landscape to 28,963 ha currently. The other major cover types on the pre-European landscape have decreased in the KWMAs, indicating homogenization of the landscape over time; red pine decreased 29% from 3,816 ha to 2,707 ha, and barrens have been reduced by approximately 67% (9,650 ha to 3,188 ha) from their pre-European distribution.

Determination of jack pine stand ages

The ages of field-sampled trees ranged from 5 to 105 years, and diameters ranged from 0.2 to 50.5 cm ($Y = (289.43 x) / (83.24 + x)$). The coefficient of determination between tree age and diameter was high for all 1,790 trees ($R^2 = 0.81$, $p < 0.001$), although variation of diameter at a given age increased with stand age (Figure 2). These trends suggest that size inequality, or size hierarchies, for jack pine are more common in older stands (Kenkel et al. 1997), and thus prediction of tree age from diameter is most accurate for younger stands.

Differences in means between the original input data and the validation points predicted from the model were not statistically significant. Kappa statistics and error matrices showed moderate agreement between the data sets and overall accuracy of the kriged values (see Landis and Koch 1977). We constructed two matrices using the three management-based age classes (< 20, 21-50, > 50 years; Table 1a) and also using five, equal-interval age classes to more precisely determine age classes with the most error (Table 1b). The model tends to under-predict the age of the pre-European forest in the 3-class scenario, and to over-predict the age in the 5-class scenario. The 3-class configuration kappa was 0.494 ($T = 54.5$, $p < 0.001$), 95% CI (0.476, 0.512), and overall accuracy was 69.8%. The 5-class configuration showed kappa was 0.516 ($T = 77.5$, $p < 0.001$), 95% CI (0.500, 0.532), and overall accuracy was 63.0%. The 3-class matrix exhibited the most error in the middle (21-50 years) age class, whereas the 5-class matrix displayed a more uniform distribution of disagreement (Tables 1a, 1b). Error in the 21-50 year age class is likely a result of a lack of data between 21-40 years, because most data (89%) in the broader 21-50 year old class is > 40 years.

Comparison of the proportions of the landscape in the three, management-based age classes within existing managed areas shows significant changes to the distribution (Wilcoxon signed-rank test; $V = 652382.5$, $p < 0.001$). The pre-European distribution had 5% of the landscape in the youngest age class, 19% in the intermediate age class, and 76% in the mature age class; the current landscape, in comparison, contains 31%, 39%, and 30% in the three classes, respectively (Figure 3a). The age distribution of the broader modeled landscape was similar to what was represented in the existing management areas: 8% of the landscape was in the youngest age class, 17% in the intermediate class, and 75% in the mature age class. Using equal, 20-year-interval age classes to more closely examine the distribution of ages, the pre-European landscape was dominated by the 61-80 year age class (47%; Figure 3b). Stands 0-20 years represented 5%, stands 21-40 years 10%, 41-60 years 36%, and stands older than 80 years represented 2% of the landscape. Similarly, the broader landscape had stands 0-20 with 8%, stands 21-40 years 10%, stands 41-60 38%, stands 61-80 years 46%, and stands older than 80 years represented 9% of the broader landscape.

Landscape patterns of stand ages

The spatial arrangement and configuration of age classes within KWMAs differed markedly between pre-European and current landscapes (Figures 4a, 4b). As a whole, the current landscape is much more fragmented than the pre-European landscape, with over twice as many patches (2029 current, 999 pre-settlement), half the mean patch size (35.8 ha, 71.3 ha), lower aggregation of stands within an age class (contagion = 47.3%, 68%), and much higher interspersion of patches (interspersion and juxtaposition index = 94.1%, 62.1%). When analyzed by age class, metrics show a pronounced change in the distribution of the three age classes between the two time periods (Table 2). The youngest age class currently has a much larger mean patch size, consistent with the establishment of large plantations in KWMAs. While the intermediate age class has exhibited the least change in mean patch size, the increase in largest patch index indicates the presence of very large patches on the modern landscape. The extent of the mature age class (which is being replaced by plantations in the current management plan) has been reduced by 60% from pre-European settlement, has had a 74% reduction in mean patch size, and has exhibited a 15-fold reduction in largest patch index, suggesting the existence of very large, mature patches on the historic landscape that are no longer present.

Discussion

Our analyses suggest that while the spatial location of KWMAs in northern Lower Michigan are consistent with that of pre-European settlement jack pine-dominated cover types, the stand age distribution of jack pine forests on the current landscape differs significantly (Figure 3). Comparatively, the current landscape is characterized by widespread reductions of mature jack pine stands and an even distribution of stands among age classes (Table 2). Assuming the landscape during the pre-European survey period (1837-1858) to be within the HRV, the current management regime of harvesting and planting jack pine on a 50-year rotation has greatly reduced the landscape-scale variability of stand ages. This supports other conclusions that extensive plantation management for KW breeding habitat is likely to homogenize the landscape (Spaulding and Rothstein 2009). Given that the management regime has resulted in a near replacement of wildfire-regenerated stands by plantations on public lands in the region (Donner et al. 2008), the effects of KW management on the landscape may be extensive.

While our study focuses on landscape structure rather than the structure of individual stands, it has been shown that plantations at young and intermediate ages differ significantly from wildfire-regenerated stands in important attributes such as the variability in stem density among stands, internal patchiness, the number of snags, the amount of coarse woody debris, and forest floor biomass (Spaulding and Rothstein 2009). These important stand structural components begin to resemble those of wildfire-regenerated stands after approximately 40 years, but mature stands older than 50 years have been significantly reduced (Figures 3, 4). Mature jack pine forests in the region are important for ecosystem services such as carbon storage and nutrient accumulation over time (Rothstein et al. 2004; LeDuc and Rothstein 2010), and may affect biodiversity of both bird (Corace et al. 2010a; Corace et al. 2016) and plant communities (Kashian et al. 2003b). Together with these results, our data suggest that KW habitat management using a short rotation age and targeted removal of stands > 50 years old has created a landscape that at multiple spatial scales departs markedly from that resulting from the natural disturbance regime in NLM.

Despite dominance by a short-lived tree species and a frequent, stand-replacing fire regime (Simard and Blank 1982; Cleland et al. 2004), our analyses suggest that the pre-European landscape was not dominated by early-successional forests during the period of the GLO surveys. We acknowledge that the 20-year period of the survey represents only a short period of time, but we suggest that the landscape is perhaps better characterized as dynamic, or temporally variable, rather than strictly early-successional. The dominance of the landscape by older age classes may have resulted from a single large fire or a series of fires in close succession, but the landscape was clearly dominated by young stands just a few decades prior to the GLO surveys. Thus, the pre-European stand age distribution likely varied through time rather than remaining at any one age distribution or successional stage, and that variation may have been important for maintaining ecosystem processes and biodiversity over long temporal scales (Petraitis et al. 1989). This temporal variability is lacking on the current landscape because of consistent annual harvesting and planting that maintains a relatively constant, or slowly increasing, proportion of young stands. While a 50-year harvesting rotation may approximate the historical 59-year fire rotation (Cleland et al. 2004), annual and decadal variability in the area burned, with much area burned in some years but little or none in others, is equally important for re-creating the stand age HRV. Fire rotations are determined by the overall amount of burned land over time, but do not necessarily indicate that the entire landscape has burned within that time frame. Overlapping fires in the same locations (perhaps driven by locally shorter rotations at smaller scales) would lead to variably-burned landscapes, with some areas remaining unburned and others remaining relatively young for long periods of time. Current management practices have modified the age distribution of large swaths of the landscape, without the variability in age that would likely characterize a landscape produced by a historically-relevant fire regime. Although the current proportion of older stands on the landscape may be within the HRV when large fire years are considered, harvesting and planting an equal area of jack pine each year will dampen and eventually eliminate the variability of stand ages over time (Figure 5).

Our analyses further suggest that the spatial configuration of stand ages in current jack pine forests has been affected by prolonged KW breeding habitat management. Patches of young forests are much larger, on average, than during the pre-European period (Table 2). This suggests that the current distribution of large plantations does not reflect the variability of a natural fire regime, where a range of fire sizes over time would likely yield some large stands but also many smaller stands. Conversely, the average sizes of intermediate and, more dramatically, mature patches have been reduced over this time period (Table 2). Smaller patches result in the loss of forest interior areas, and could have implications for wildlife or plant communities that depend upon such sites (White and Host, 2008; Cullinane-Anthony et al. 2014). This observation is reinforced by the reduction in landscape contagion over this time period, suggesting that similarly-aged patches are overall less aggregated into large stands, even as the size of young stands has increased. The current management protocol recommends plantations of at least 121 ha, but preferably 202 ha, for the provision of KW breeding habitat (MDNR et al. 2015); this will likely continue to increase the mean patch size of young forests, reduce the size of older forests as more old stands are converted to plantations, and further reduce the variability of stand sizes. Thus, in addition to a homogenization of stand-level characteristics (Spaulding and Rothstein 2009), our data suggest that landscape composition and structure have been homogenized by KW breeding habitat management in terms of the extent and configuration of stand ages.

We acknowledge that limitations exist in the use of GLO notes to characterize pre-European settlement landscapes, such as surveyor biases in tree species and size selection (Manies et al. 2001), and uncertainty in the quality of data recorded by individual surveyors who were not trained botanists or ecologists (Schulte and Mladenoff 2001). However, relatively homogenous site conditions consisting of nearly-monotypic jack pine stands persist across much of the Grayling Sub-subsection, such that gross misidentification errors were likely minimal. Bias against using jack pines as marker trees have been reported for GLO notes in Wisconsin, suggesting that surveyors chose trees of larger, more easily marked species where possible (Liu et al. 2011). Although such a bias would underreport the presence of jack pines in a given area, our focus on monotypic jack pine stands, rather than mixed-pine stands, reduces the importance of this bias for our results. Further, our exclusive use of surveyed line trees reduces the risk of biases associated with blazing, as these trees were not required to be marked (Liu et al. 2011).

Of greater concern is the lack of small, young jack pine in the survey notes, which fell beneath the minimum diameter for measurement along section lines; 3 in. (7.6 cm) dbh was the smallest reported in our dataset (Manies et al. 2001). Our representation of surveyed, recently burned areas as young stands (three years old) added young forest to the landscape to ensure representation of young stands that were described by surveyors but would not be otherwise captured by GLO data. The distinct lack of trees in the 21-40 year age class (Table 1b) is associated solely with the survey data, and demonstrates the paucity of young trees in the survey notes. The misinterpretation of the 21-50 year age class by the model (Table 1a), which inaccurately classified most of the trees in the age class, is likely because the majority of the surveyed trees in that class (89%) were older than 40 years (Table 1b). This would cause even relatively small errors in the modeled estimates to frequently fall above the upper limit of the 21-50 year age class. While this sampled age distribution may have implications for the modeling process, it also likely represents a lack of young stands on the actual pre-European landscape. Overall, the frequent, high-severity fire regime in NLM created a landscape composed chiefly of patches of even-aged stands. This would have offered little size variation at scales small enough to warrant much bias in surveyor preference for age or size. Wildfire-produced stands in the region often include unburned living trees within burned areas (Kashian et al. 2012), but the number of data points that were surveyed as old trees cannot be accounted for by this heterogeneity alone. While uncertainty exists, the relative simplicity of the study area and the considerations made to add young trees likely ameliorate many of the effects of that uncertainty.

It is increasingly recognized that variability in landscape structure and successional stage is intimately associated with ecosystem function and sustainability (Franklin 1993; Lindenmayer et al. 2000). Landscape heterogeneity is important for maintaining both resistance and resilience to disturbances (Churchill et al. 2013; Moritz et al. 2014; Seidl et al. 2014), and components of stand structure such as complexity and heterogeneity have been associated with increased landscape biodiversity (Lindenmayer et al. 2000). Therefore, historically-relevant variability may be vital for the future sustainability of managed ecosystems (Grumbine 1994; Keane et al. 2009). The efficacy of managing for HRV objectives has been questioned given the overwhelming effects of global climate change on ecosystems (Millar et al. 2007). Indeed, there is much uncertainty about the effects of climate change on the region (Handler et al. 2014). Given this uncertainty, restoration of historic heterogeneity may be a way to create robust ecosystems that are resilient given the ecosystem properties that are known and documented, while allowing for adaptive management practices and future research and projections of climate effects to shape management practices going forward (Keane et al. 2009).

In NLM in particular, restoration of historically relevant patterns and processes may aid in management both ecologically and financially; current management is not self-sustaining in that the young jack pines scheduled for harvest under the current protocol have little economic value. Although jack pine is an important pulpwood species, there has been little pressure to harvest for that purpose due to protection of the area as KW breeding habitat under the ESA. As KW delisting approaches, there may be an increase in harvesting for pulpwood or a burgeoning biomass market, though KW habitat protection will continue and agreements have been made to restore or increase more traditional KW management should the population begin to fall (MDNR et al. 2015). Future management will be overseen by a conservation team comprised of management practitioners from multiple agencies and other interested parties, and non-profit fundraising is already under way (MDNR et al 2015). These efforts can be facilitated by restoring historic ecosystem heterogeneity across properties (age, structure, disturbance processes, etc.) to provide a stable and sustainable ecosystem.

This study highlights a need to reconcile endangered species management with the heterogeneity created by natural disturbance regimes in systems often tightly managed for very specific objectives. In the case of KW, there exists a complex tradeoff between the recovery and maintenance of an endangered species and the conservation and restoration of a forested landscape within the historical range of age variability, as represented by the relatively old stand-ages of the survey period. We have shown that the spatial and temporal variability of the age distribution of jack pine forests has been homogenized by decades of intensive and extensive management, resulting in a fixed, young landscape that has little historically-consistent age variability. As the overwhelming success of KW recovery moves it towards removal from ESA listing, there is an opportunity to re-evaluate the management regime of the region while maintaining the knowledge gained from a highly successful recovery program. Management that better emulates historic spatial and temporal age variability may provide a foundation for a more ecosystem-based management plan moving forward that supports both the KW population and the viability of jack pine-dominated ecosystems in the region.

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Table 1. Error matrix of original survey points and validation points generated from the prediction surface using (a) three age classes [kappa = 0.494 (*T = 54.5*, *p<0.001*), 95% CI (0.476, 0.512), overall accuracy = 69.8%], and (b) five age classes [kappa = 0.516 (*T = 77.5*, *p<0.001*), 95% CI (0.500, 0.532), overall accuracy = 63.0%. Classification errors in the model tended to under-predict forest age in the 3-class configuration, and to over-predict forest age in the 5-class configuration.

1a)

		Surveyed			
		0-20	21-50	>50	Total
Predicted	0-20	*1200*	32	69	1301
	21-50	578	*481*	490	1549
	>50	4	931	*3062*	3997
	Total	1782	1444	3621	*6847*

1b)

		Surveyed					
		0-20	21-40	41-60	61-80	>80	Total
Predicted	0-20	*1200*	14	50	35	2	1301
	21-40	562	*80*	210	186	39	1077
	41-60	20	63	*1287*	453	57	1880
	61-80	0	8	434	*1360*	391	2193
	>80	0	0	0	25	*370*	395
	Total	1782	165	1981	2059	859	*6846*

Table 2. Class-level landscape metrics of the pre-European settlement compared to current landscapes within Kirtland's Warbler Management Areas in northern Lower Michigan detailing marked changes between the 2 time periods.

Age Class	*% Landscape*	*# Patches*	*Mean Patch Size (ha)*	*Largest Patch Index (%)*	*Euclidean Nearest Neighbor (m)*
0-20					
Pre-settlement	5.4	77	50.1	0.97	356.4
Current	30.8	285	78.5	1.7	453.3
21-50					
Pre-settlement	19.0	237	57.2	1.9	242.4
Current	39.3	671	42.5	4.3	317.8
> 50					
Pre-settlement	75.6	685	78.6	9.9	221.9
Current	29.9	1073	20.2	0.65	273.7

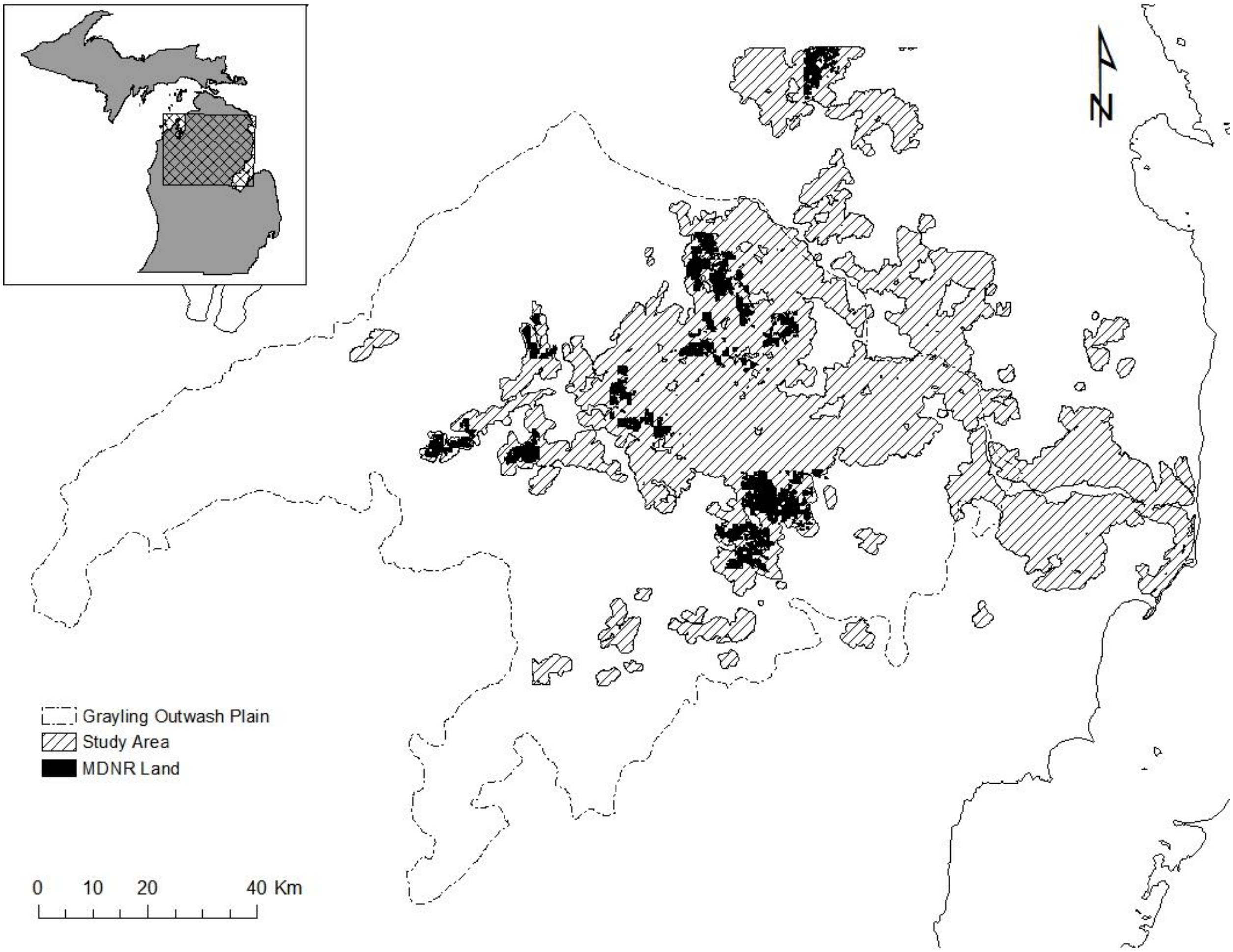

Figure 1. The study area used to characterize the pre-European settlement distribution of jack pine forests in northern Lower Michigan (U.S.A.) and the distribution of Michigan Department of Natural Resources land used for cover type analyses. The majority of the study area is encompassed by the Grayling Outwash Plain.

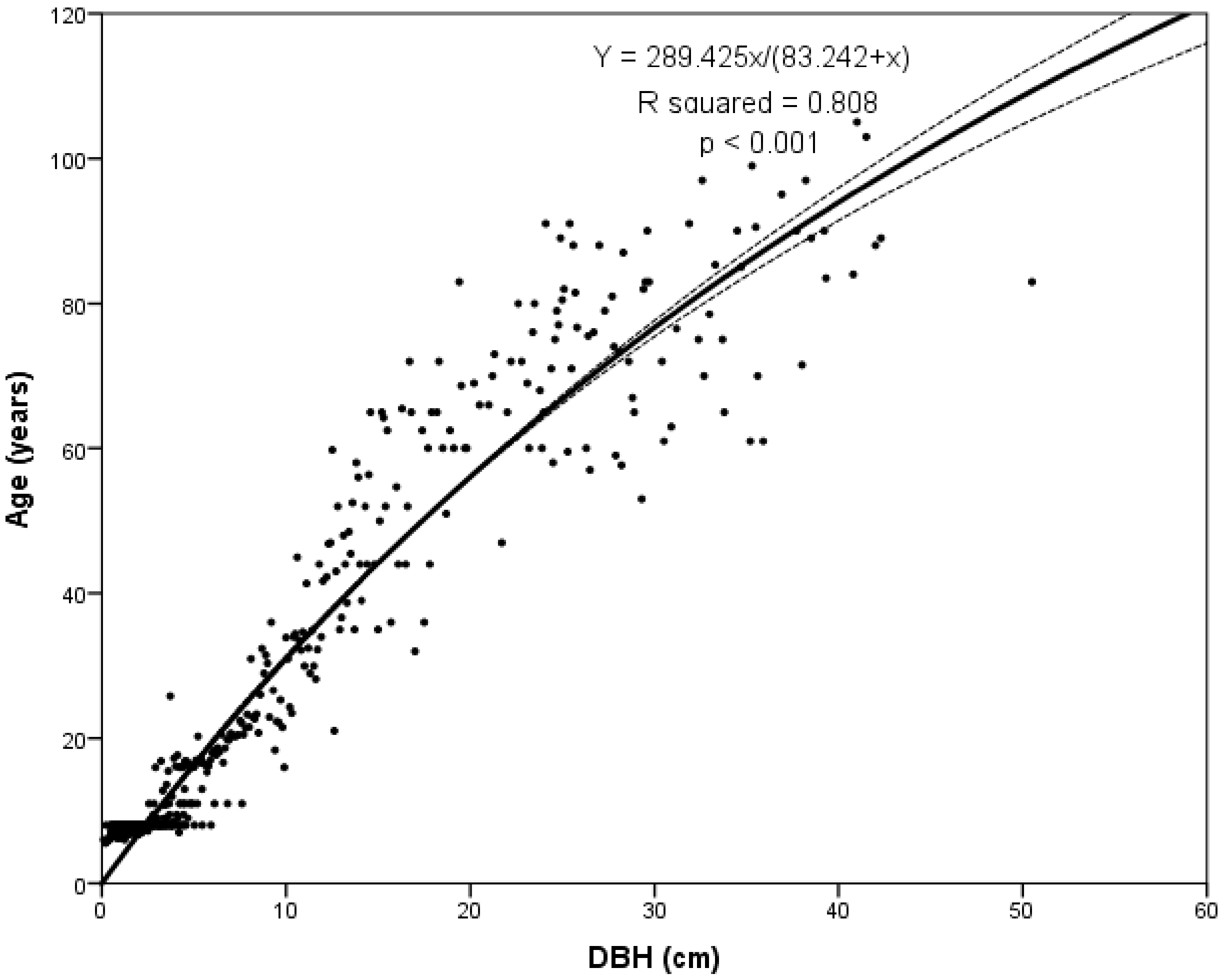

Figure 2. Age and diameter at breast height (dbh) of field-collected data, showing Michaelis-Menten regression line and 95% CI ($R^2 = 0.808$, $p < 0.001$). The data range from 5-100 years. Presettlement data derived from the equation range from 3-161 years.

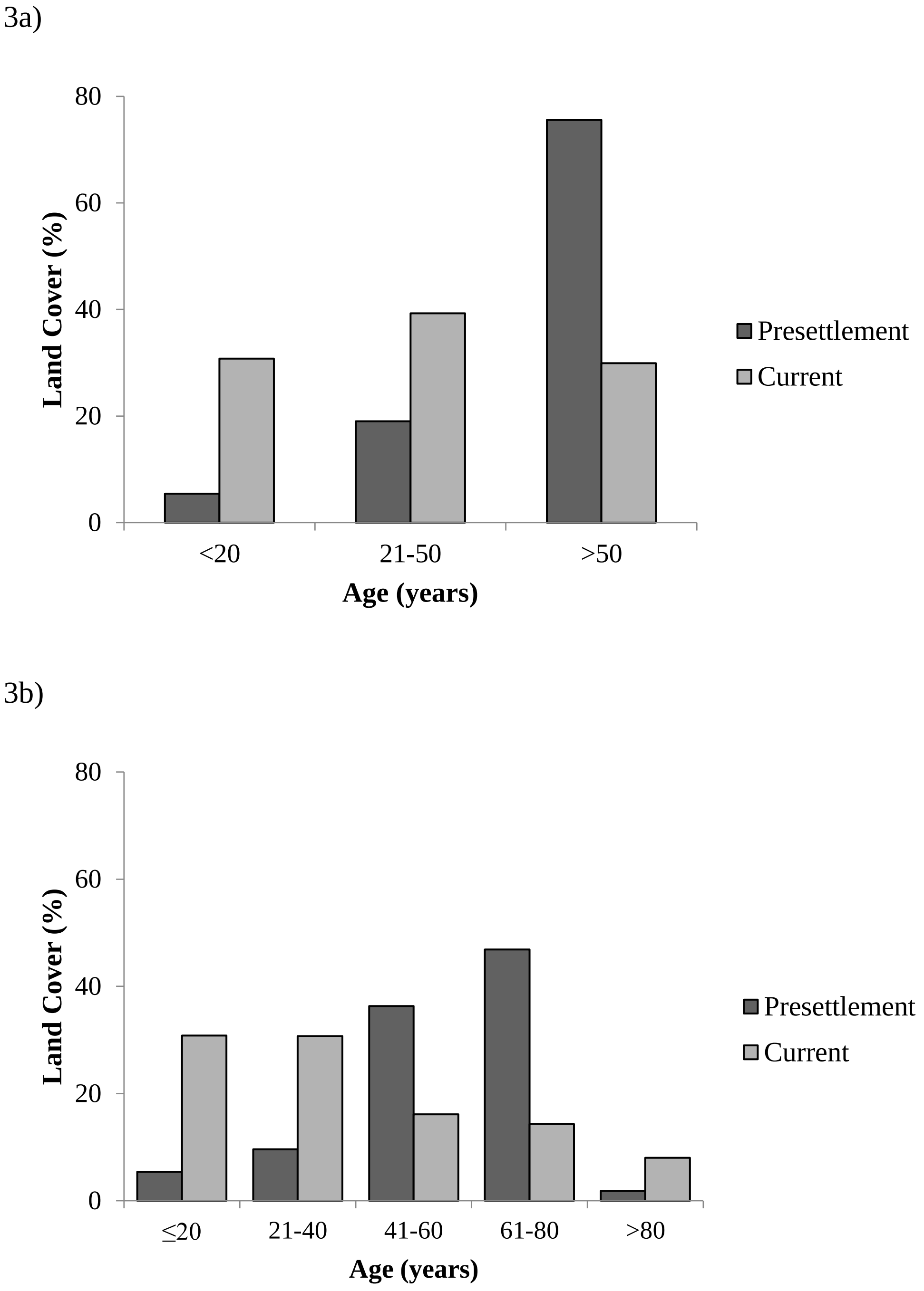

Figure 3. Percent cover of pre-European settlement and current jack pine stand-age classes within current Kirtland’s warbler management areas, illustrating a marked decrease in the coverage of older (> 50 years) stand ages on the current landscape. Figure 3a shows three, management-based age classes, figure 3b shows the same data in 20-year intervals.

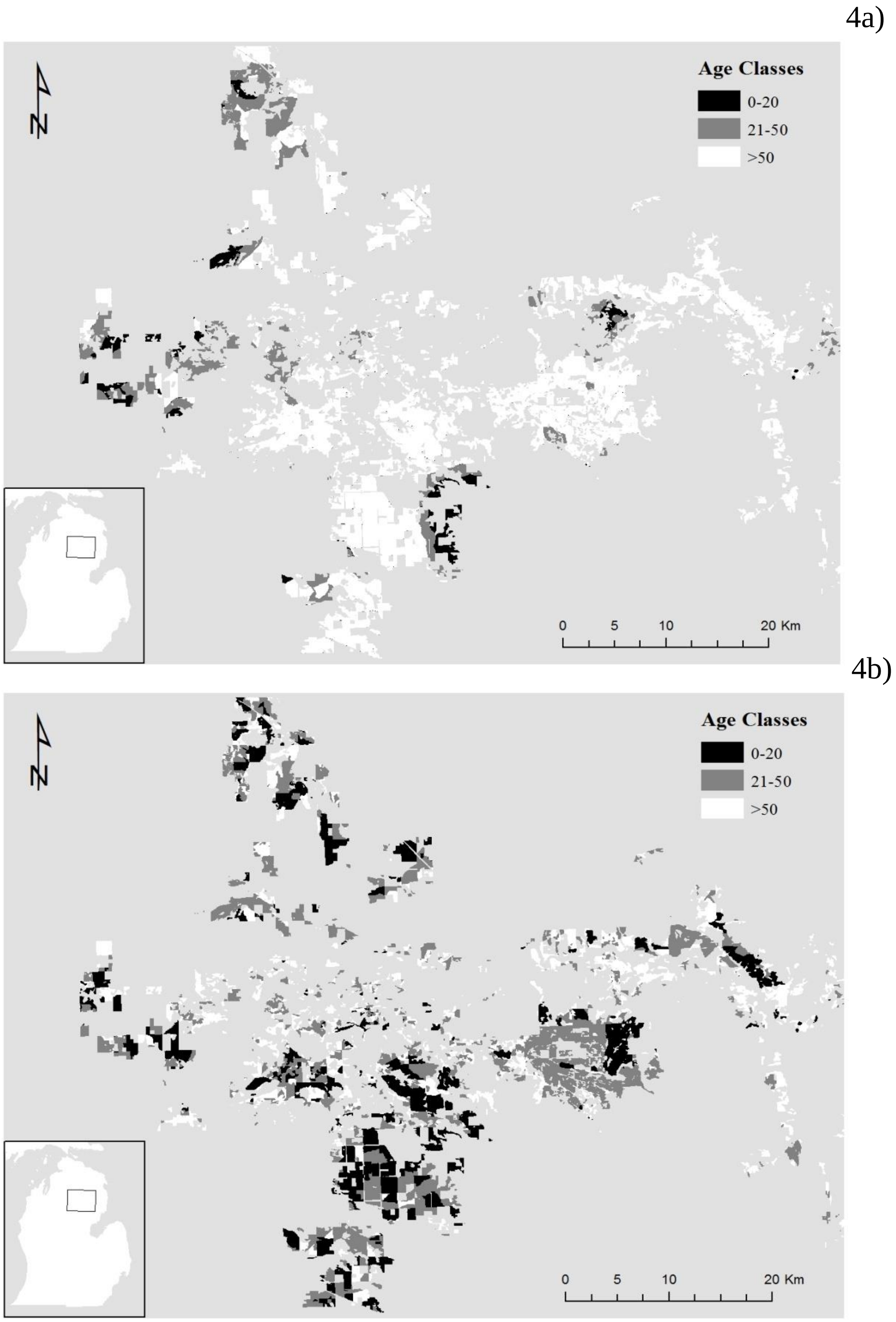

Figure 4. Pre-European settlement (a) and current (b) distribution of jack pine stand age classes in Kirtland’s warbler management areas. The extent represents Michigan Department of Natural Resources, USDA Forest Service, and USDI Fish and Wildlife Service management areas in northern Lower Michigan (U.S.A.).

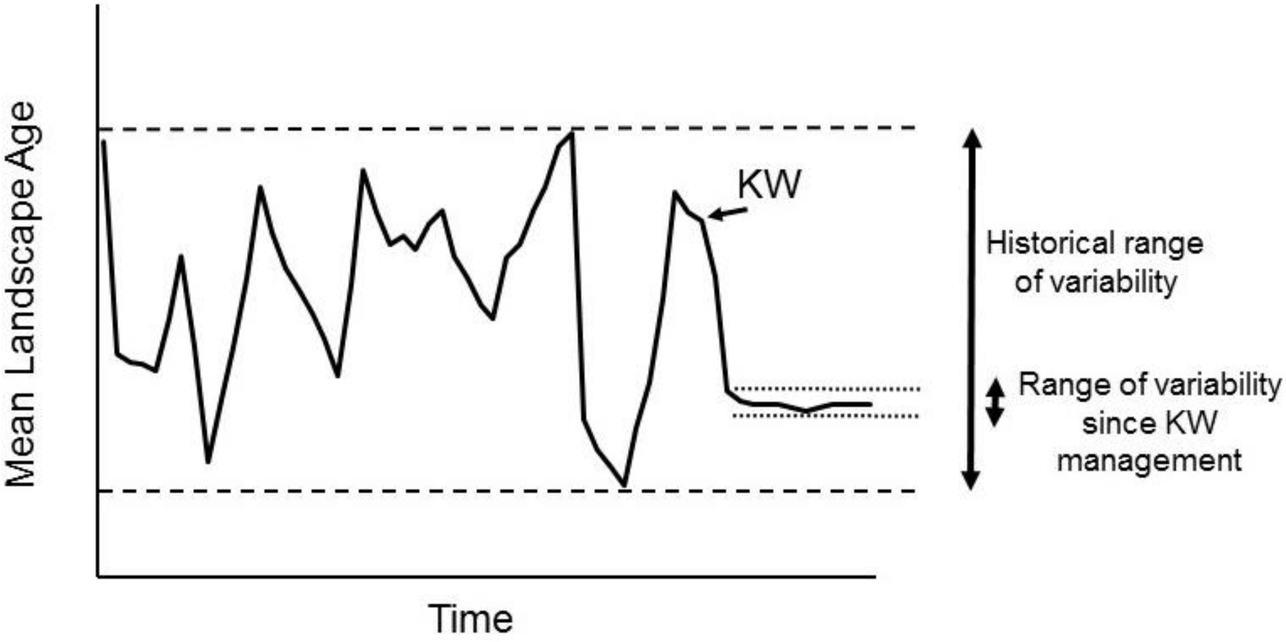

Figure 5. Conceptual representation of the historic range of jack pine stand-age variability in northern Lower Michigan (U.S.A.), illustrating the effects of warbler habitat management on the temporal variability of stand age-distributions. “KW” indicates the beginning of Kirtland’s warbler habitat management using plantations. Representation of landscape age prior to warbler management is hypothetical based on the periodic occurrence of large wildfires of variable size and timing on a 59-year rotation.

CHAPTER 3 - PRE-FIRE FOREST REMNANTS AFFECT POST-FIRE PLANT COMMUNITY COMPOSITION AND STRUCTURE [2]

Introduction

Biological legacies are remnants of pre-disturbance conditions that persist on post-disturbance landscapes (Foster et al. 1998, Franklin et al. 2000). The spatial and temporal variability of disturbances generated by climate, physiography, soil, vegetation, and other factors create patterns of post-disturbance biological legacies (Foster et al. 1998; Swanson et al. 2010). Biological legacies have been observed following even extreme disturbance events, such as large wildfires, volcanoes, hurricanes, and floods (Foster et al. 1998). The biological legacies that remain provide a host of services to the post-disturbance ecosystem. For example, post-fire landscape structure, site productivity, and soil properties are influenced by the amount and persistence of coarse woody debris (Harmon et al. 1986). Standing dead trees (snags) and downed wood may act as substrate for new seedlings, vegetatively reproduce to repopulate plant communities, or may provide habitat or food sources for wildlife (Harmon et al. 1986; Hutto 2006). Living remnants of the pre-fire ecosystem such as patches of unburned forests, while less well understood, also have the potential to affect post-fire stand structure (Arseneault 2001; Kashian et al. 2012), biodiversity (Franklin and MacMahon 2000; Cullinane-Anthony et al. 2014), and broad-scale ecosystem resilience (Churchill et al. 2013; Seidl et al. 2014). Living biological legacies may act as seed sources for post-fire regeneration, as refugia for late-successional species within an early-successional landscape, or may produce micro-climate variability on the post-disturbance landscape (Franklin et al. 2002; Swanson et al. 2010). In these ways, pre-fire forest remnants maintain continuity between the pre- and post-disturbance ecosystems.

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Unburned patches on a landscape may persist through several subsequent disturbance events, and these refugia may provide unique ecosystems for decades to centuries (Camp et al. 1997). Areas may burn less frequently than the surrounding landscape due to topographic or physiographic features or vegetation structure, but not all post-disturbance remnants are related to physiographic or topographic features. In northern Lower Michigan, USA, the stand-replacing fire regime of jack pine (*Pinus banksiana* Lamb.)-dominated ecosystems frequently leaves strips of living trees after large fires, hereafter called "stringers" (Kashian et al. 2012). Stringers are typically oriented in the direction of the spread of the fire (Simard et al. 1983; Arseneault 2001), occur most frequently when fires are large and intense (> 1,000 ha; Kashian et al. 2012), and have been documented in northern Michigan as long ago as early European settlement (Pyne 1982). Unlike landform-related refugia, stringers typically persist only until the occurrence of subsequent disturbances. Stringer creation is hypothesized to be a result of fire-created weather events; variably-heated air masses cause horizontal roll vortices that result in large downbursts that extinguish the fire below (Haines and Smith 1983; Simard et al. 1983). The stringers themselves retain evidence of a high severity burn along their edges (e.g. scorch marks, pers. obs.), but the trees within remain unburned. Although the mechanisms of stringer formation are not definitively known, fire behavior rather than topography or vegetation is likely the cause of the differential burn severity.

Fire suppression and exclusion dominated forest management in northern Lower Michigan throughout the 20th century (Dickmann and Leefers 2003). Reduced fire occurrence in the region limited the extent of young jack pine stands on the landscape, as the vast majority of naturally regenerated jack pines are produced through post-fire seed dispersal from serotinous cones. Widespread increases in stand age resulted in breeding habitat loss for Kirtland's warblers

(*Setophaga kirtlandii* Baird), neo-tropical migratory songbirds which require large (> 32 ha), young (< 20 years old) stands of dense jack pines interspersed with open foraging areas (Walkinshaw 1983). Kirtland's warblers are federally endangered and nest mostly in northern Lower Michigan (Donner et al. 2008). To account for the reduction in young stands due to fire suppression, extensive habitat management has provided breeding habitat using clear-cut harvesting followed by planting of jack pine plantations since the mid-20th century. Plantation establishment and management is largely responsible for recovery of the Kirtland's warbler population, which currently is more than 2.5 times the original management objective proposed by the Kirtland's Warbler Recovery Team (MDNR et al. 2015).

Plantation management has also had significant effects on several stand- and landscape-level forest attributes in the region, such as reduced stand-age heterogeneity (Tucker et al. 2016), increased stem density (Kashian et al. 2017), reduced snag retention and forest floor biomass (Spaulding and Rothstein 2009), and reduced bird community diversity (Corace et al. 2010b). Plantation designs have not prioritized the inclusion of stringers, and those created by wildfires have frequently been harvested from the landscape. Therefore, although plantation management has largely replaced fire-regenerated forests across the region (Donner et al. 2008), the recent recovery of the Kirtland's warbler population has facilitated a stronger emphasis on ecosystem-based, adaptive management practices which might include retention of stringers (Bocetti et al. 2012; MDNR et al. 2015).

This study examines the potential of stringers to affect post-fire regeneration and community composition. Stringers provide heterogeneity of structure and vegetation on a landscape characterized by relatively homogeneous topography, soils, vegetation, and disturbance regime (Whitney 1986, Cleland et al. 2004). Given the likely preponderance of stringers on the historical landscape, reduction of these naturally-produced structures on the current landscape could have critical impacts on succession and overall biodiversity. Similar pre-fire remnants alter long-term, post-fire vertical stand structure in homogeneous jack pine and black spruce- (*Picea mariana* (Mill.) BSP) dominated boreal forests (Arseneault 2001). Effects of seed dispersal from unburned patches on post-fire plant communities have been documented in western coniferous forests (Lentile et al. 2007). Stringers may likewise affect succession if they act as refugia for later-successional species, provide a prolonged post-fire seed source, or provide microclimate differences on the burned landscape. Effects of stringers on post-fire plant community composition and structure have not previously been studied, but may offer important insights for future landscape management. Therefore, we asked: 1) What effects do stringers have on post-fire plant community composition? We hypothesized that seed sources within the stringers would affect the burned areas immediately adjacent to the stringers, such that plant community composition would change with increasing distance from stringers; and 2) How do stringers impact post-fire structural development of adjacent stands? We hypothesized higher sapling density and broader age distributions adjacent to the stringer, as the mature stringer trees would provide a continuous post-fire seed source into the adjacent burned area.

Methods

Study Area

The study area lies within the Grayling Outwash Plain (sub-subsection VII.2.2), in the Highplains subsection (VII.2) of the Northern Lacustrine-Influenced Lower Michigan Section (VII) of Region II (NLM; 44º30’N, 84º30’W) per Albert (1995). Soils are excessively- to well-drained sands, with sandy ice-contact ridges scattered throughout the outwash plain. Vegetation is dominated by largely monotypic stands of jack pine, occasionally interspersed with northern pin oak (*Quercus ellipsoidalis* EJ Hill) and bigtooth aspen (*Populus grandidentata* Michx.). Groundcover flora is dominated by blueberry (*Vaccinium spp*.), bearberry (*Arctostaphylos uva-ursi* L.), sand cherry (*Prunus pumila* L.), and Pennsylvania sedge (*Carex pensylvanica* Lam.) among other species of woody plants, forbs, and grasses (Kashian et al. 2003b). Jack pine dominance was historically maintained by frequent stand-replacing fires, with a pre-European settlement fire rotation of 59 years (Cleland et al. 2004). The serotinous habit of jack pine, which stores seeds in closed cones that open with the heat of a fire, provide a post-fire, early-successional advantage for seed dispersal and germination in the absence of competition from more shade-tolerant species that otherwise displace jack pines on more productive sites (Burns and Honkala 1990).

We examined the compositional and structural differences of plant communities adjacent to stringers found in four burned areas in northern Lower Michigan representing a gradient of successional ages (Figure 6): Damon (burned in 1966; 481 ha), Mack Lake (1980; 9825 ha), No Pablo (2000; 2104 ha), and Hughes Lake (2006; 2345 ha). The percent of the burned area represented by stringers (from Kashian et al. 2012) was Damon – 8.1%, Mack Lake – 5.7%, No Pablo – 5.0%, and Hughes Lake – 5.8%. The number of stringers sampled for each burn represented the overall size of the burned area and the suite of management activities (such as harvesting and plantation establishment) that often limited the number of remaining stringers on the landscape. The Damon burn was most heavily impacted by harvesting, so we sampled one stringer that was dominated by planted red pine (*Pinus resinosa* Sol ex. Aiton) and mature post-fire jack pine. At Mack Lake, both plantation-origin red pine- (n = 4) and jack pine- dominated (n = 2; hereafter identified as “JP Mack Lake”) stringers were sampled. We analyzed all six Mack Lake stringers together to represent the full variability of the burn, and then the two at JP Mack

Lake separately to determine specific effects of the prolonged jack pine seed source. Five jack pine-dominated stringers were sampled at No Pablo, composed of jack pines established post-fire after the Mack Lake burn. Three stringers were sampled at Hughes Lake, all dominated by planted jack pine.

Field Methods

The experimental unit for the study was the individual stringer, sampled with three replicate transects per stringer. Along each transect we sampled nine 100 m^2 plots that consisted of a single plot in the center of the stringer and four plots in each direction perpendicular to the stringer at distances of 0.5, 1, 2, and 3 times the average height of the trees within the stringer (Figure 7). We varied the length of the transects based on the height of the mature trees in the stringer to allow us to capture areas within the effective dispersal distance of jack pines (less than two tree heights; Burns and Honkala 1990). Doing so adjusted the sampling distance to reflect the age and compositional differences within stringers while keeping the farthest plots outside the effective dispersal distance of mature jack pines. At each 100 m^2 plot we counted overstory (> 9.0 cm diameter at breast height, DBH) and understory (1.5 – 9.0 cm DBH) jack pines to calculate tree density (stems/ha). We used a basal area prism (basal area factor = 10 ft^2/acre, 2.3 m^2/ha) from the center of the plot to randomly select at least 10 jack pines for aging. We then aged those trees using increment cores or by counting whorls on trees too small to core. Increment cores were mounted and sanded in the lab per standard techniques (Speer 2010) and rings counted using a dissecting microscope. We also sampled vegetation within three replicate 1 m^2 quadrats surrounding the center point of each plot to determine aerial cover classes of the ground cover community. We identified all specimens to species after Voss and Reznicek (2012) except in the case of mosses, which were identified to genus for clubmosses (*Lycopodium*) or termed Bryophytes for all others.

We used cover classes of: class 1: trace amount-1%; class 2: 1-2%; class 3: 2-4%; class 4: 4-8%; class 5: 8-16%; class 6: 16-32%; class 7: 32-64%; class 8: 64-100% (adapted from Walker et al. 2003). To examine microclimate effects, we used temperature and light intensity data from HOBO data loggers that had been deployed in 2011. The HOBOs sampled data every four hours during the month of August along transects across two stringers at No Pablo with representative directional orientation and structure. HOBOs were placed at 10 m outside the stringer on each side, 5 m outside on each side, at the stringer edges, and four HOBOs spaced evenly along the transect within the stringer.

Data Analysis

To determine the extent that stringers affect post-fire plant community composition, differences in community composition between plots nearest to stringers (0.5x and 1x the tree height of mature trees in the stringer) and farthest plots (2x and 3x) were assessed using non-metric multidimensional scaling (NMDS) ordinations (Kruskal 1964). For each stringer, ground cover aerial cover class was converted to abundance using the midpoint of the cover class as the percent cover of each measured species (after Walker et al. 2003). Replicate transects within each stringer were averaged, and then all stringers at each burn were averaged to provide a mean value of species abundance for plots at increasing distances from stringers. NMDS ordinations were produced using the Bray-Curtis dissimilarity as the distance measure between plots (Bray and Curtis 1957). Ordinations were generated for each burn individually and a single ordination was generated with all burns collectively using the vegan package (metaMDS, k = 2 for all ordinations; Oksanen et al. 2016) in R (v. 3.1.1; R Core Team 2014).

For the individual burns, plots were grouped and displayed using hulls (ordihull, vegan package) drawn around the nearest plots (0.5x and 1x) and the farthest plots (2x and 3x), with the center stringer point separate on all ordinations. Configuring the NMDS in this way allowed us to display the community dissimilarity of plots within the dispersal distance of the stringer trees and those outside the dispersal distance, and thus assessed differences in community composition attributable to distance from the stringer. After testing for homogeneity of dispersions of the Bray-Curtis dissimilarity matrices (betadisper tool, vegan package) and finding no meaningful violations, we tested for differences between the nearest plots and farthest plots using the adonis function in vegan, a permutational multivariate ANOVA (perMANOVA) designed for use with distance matrices (Oksanen et al. 2016). Pairwise comparisons between the composition of center, nearest, and farthest plots at each burn were assessed using the false discovery rate (fdr) method (pairwise.perm.manova in RVAideMemoire package; Hervé 2017). The contribution of individual species to the observed differences in plant communities between inner and outer plots was analyzed using a similarity percentage (SIMPER) analysis of plant community matrices (simper in vegan package).

The ordination displaying all burns was grouped by site, with hulls drawn around all plots for each, individual burn. This configuration allowed us to more broadly compare the community composition between burned areas, which helped us to determine whether differences found within sites were unique to the burns or common among all burns across the study area. To determine whether differences in communities were driven by factors other than random chance, we conducted permutation tests (ordiareatest, vegan package) to determine whether the areas of the hulls grouped by burn were significantly smaller than randomly generated hulls (Oksanen et al. 2016). We again compared the distance matrices using perMANOVA and used pairwise comparisons to investigate differences in communities between burns.

To test whether mature jack pine in stringers act as a prolonged seed source and affect stand structure outside of stringers, we assessed stand density, mean stand age, and age distributions of post-fire jack pine regeneration in plots at increasing distances from the stringer. The assumption of independence of samples for both density and age was confirmed by testing for spatial autocorrelation between plots using a Moran's I test (ape package v. 4.1 for R; Paradis et al. 2004). We assessed normality and homogeneity of variances using the Shapiro-Wilk test (Shapiro and Wilk 1965) and the Levene's test (Levene 1960), respectively, in SPSS (v. 23; IBM Corp. 2015) for both age and density within plots; these assumptions could not be met for all plots. Therefore, we compared density and mean age along transects using the GLIMMIX procedure in SAS Studio (v. 3.5; SAS Institute 2016) using either the Gaussian or Poisson distribution upon inspection of the Pearson residuals produced by the post-hoc UNIVARIATE procedure. Replicate transects within individual stringers were considered random effects, and stringers and plots were fixed effects. The mean ages of the plots within stringers and those outside varied greatly, so we compared mean ages using the generalized linear mixed model with all plots to determine differences between stringer plots and those in the burned area, and then again using only the plots outside the stringer to compare differences along transects.

To examine effects of prolonged seeding on the age distribution of post-fire regeneration, age distributions of the nearest and farthest plots (0.5 x and 3 x tree heights, respectively) were visually inspected and statistically compared using the standardized Anderson-Darling test in R (ad.test, kSamples package v. 1.2-4; Scholz & Zhu 2016). Comparing the nearest plots (those likely to be most affected by the prolonged seed source provided by stringers) with the farthest plots (those likely to not be affected) provided the starkest comparison of plots to test for effects. Our focus on the extreme differences between plots is particularly important because the magnitudes of observed differences in structural metrics are likely to be small given the relatively minor amount of gradual infilling compared to the abundance of immediate, episodic post-fire regeneration in these forests. Appropriately, the Anderson-Darling statistic is sensitive to the tails of distributions, which makes it an ideal test in this case, as deviations from the even-aged distribution would most likely be found in the tails, where younger seedlings that did not establish immediately post-fire would be observed.

To investigate potential effects of stringers on microclimate we calculated the average temperature (degrees C) and light intensity (lux) at 16:00 for the month of August, 2011 using data collected from HOBO data loggers. Data were analyzed for differences using Welch's ANOVA in SPSS (Welch 1951), as Levene's test revealed heterogeneity of variances. Post-hoc pairwise comparisons were made with Games-Howell tests (Games and Howell 1976). An alpha of 0.05 was used for all statistical analyses.

Results

Community Composition

NMDS ordinations of the individual burns qualitatively showed dissimilarity of community composition between plots nearest to (0.5 x and 1 x) and farthest from (2 x and 3 x) the stringers in some of the burns. Dissimilarity of the nearest and farthest plots from the center stringer plots were evident at all burns. Complete dissimilarity between nearest and farthest plots was observed at No Pablo and partial dissimilarity was observed at Damon and JP Mack Lake, but almost complete similarity was displayed at Mack Lake and Hughes Lake (Figure 8). Stress in the ordinations ranged from 0.08 for Mack Lake to 0.14 at No Pablo, representing a good to fair ordination for all sites (Kruskal 1964). Results of perMANOVA analyses showed significant differences of Bray-Curtis dissimilarity between the nearest and farthest plots only at JP Mack Lake ($F_{(2)} = 2.028$, $p < 0.05$, $R^2 = 0.403$); post-hoc pairwise comparisons between center, nearest, and farthest plots were not significant. Although not significant at $\alpha = 0.05$, community differences between the nearest and farthest plots at both Mack Lake ($F_{(2)} = 1.649$, $p = 0.12$, $R^2 = 0.355$) and No Pablo ($F_{(2)} = 1.832$, $p = 0.11$, $R^2 = 0.379$) were explained by location nearly as robustly as at JP Mack Lake when examining the R^2 values.

Similarity percentage (SIMPER) analyses of sites showed the species most responsible for differences between near and far plots, and the percent contribution of each species (Table 3). At Mack Lake and JP Mack Lake the percent cover of bryophytes was markedly higher in the farthest plots and explained 35.4% and 31.4% of the difference between plots, respectively. *Vaccinium angustifolium* cover was higher in the nearest plots at Mack Lake (11.8% of the observed difference), JP Mack Lake (17.6%) and No Pablo (40.7%). At Hughes Lake, *Carex pensylvanica*, *Deschampsia flexuosa*, and *Vaccinium myrtilloides* were all more abundant in the nearest plots (20.5%, 14.6%, and 11.6% of the difference). At Damon, *Lycopodium spp.*, (27.5%) and *Pteridium aquilinium* (7.9%) were more abundant in the nearest plots, and *Vaccinium angustifolium* was more abundant in the farther plots (11.3%).

The NMDS of all burns combined (Figure 4) qualitatively showed dissimilarity of the plant communities among all burns except Mack Lake and JP Mack Lake (stress = 0.20). Permutation tests for the hull sizes of the burns were significantly smaller than random in all cases ($p < 0.01$ for all burns). PerMANOVA analyses showed significantly different communities among burns overall ($F_{(4)} = 15.662$, $p < 0.001$, $R^2 = 0.610$) and pairwise comparisons between burns were significant ($p < 0.007$) for all comparisons.

Stand Structure

Jack pine tree density inside stringers was significantly lower than all the surrounding plots at Mack Lake ($-3.8 < t_{157} < -3.0$; $p < 0.003$ for all sites) and No Pablo ($-3.0 < t_{130} < -2.3$; $p < 0.02$) and was lower than the nearest plot at Damon ($t_{22} = -2.2$; $p < 0.04$) (Table 4). However, regeneration density along transects was not significantly affected by the sustained seed source (Table 4). Overall, density was highly variable among the plots outside stringers and showed no consistent patterns.

Prolonged post-fire seeding would be expected to produce more continuous post-fire establishment of seedlings near stringers compared to episodic establishment in plots farther from stringers, where saplings predominantly established immediately post-fire. The average ages of saplings in plots along transects did not differ except at No Pablo and Hughes Lake (Table 4). However, age distributions of the nearest and farthest plots were significantly different at No Pablo (T.AD = 18.39, $p < 0.001$), Hughes Lake (T.AD = 29.37, $p < 0.001$), and JP Mack Lake (T.AD = 3.658, $p < 0.05$), with broader and flatter age distributions found at the nearer plots.

Microclimate

Temperature and light intensity were both significantly reduced by stringers (temperature: $F_{(9,\ 121.884)} = 8.518$, $p < 0.001$; intensity: $F(_{9,\ 120.081)} = 21.865$, $p < 0.001$). Pairwise comparisons between the sites along the HOBO transects revealed that temperatures and light intensities sampled within the stringers were significantly lower than those sampled adjacent to the stringers, and that those effects varied on the two sides of the stringers. The most consistent effects were demonstrated between the plots within the stringers and those adjacent to the stringers (Figure 10).

Discussion

Our results suggest that stringers may affect post-fire plant community composition, and that the impact decreases with distance from the stringer, though the successional stage (time since burn) of the area surrounding the stringer is an important factor mediating this effect. NMDS ordinations of whole burns indicated that plant communities differed among burns, and that those communities were not randomly assembled (Figure 9). These trends suggest that plant communities are likely to differ based upon time-since-fire and site conditions represented by individual burns, and thus stringer effects on plant communities are likely to vary across burns dependent in part upon their stage of succession. Ordinations of individual burns showed dissimilarity between plots nearest the stringers and those farthest away at all burns except Mack Lake and Hughes Lake (Figure 8). Plots nearest and farthest from the jack pine-dominated stringers at Mack Lake (JP Mack Lake) differed significantly in species composition, and over 35% of the differences between the nearest and farthest plant communities at Mack Lake and No Pablo were explained by distance. Lack of dissimilarity at Hughes Lake may result from the young age of the burn when sampled (6 – 7 years post-fire), reducing potential dispersal time into the burned area. Given the short amount of time since fire, plant communities at Hughes Lake are more likely to have featured the emergence of post-fire vegetative sprouters (Ahlgren 1960, Abrams and Dickmann 1982, Turner et al. 1997) that would be less likely to vary with distance from the stringer. At Damon, the advanced age of the burn (47 years) might also have led to a more homogeneous community composition following canopy closure, which typically occurs in jack pine stands in the Lake States between 20-60 years (Frelich 2002). Thus, effects of stringers on community composition are likely transient or at least reduced as post-fire regeneration matures and creates consistent conditions with distance from the stringer.

Comparison of dominant species in near and far plots using SIMPER analyses revealed that small differences in coverage of individual species may explain much of the variability at a given site. For example at JP Mack Lake, significant differences between near and far plots were largely explained by a 25.7% increase in Bryophyte coverage in the far plots. However, a 3% change in coverage of *Vaccinium angustifolium* accounted for 17.6% of the observed difference at the same site (Table 3). Further, the youngest site, Hughes Lake, was dominated by plants less common at any of the other sites (*Carex pensylvanica*, *Deschampsia flexuosa*, and *Vaccinium myrtilloides*). Other researchers have also suggested that minor differences in plant community composition in these xeric forests may have large impacts on successional trajectories. Abrams et al. (1985) showed that plant communities in this region were likely to follow diverging successional trends depending on small differences in post-disturbance plant establishment; small early differences in shrub cover, for example, could eventually lead to very different late-successional differences in plant community structure ranging from Pennsylvania sedge “meadows” to stand replacement by jack pines. Thus minor differences in species coverage at a site may have lasting ecological impacts, particularly where plant species diversity is generally low.

Microclimatic variability is an important factor in post-fire germination and establishment, and in persistence of surviving flora (Eyre and LeBarron 1944). Differences in mean afternoon temperature within, on the edge of, and outside of stringers (Figure 10) creates variability that may have important effects on germination rates or overwinter survival that vary by species, especially on the Grayling Outwash Plain where late spring frosts and short growing seasons are common (Albert 1995). At the edge of stringers, temperatures were higher than both the stringer itself and the plots farthest from the stringers. This temperature difference may be due to reduced wind velocity at the forest edge that allows the relatively still air to be heated more than the surrounding area (see Chen et al 1993). While our HOBO data for 16:00 describe high light intensity adjacent to stringers (Figure 10), there is temporal variability, and as the sun moves shade is provided to these plots by the stringers. Variations in light intensity adjacent to stringers may further facilitate variability in community composition, as shade-tolerant species persist within stringers while shade-intolerant species dominate the adjacent burned areas. The edge between stringers and the surrounding burned areas may offer an intermediate area between the two extremes. For example, *Vaccinium sp.* occurred with higher percent cover in plots nearest the stringer at all sites except Damon (where canopy-closure of jack pines established post-fire would likely make light levels less important). These blueberry species are typically described as shade intolerant (Humbert et al. 2007) but can be sensitive to full sun conditions, and have been documented to grow well in the partial shade of slash piles (Abrams and Dickmann 1982). In northern Lower Michigan, stringers appear to provide enough light variability to promote blueberry establishment in nearby plots. In this way, stringers may act as refugia for more shade intolerant species and affect variability in plant community composition at relatively small scales, and their effects on the overall diversity of the broader landscape should be investigated further (see Brosofske et al. 1999).

Jack pine density in the region has been shown to be highly heterogeneous, both historically and currently (Whitney 1987; Kashian et al. 2017). As expected, density of post-fire regeneration was significantly lower inside the stringers than in the burned areas at No Pablo and Mack Lake, and in the farthest plot at Damon. Our results do not suggest a significant effect of stringers on post-fire density of regenerating jack pines along our transects, but measurement variability was uniformly high, suggesting a need for further research at a smaller or more categorized scale (i.e. comparing overall less-dense stands with each other rather than comparing all stands regardless of stocking density). Careful consideration of the degree of cone serotiny in the stringer trees may also further address the variation in density measurements, as pre-fire serotiny in stands has been shown to affect post-fire density in other closed-cone coniferous systems (Tinker et al. 1994).

Post-fire regeneration of jack pines in the region typically occurs episodically in the first few years after stand-replacing fires. Episodic regeneration produces a mosaic of even-aged stands where fires have burned at different times, though uneven-aged distributions have also been documented in fire-origin jack pine stands (Abrams 1984). Further, Abrams (1984) found that post-fire seeding from remnant living trees can be a source of age heterogeneity in the region. Structural heterogeneity provided by the presence of the stringers themselves as well as variability in tree age resulting from seed dispersal from the stringer into burned areas each contribute to the overall structural diversity of the landscape. We detected effects of seeding from stringers on the age distribution of plots at Hughes Lake, No Pablo, and JP Mack Lake (Table 4), where plots nearer the stringers exhibited broader age distributions likely from prolonged seeding over time. Though a less useful metric than age distributions, mean age of jack pine was younger nearest compared to farthest from the stringers only at Hughes Lake and No Pablo. Neither mean age nor age distributions differed among plots at Mack Lake and Damon, each of which had stringers dominated by red pines that are less likely to seed into the surrounding burned areas. Therefore, in the younger burns and those with jack pine-dominated stringers, we conclude that sustained post-fire seeding from cones on live jack pine trees in the stringer affects the age of the regenerating forest. Irrespective of the long-term effect of the stringer seed source on the surrounding burned area, however, the stringers themselves clearly provide heterogeneity in age structure that is contrary to the even-aged, early-successional landscape often assumed by traditional jack pine management regimes in the region (MDNR 2015).

Kirtland’s warbler breeding habitat provided by jack pine plantations reaches peak warbler productivity between 5 and 20 years of age, and forest management in the region focuses on producing stands in this age range (MDNR 2015). In this study, the No Pablo burn best represents the target stand age for Kirtland’s warbler habitat at the time of sampling (12-13 years). Importantly, our results show that stringers had the greatest effects on sites sampled at No Pablo, where the age distribution was less even-aged adjacent to stringers, mean age was affected by prolonged seeding into the burned area, and stringers were found to be significantly less dense than the surrounding burned area (Table 4). In addition, plant community composition was dissimilar between plots near and far from the stringer (Figure 8) and distance from the stringer explained nearly 40% of the observed dissimilarity. We therefore found that the effects of stringers on post-fire vegetation are most prominent during precisely the age range targeted for Kirtland’s warbler habitat.

Currently, more than 88,000 ha are managed for Kirtland’s warbler habitat in the region, and the Michigan DNR, the US Forest Service, and the US Fish and Wildlife Service collectively have an annual objective to produce more than 1,500 ha for breeding habitat (MDNR et al. 2015). Kirtland’s warbler habitat plantations are therefore ubiquitous in the region, yet stringers, or structures that emulate stringers, are rarely included in plantations. Managers have recently recognized a need for management prescriptions that better emulate wildfire-regenerated forests, and as much as 25% of managed lands have been designated for experimental treatments in the latest Kirtland’s Warbler Conservation Plan (MDNR et al. 2015). Spatial heterogeneity created by clusters of living trees has been well documented in other fire-adapted systems (Arseneault 2001; Franklin et al. 2002; Larson and Churchill 2012), and retention of naturally-produced stringers or emulation of similar structures using variable-retention or similar harvesting techniques (Franklin et al. 1997) could be incorporated into experimental designs to provide the inputs of stringers on this intensely managed landscape.

Conclusions

More than purely biological legacies such as snags or individual surviving trees, stringers are remnants of the pre-fire ecosystem that retain important structural, compositional, and climatological elements. Along with the obvious effects of mature stringer trees on post-fire structure and stand-age, effects of prolonged seeding from the living stringer trees can more subtly influence the age distribution and community composition of the regenerating landscape. As has been demonstrated in many fire-prone ecosystems, heterogeneity can provide variable habitat for wildlife (Schieck and Song 2006; Cullinane-Anthony et al. 2014; MDNR 2015), and has the potential to promote resilience to future disturbances, both natural and anthropogenic (Churchill et al. 2013; DeRose and Long 2014; Seidl et al. 2014). Variability provided by stringers may be particularly important given the broad scale homogenization resulting from decades of extensive Kirtland's warbler habitat plantation management in the region (Donner et al. 2008; Spaulding and Rothstein, 2009; Tucker et al. 2016; Kashian et al. 2017). With the continued recovery of the Kirtland's warbler population, management agencies have an opportunity to develop new management practices that more closely emulate the patterns and processes of naturally-produced landscapes and may have important implications for future biodiversity.

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Table 3. Results of percent similarity analyses (SIMPER) showing the three species most responsible for contributing to differences in plant communities between the nearest plots (0.5 x and 1 x) and farthest plots (2x and 3x). No Pablo only had two species that contributed to differences, therefore only two are shown. (**) indicates sites where results of perMANOVA found significant differences between the near and far plots ($p < 0.05$). (*) indicates sites where distance explained at least 35% of the difference in plant communities ($R^2 > 0.35$) but significance at $p < 0.05$ was not achieved.

Site	**Species**	**Average Abundance (Percent Cover)**		**Percent Contribution**
		Near Plots	**Far Plots**	
Damon	*Lycopodium sp.*	11.25	5.25	27.5
Damon	*Vaccinium angustifolium*	4.25	6.00	11.3
Damon	*Pteridium aquilinum*	3.75	1.50	7.9
Mack Lake*	*Bryophyte*	16.25	40.29	35.4
Mack Lake*	*Vaccinium angustifolium*	26.00	14.29	11.8
Mack Lake*	*Pteridium aquilinum*	14.83	14.54	10.2
JP Mack Lake**	*Bryophyte*	9.17	34.92	31.4
JP Mack Lake**	*Vaccinium angustifolium*	20.17	17.17	17.6
JP Mack Lake**	*Quercus ellipsoidalis*	8.08	10.50	4.7
No Pablo*	*Vaccinium angustifolium*	17.73	12.25	40.7
No Pablo*	*Comptonia perigrina*	3.65	3.18	7.0
Hughes Lake	*Carex pensylvanica*	14.83	4.75	20.5
Hughes Lake	*Deschampsia flexuosa*	7.33	5.50	14.6
Hughes Lake	*Vaccinium myrtilloides*	6.92	3.75	11.6

Table 4. Structural metrics of burned areas. “Nearest” refers to plots 0.5 x the height of stringer trees, “farthest” refers to 3 x plots, and “stringer” refers to plots within stringers. JP Mack Lake represents jack pine-dominated stringers at Mack Lake only, whereas Mack Lake (all) represents all stringers sampled at Mack Lake, both jack pine- and red pine-dominated. The Anderson-Darling statistic represents comparisons of age distributions between the nearest and farthest plots only. Ages within stringers were significantly older than the surrounding plots at all sites ($p < 0.001$). (**) indicates significance at $p < 0.001$, (*) indicates significance at $p < 0.05$. Plot types (nearest, farthest, stringer) with different letters indicate significant differences ($p < 0.05$).

	Mean age: years (SE)	**Range: years**	**Anderson-Darling statistic (T.AD)**	**Mean density: stems/ha (SE)**
Hughes Lake			29.37 **	
Nearest	6.9 (1.2)	6.0		122 (53)
Farthest	7.8 (1.2)	6.0		100 (53)
Stringer	34.5 (1.3)	40.0		11 (75)
No Pablo			18.39 **	
Nearest	12.9 (0.1) ^{a} **	9.0		3510 (719) ^{b}**
Farthest	13.9 (0.1) ^{b} **	7.0		3513 (719) ^{b}**
Stringer	30.4 (0.2)	11.0		107 (1018) ^{a} **
JP Mack Lake			3.658 *	
Nearest	26.1 (0.7)	12.0		1000 (186)
Farthest	27.7 (0.7)	17.0		1325 (186)
Stringer	61.6 (0.8)	24.0		717 (251)
Mack Lake (all)			0.9652	
Nearest	28.2 (0.5)	15.0		1381 (119) ^{b} **
Farthest	29.0 (0.5)	19.0		1494 (119) ^{b} **
Stringer	56.3 (0.7)	56.0		761 (168) ^{a} **
Damon			-0.5723	
Nearest	38.1 (1.1)	16.0		1517 (268) ^{b} *
Farthest	38.5 (1.0)	26.0		1000 (268)
Stringer	63.0 (2.67)	52.0		500 (380) ^{a} *

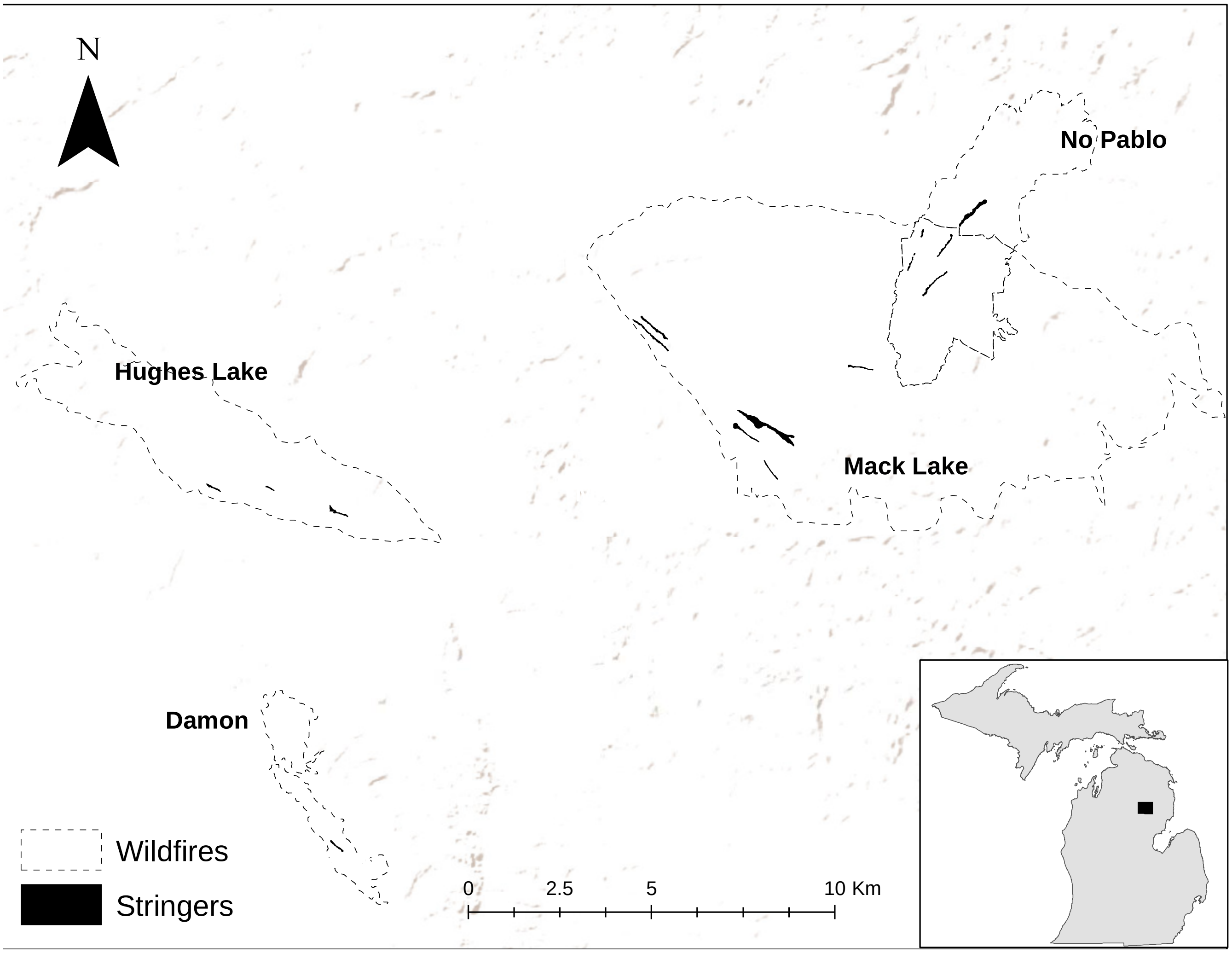


Figure 6. The four sampled burns and 15 sampled stringers in the study area in northern Lower Michigan, USA.

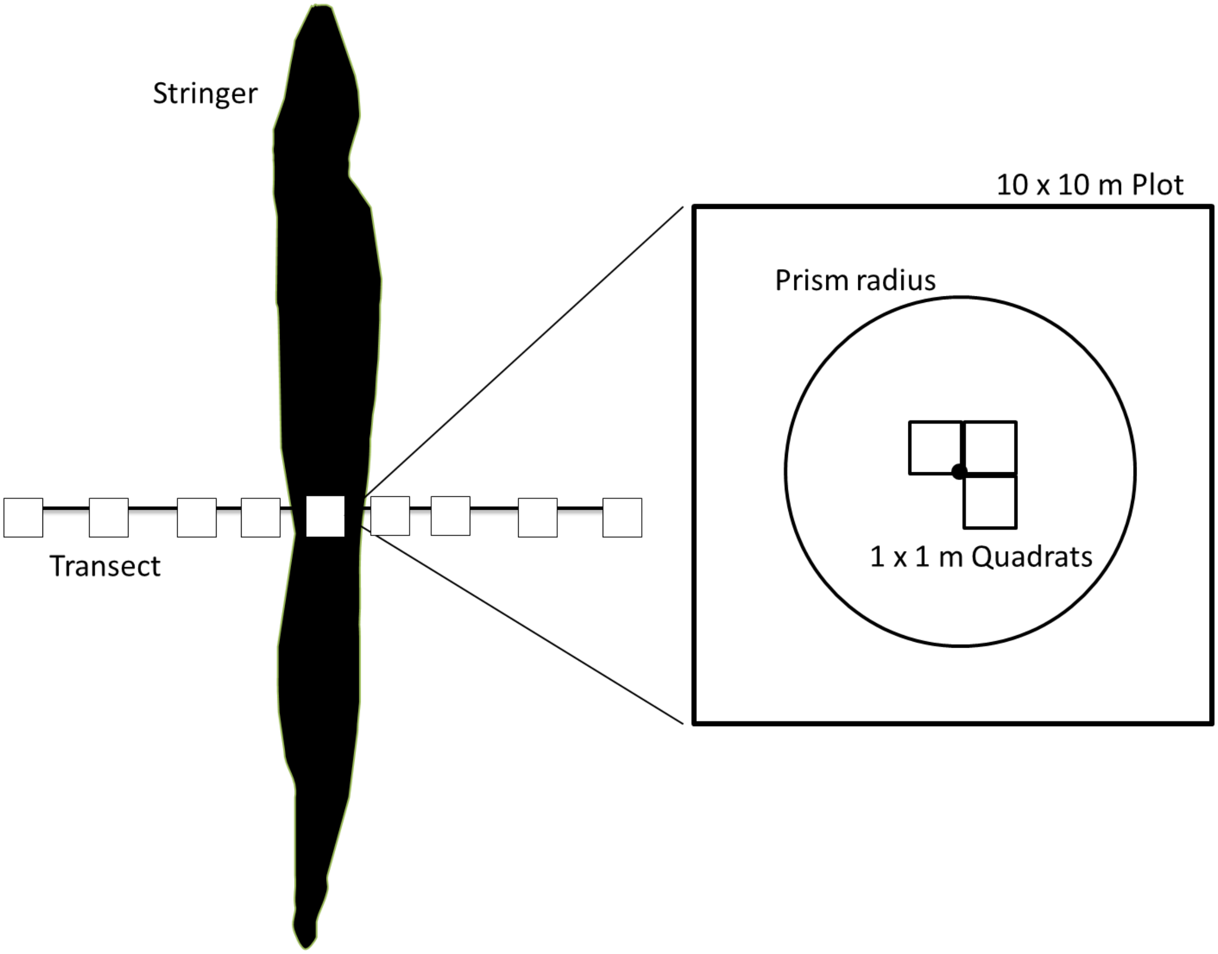
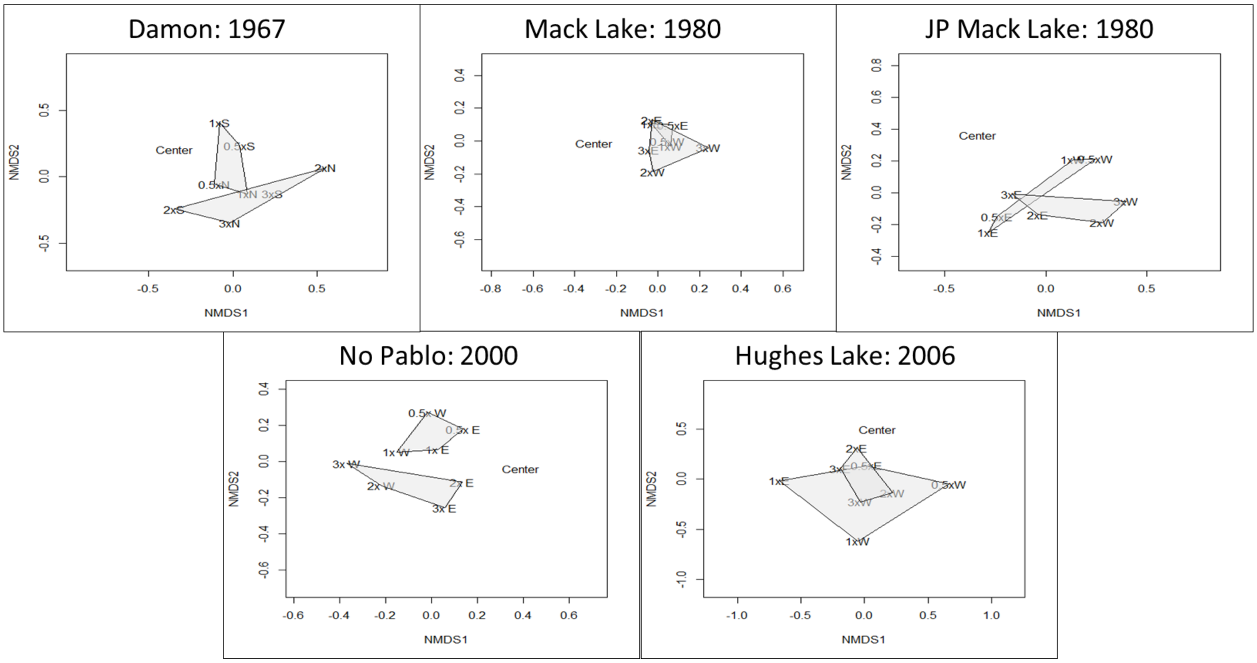


Figure 7. Schematic of sampling protocol used in the field. Plots along transects were sampled for density and over/understory composition, while quadrats within plots were sampled for aerial cover class of groundcover plant composition. Trees within the basal area prism radius were sampled for age (increment cores or counted whorls). Plots were arranged at intervals along the transect corresponding to 0.5, 1, 2, and 3 times the height of the dominant trees within the stringer, and a plot at the center of the stringer.



Damon: 1967

Mack Lake: 1980

JP Mack Lake: 1980

No Pablo: 2000

Hughes Lake: 2006

Figure 8. Non-metric multidimensional scaling using the Bray-Curtis dissimilarities of plant communities at each burn. Plots nearest the stringers (0.5x and 1x) and farthest from the stringers (2x and 3x) in both directions are enclosed with hulls, center points within stringers are separate. JP Mack Lake shows only the stringers at Mack Lake that were dominated by jack pine.

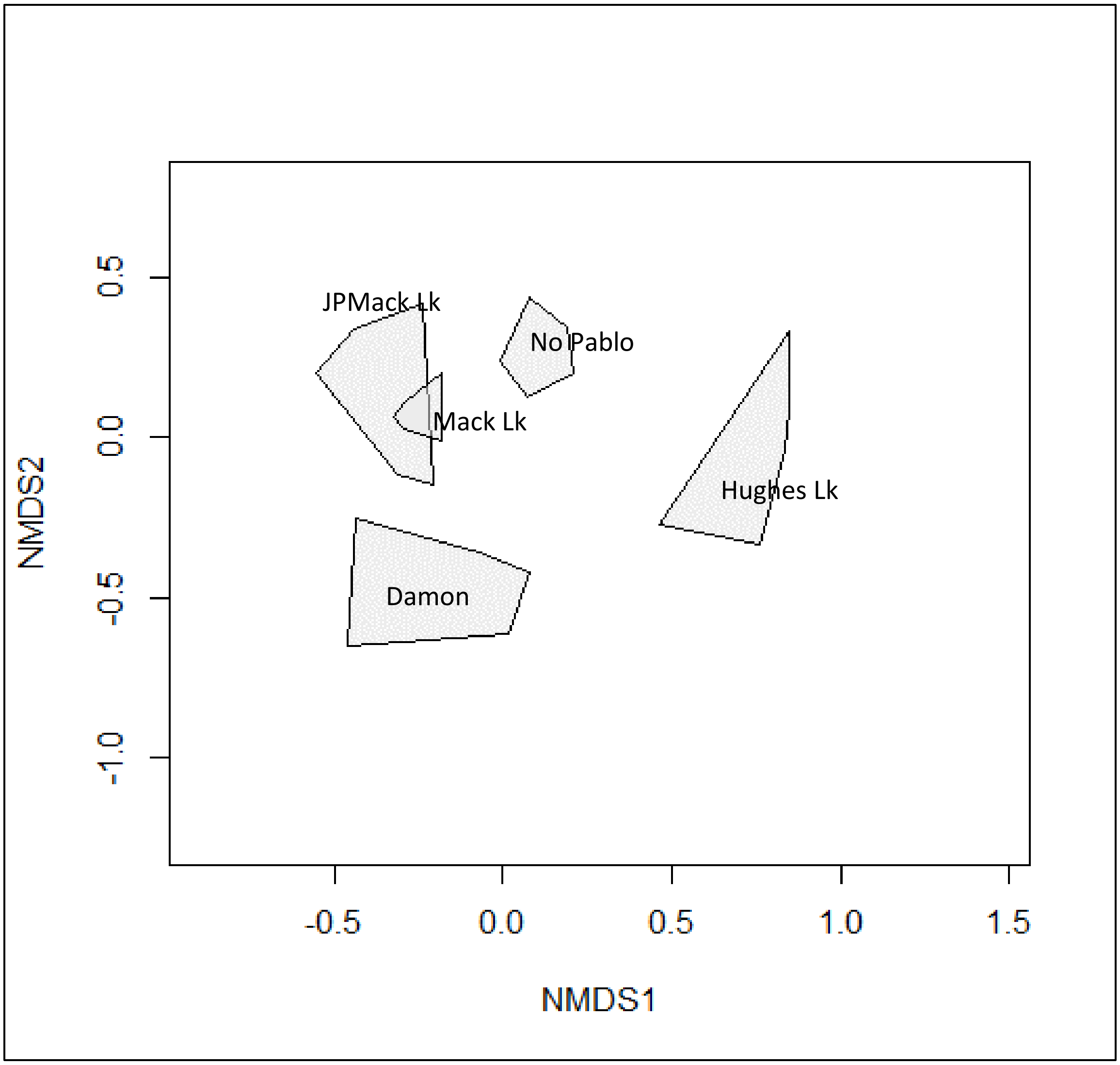


Figure 9. Non-metric multidimensional scaling using Bray-Curtis dissimilarities of all burns combined. Hulls are drawn around individual burns. JP Mack Lk shows only the stringers at Mack Lake that were dominated by jack pine.

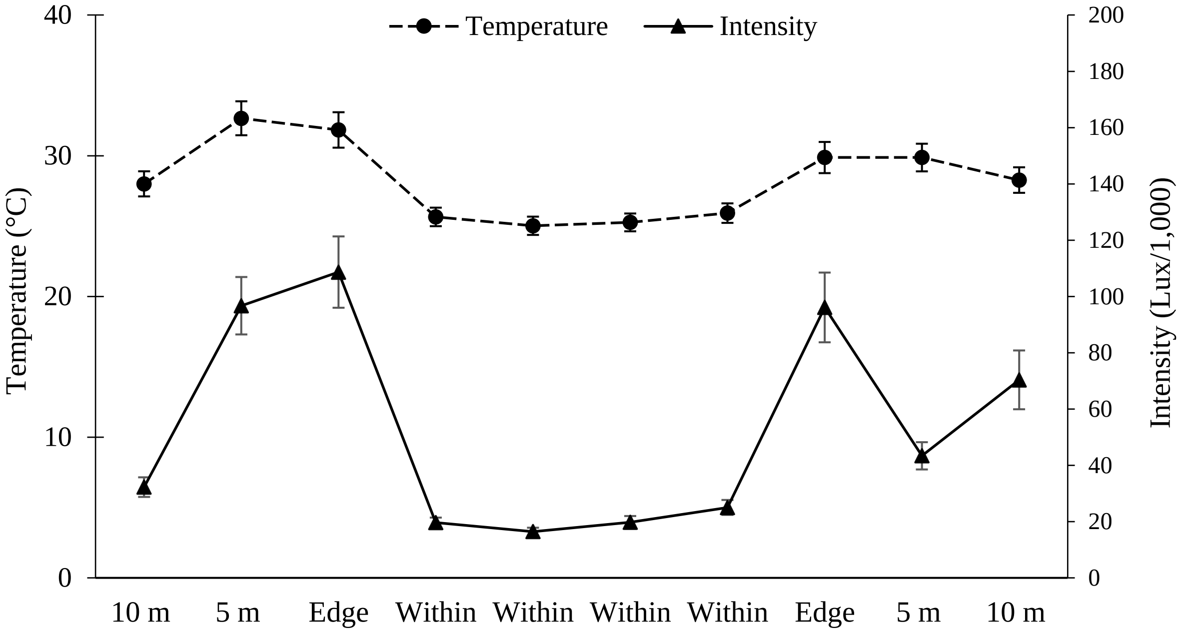


Figure 10. Average temperature and light intensity at 16:00 during the month of August, 2011 as sampled by HOBO sampling devices. Plots are labeled along transects from 10 m and 5 m outside a stringer, at the edge of and within a stringer, and again outside the other side of the stringer. Plots are displayed from West (left) to East (right). Error bars represent standard error.

CHAPTER 4 – INTERACTING EFFECTS OF WILDFIRE AND CLIMATE CHANGE ON THE DISTRIBUTION AND ABUNDANCE OF JACK PINE BARRENS IN NORTHERN LOWER MICHIGAN

Introduction

As effects of climate change become increasingly evident across temperate zones, forest management agencies are being charged with stewardship of landscapes that exist in a state of flux (Millar et al. 2007; Stephens et al. 2013). Along with changes in temperature and precipitation (Melillo et al. 2014), climate change has been predicted to cause changes in tree species distributions (Scheller and Mladenoff 2005; Iverson and McKenzie 2013) and fire regimes (Flannigan et al. 2009; deGroot et al. 2013; Flannigan et al. 2013). Investigating these effects may inform long-term management decisions, but effects of climate change on stand structure and landscape pattern have not been thoroughly investigated. This project examines effects of climate change on jack pine (*Pinus banksiana* Lamb.) barrens distribution and wildfire severity in northern Lower Michigan.

Jack pine barrens were historically common in northern Lower Michigan, where fire-adapted landscapes consisted of dense stands of even-aged jack pine fragmented by open, often large barrens dominated by sedges, grasses, and low shrubs more typical of savannas than forests (Whitney 1986; Houseman and Anderson 2002). Barrens in this region persisted within a complex structural mosaic that varied from sparse tree cover to closed-canopy jack pine forests resulting from a combination of site factors and disturbance legacies (Whitney 1987; Albert 1995; Leahy and Pregitzer 2003). This landscape structure was maintained by frequent, severe wildfires, but fire suppression and land cover changes in the 20th century altered the frequency and intensity of this structuring force (Cleland et al. 2004). The subsequent reduction in coverage of early-successional jack pine-dominated forests also reduced young stands used as breeding habitat by Kirtland’s warblers (*Setophaga kirtlandii* Baird). Kirtland’s warblers were listed as federally endangered in 1973, resulting in widespread planting of jack pine plantations to provide habitat. Currently nearly 80,000 ha of land are managed for Kirtland’s warbler habitat in northern Lower Michigan (MDNR 2015), and regional forest management has largely replaced open barrens with jack pine plantations (Donner et al. 2008). Jack pine barrens have been reduced by nearly 70% on state-owned land in the region since pre-European settlement largely due to fire suppression and Kirtland’s warbler management (Tucker et al. 2016). This reduction is significant because non-forested cover types are some of the most critically imperiled ecoregions globally (Hoekstra et al. 2005), and in northern Lower Michigan these open, non-forested areas may serve as critical refugia for rarer or threatened grassland and prairie species (Houseman and Anderson 2002; Tucker and Kashian 2018).

Jack pine barrens have been assumed to be characterized by severe fires occurring at intervals < 10 years (Frelich 2002), but there is relatively little evidence that fire frequency varies at the spatial scale that currently exists in barrens vegetation. While the mechanisms involved in the creation of barrens are not well understood, two hypotheses have been suggested that may be applicable to northern Lower Michigan. First, low-lying, colder areas on the landscape (“frost pockets”) may cause post-fire regeneration failure of trees, resulting in open conditions (Albert 1995; Kashian and Barnes 2000; Motzkin et al. 2002). Alternatively, a single fire event may produce barrens in areas where fire severity is particularly high, or where two or more fire events overlap spatially or occur at short intervals and cause tree regeneration failure (Radeloff et al. 1999). It is likely both these processes occurred on the historical landscape, creating the documented mosaic of open barrens and dense jack pine “thickets” (Whitney 1987; Albert 1995; Leahy and Pregitzer 2003).

In the context of climate change, interacting effects of barrens and wildfire behavior may be altered if climate change impacts the extent and function of barrens. Larger, more frequent fires predicted to accompany climate change in the region (Flannigan et al. 2000; Dale et al. 2001) may concomitantly increase the amount of fire-created pine barrens on the landscape. However, if barrens act as fuel breaks and fire severity is reduced by the lower-fuel cover type, an increased presence of barrens would be expected to act as a negative feedback, eventually reducing wildfire occurrence and severity across the landscape (Figure 11). Climatic interactions could also reduce barrens formation if warmer temperatures are accompanied by increased precipitation (Dale et al. 2001) or if increased temperatures moderate the deleterious effects of frost pockets on vegetation germination and establishment. Clearly, further investigation of the effects of climate change on jack pine-dominated ecosystems is needed.

In the absence of long-term ecological studies, General Land Office (GLO) public land surveys have been used successfully to reconstruct and characterize forests as they existed prior to European settlement (Whitney 1986; Schulte and Mladenoff 2001; Copenheaver and Abrams 2002). GLO surveys in northern Lower Michigan serve as a snapshot of the forest prior to significant land clearing, logging, land cover conversion, or other European influence. As such, GLO surveys have the potential to serve as an ecological baseline that may inform modern restoration efforts and management decisions (Schulte et al. 2002; Sturtevant et al. 2012). Specifically, GLO surveys may be useful to reveal the extent and arrangement of barrens across the historical landscape. Many federal and regional management strategies have cited the restoration of forest structure in fire-adapted ecosystems towards its historic range of variability as a priority, and local land managers in the region have shown interest in barrens restoration efforts (Solomon 1998; MDNR 2015). Thus, the inclusion of barrens into management areas, including those managed for Kirtland's warbler habitat, could allow managed areas to better represent natural landscape variability and structure.

Spatially explicit simulations of forest cover and disturbance processes via landscape models allow for quantification of landscape structure and disturbances at large spatial scales. Such models are therefore useful for predicting landscape changes due to land use, alteration of disturbance regimes, or global climate change (Scheller and Mladenoff 2005; Scheller et al. 2007; Duveneck et al. 2014). LANDIS-II (Scheller et al. 2007) is a landscape disturbance and succession model that uses empirically-derived parameters to model forest processes and patterns such as tree establishment, plant growth, and disturbances over time and space (Scheller et al. 2007; Sturtevant et al. 2009). User-specified iterations simulate the input landscape parameters over discrete time-steps to generate maps and output logs that report variables such as fire severity, fuel types, and vegetation age and distribution. LANDIS-II is particularly useful for investigating effects of climate change on forested and semi-forested landscapes because of its emphasis on simulation of multiple spatial processes and the interactions of these processes with spatial pattern (Scheller et al. 2007; He 2008).

Using comparisons between historical, current, and climate change-affected landscapes, this study examines the potential for climate change to alter fire severity and the distribution and arrangement of jack pine barrens on the landscape. I combined the largely unaltered, historical conditions referenced from GLO survey notes with the forecasting capabilities of LANDIS-II to examine the distribution of pine barrens on landscapes modeled with historical, current, and projected climate parameters to answer the following questions:

1) How are the distribution and arrangement of jack pine barrens affected by wildfire severity? I hypothesized that higher severity fires would yield larger, more aggregated, and more numerous barrens.
2) How might climate change affect fire severity, and how might that affect the distribution of barrens on the landscape? Factoring in the effects of climate change, I expected that overall fire severity would increase under the climate change scenarios. I expected that more severe fires would produce barrens at a higher rate, thus increasing the area of barrens. I further hypothesized that the more severe climate scenarios (those with greater predicted changes in temperature and/or precipitation) would produce the highest fire severities and greatest extent of barrens.

Methods

Study Area

The study area is situated on the Grayling Outwash Plain (Sub-subsection VII.2.2) within the Highplains Subsection (VII.2) of the Northern Lacustrine-Influenced Lower Michigan Section (VII) of Region II (NLM; 44º30’N, 84º30’W; Albert 1995). The Grayling Outwash Plain is a large physiographic system that covers approximately 1 million ha in northern Lower Michigan (Figure 12). Perched at a high elevation relative to the rest of the Lower Peninsula, the area has a continental climate with little lake-effect influence on either temperature or precipitation. Winters are cold, and frosts commonly occur well into the growing season (Albert 1995). Soils are predominantly excessively- to well-drained sands, and topography is overall gently sloping with scattered, steep (19-25 percent slope) ice-contact ridges (Albert 1995). The study area occupies 373,473 ha in the central region of the outwash plain and was explicitly chosen to encompass areas most commonly dominated by jack pine forests and barrens prior to extensive European settlement of the region (Comer et al. 1995).

The disturbance regime of the historical landscape was dominated by stand-replacing wildfires that burned in an approximately 60-year rotation (Cleland et al. 2004). This fire regime contributed to the persistence and dominance of a mosaic of stands of even-aged jack pine interspersed with open, dry prairies dominated by low shrubs (e.g. *Vaccinium sp.* and *Prunus pumila* L.) and sedges (*Carex pensylvanica* Lamb.). Sparsely-scattered red pine (*Pinus resinosa* Sol ex. Aiton) and multiple-stemmed, fire-affected northern pin oak (*Quercus ellipsoidalis* EJ Hill) were frequent co-dominants (Kashian et al. 2003b).

Though much of the historically-dominant forest community persists on the current landscape, the extent and distribution of barrens has been thoroughly altered by modern land management, including Kirtland’s warbler habitat management. I therefore used a historical landscape derived from General Land Office (GLO) public land survey notes as the starting point for landscape simulations. These surveys were conducted in the study area between 1837-1858, prior to widespread European settlement (Whitney 1987). Surveyors recorded the species and diameter (dbh) of trees at one-square-mile section corners, quarter corners, and meander trees that occurred along the line between corners, as well as bearing trees near the corners (Schulte and Mladenoff 2001). Areas of notable disturbance such as recent wildfire or windthrow were also recorded by surveyors. I used a digitized dataset of GLO points (Maclean and Cleland 2003) within the study area to determine spatially-explicit, historical forest community composition of the landscape. This allowed me to observe historical barrens distribution in the region, and to examine interactions between barrens and wildfire severity without the confounding factors of modern land use and management.

Description of climate data

The historical climate scenario was generated using climate estimates derived from PRISM (Parameter-elevation Regressions on Independent Slopes Model) data (PRISM Climate Group). These data are derived from available weather station readings and interpolated using climatologically-aided interpolation based on a combination of long-term average patterns and weather station readings. To reduce effects of anomalous data (e.g. a droughty summer or warm winter) I randomly selected readings of months between the years of 1895-1905 (B. Miranda USFS, *pers. comm.*). Climate data for the current climate scenario was compiled and averaged for the most recent 10-years of readings (2007-2017) using remote automated weather stations (RAWS; Western Regional Climate Center). Weather data from the weather station in Mio, MI was used, which approximates the center of the study area.

To project effects of climate change on the landscape I used two different general circulation models (GCMs) to generate predictions of future climate for the year 2099. I accessed the CMIP5 (Coupled Model Intercomparison Project) multi-model ensemble dataset to retrieve data from the Community Climate System model (hereafter CCSM4; CCSM version 4.1, National Center for Atmospheric Research) and the Canadian Centre for Climate Modelling and Analysis model (CanESM2; CanESM second generation, Climate Research Division). These specific models are both based in North America and are robust across scales, making them good models for representing the study area (Ahmadalipour et al. 2017). The CanESM2 model predicts higher temperatures on average and higher rates of precipitation, while the CCSM4 model predicts higher temperatures but little change in average precipitation (Table 5).

Future climate projections are dependent upon, and consequences of, current and future climate policies and behaviors. To investigate effects of climate change under various scenarios of continued greenhouse gas emissions, I used three representative concentration pathways (RCPs) for each GCM. RCP 2.6 represents the lowest emissions scenario, RCP 4.5 is a mid-low scenario, and RCP 8.5 reflects the highest emissions scenario (Stocker et al. 2013). RCP values represent the amount of radiative forcing (in watts per square meter) associated with greenhouse gas accumulation by year 2100, and many of the RCPs are roughly equivalent to previous scenarios developed in the IPCC Special Report on Emissions Scenarios (Nakicenovic et al. 2000). SRES scenarios describe geopolitical and technological conditions that produce changes in climate and can be more intuitive than RCPs. RCP 2.6 is the lowest emissions scenario and represents reduced carbon emissions over time combined with global carbon mitigation activities, which is not expected but offers a low value for comparison (Melillo et al. 2014). There is no comparable SRES scenario for RCP 2.6. RCP 4.5 is similar to SRES B1, which simulates introduction of clean, efficient technologies, global economic and environmental cooperation, and an accompanying slowing of greenhouse gas emissions. RCP 8.5 represents a scenario similar to SRES A1Fi, a "business-as-usual" scenario with continued dependence on fossil fuels (Nakicenovic et al. 2000). These scenarios represent a range of policy and technology decisions from inaction to global mitigation and are used here to present a range of outcomes that may influence future forest management.

Experimental Design

I used LANDIS-II v. 6 (Scheller et al. 2007) to model effects of climate change across the study area. LANDIS-II is a disturbance and succession model that enables researchers to model landscape-scale processes based upon detailed inputs including climate data (Table 5), species and site variables (Tables 6 and 7), and disturbance and community structure parameters. Extensions are added to the base model to address specific successional and disturbance pathways. I used the

Dynamic Fire and Fuels (v. 2; Sturtevant et al. 2009) and Age-Only Succession (v. 4.1; Mladenoff and He 1999) extensions to simulate wildfires and post-fire regeneration under the various climate scenarios. I used a size-based approach to simulate fires in the Dynmic Fire and Fuels model, which randomly draws from a lognormal distribution to determine the size of fires. The size distribution was determined from historical records of fires (Comer et al. 1995; Austin et al. 1999) and calibrated to reflect the appropriate fire regime. I used the Maximum Species Age output extension (v. 3.0; Scheller and Domingo 2018) to produce maps of species age for each timestep. All simulations were run for 200 years using a 10-year timestep and 50 m cell size.

The Dynamic Fire and Fuels extension allows for complex interactions between community composition, substrate, and wildfire severity. These qualities are particularly important in the study region, where the dominant jack pine cover type and sandy soils are fundamental in determining the disturbance regime (Whitney 1987). To provide input for disturbances, I used daily values of temperature (°C) and precipitation (mm) combined with wind speed and direction to calibrate fire weather databases for the Dynamic Fire extension. Wind speed and direction are not readily available in projected climate data, so I used weather station (RAWS) data from recent years to initiate the weather databases for all simulations. Fuel types for the extension followed the Canadian Fuels Behavior Prediction system (CFBP; Forestry Canada Fire Danger Group 1992) which are primarily based on community composition and age. The barrens fuel type was categorized as immature jack pine-dominated forest (fuel type C4 in the CFBP) but with fuel parameters that corresponded more closely to a treeless cover type, similar to the grassland fuel types in the CFBP (e.g. low build-up index and crown base height, high ignition probability).

The Age-Only Succession extension groups cohorts by species and age and is calibrated using probabilities of tree species establishment that vary by ecoregion. Variation in the probability of establishment (Pest) produces the observed landscape differences between climate scenarios. To generate species-specific establishment probabilities, I used historical, current, or projected scenario climate parameters within the Pest Calculator tool (Gustafson et al. 2010). The Pest Calculator combines climate data (monthly average maximum and minimum temperature and standard deviation in °C, average precipitation and standard deviation in cm) with species-specific information (nitrogen, drought, and cold tolerance, maximum and minimum growing degree days) and site-specific parameters (longitude/latitude, field capacity, wilting point, and base soil nitrogen) to produce probabilities of establishment for each input species.

Several tree species could not be simulated using the Pest Calculator. As barrens are mostly devoid of trees, I created a graminoid pseudospecies (“gram”) to represent the sedges, shrubs, and grasses dominant within barrens. I used typical characteristics of graminoids (mostly *C. pensylvanica*) in the study area: a short lifespan with early maturity and re-sprouting capabilities, very low shade and fire tolerance, and universal seed availability as seeding does not appear to restrict the range of barrens species in the region (Abrams et al. 1985; Table 2). For the gram pseudospecies I assumed the Pest of the historical landscape to be equal to that of jack pine, as the barrens community occupies a similar niche as post-fire, early-successional colonizers. Four other species that represented small numbers of trees in the records (< 2% of trees in the records each) were assigned establishment probabilities using a proportion of their relative occurrence within the historical records. I adjusted the Pest for those species for the various climate scenarios by adding the average change in Pest of co-occurring species for each scenario to the calculated historical proportion. Similarly, due to the difficulty in estimating input parameters for the Pest Calculator and the small size of the ecoregion (< 3% of the landscape), establishment probabilities for the entire lowland wet ecoregion were estimated using historical proportions of species distributions. For climate-caused species change in the lowland wet ecoregion I used the species change for the low outwash ecoregion as a proxy and adjusted based on the historical proportions accordingly.

Initial Communities

I established initial conditions of the LANDIS-II model using stratified categorization of digitized GLO meander and corner trees and the noted bearing trees (trees near the corner or meander that were also measured and recorded; Maclean and Cleland 2003). The point coverage was stratified into broad ecoregions that correlate closely with large glacial-origin landforms, with an added ecoregion for wet areas that react differently in the model (Table 7). I further stratified the points by community type, as determined by GLO surveyors (Comer et al. 1995; Austin et al. 1999). Finally, I stratified the data by unique species combinations of the corner or meander tree and the first recorded bearing tree and their age classes (class 0 = 0 years; class 1 = 1-10 years; class 2-7 in 20-year increments, and class 8 = trees >130 years). Tree ages were estimated using either a tree diameter growth model (Teck and Hilt 1991), or in the case of jack pine, by a dbh-age regression developed for the study area (Tucker et al. 2016). Areas with no trees but delineated as "very burned" or "recently burned" in the notes represented barrens and were categorized as gram pseudospecies at age class 1. This process produced a database of over 1,700 plots unique to ecoregion, forest type/community, species, and age combinations. I then input the database into the Random Landscapes Tool add-in (Fox 2017) for ArcMap 10.2 (ESRI 2011) to create a raster surface which was then used as the initial community for LANDIS-II simulations.

Simplifying Assumptions

To perform simulations on the study landscape I was required to make a number of simplifying assumptions. First, I started each scenario with identical initial communities modeled after historical conditions. This does not reflect current land use in the region but allowed me to examine changes to the landscape brought about only by the climate scenario and not relating to modern land use. Secondly, I implemented projected climate parameters as a constant condition using climate at year 2099 and did not gradually ramp-up the parameters over time. This assumption generated conditions of climatic equilibrium but may not perfectly capture subtle changes over time. Further, although future projections often predict increased occurrence of severe weather and lightning (Price and Rind 1994; Flannigan et al. 2006), I did not alter fire weather conditions for the various scenarios because of the uncertainty and variability of those projections. Therefore, to provide the most robust data, I used current fire weather data (wind speed and direction) and historical values for ignitions and area burned in the models for all climate scenarios. Given the relative homogeneity of the site and the edaphic conditions that maintain many community and disturbance regime characteristics, it is likely these assumptions are valid and do not consequentially affect the outcome of the simulations.

Data Analyses

Fire severity is output both as a table and a raster surface, which allowed me to compare differences not only in barren coverage but also in their spatial arrangement. To answer the question of how the distribution and arrangement of barrens are affected by wildfire severity, I visually inspected fire severity maps output from the model runs and compared the distribution of pine barrens fuel type (which approximates community composition) in the following timestep. Areas of overlap of increasing levels of fire severity were quantified using the combine raster tool in ArcMap. This was performed at 50-year intervals on all 3 replicates of the historical landscape only. The replicates were averaged and I calculated the percent of the landscape converted to barrens by varying fire severity classes (1: burned but no cohorts damaged; 2: ≤ 20% of cohorts killed; 3: ≤ 50% of cohorts killed; 4: ≤ 85% of cohorts killed; 5: all cohorts of all species killed).

To assess how climate change may affect fire severity and barrens distribution, I averaged the output data by timestep from 3 replicates per model for each climate scenario. I statistically compared mean fire severity for each scenario using an independent samples Kruskal-Wallis test (Kruskal and Wallis 1952) and Dunn-Bonferroni *post hoc* pairwise comparisons (Dunn 1964), as assumptions of normality could not be met for a parametric test. Stand-age for the landscape was determined using the Maximum Species Age output maps at year 200. As the barrens pseudospecies has a short longevity (15 years), I used the stand age of jack pines for my analyses to assess changes to the cover types most closely associated with barrens. I performed a Shapiro-Wilk test (Shapiro and Wilk 1965) on mean stand age by scenario. I found no meaningful violations of normality and confirmed homogeneity of variances using Levene's test (Levene 1960), then compared means using a one-way ANOVA and *post hoc* Tukey's HSD (Tukey 1977). Fire rotation can be calculated from output tables of disturbance size and frequency by dividing the total landscape area by the summed area burned per year to give the fire rotation in years. I confirmed normality and homogeneity of variances of fire rotations, compared means between scenarios using one-way ANOVA, and analyzed pairwise comparisons using Tukey's HSD test. The assumption of homogeneity of variances was not met for the number of fires burned in each scenario, so I used Welch's test (Welch 1951) to compare means, and a nonparametric Games-Howell test (Games and Howell 1976) for pairwise comparisons.

I used FRAGSTATS v3.3 (McGarigal et al. 2002) to examine changes in the spatial arrangement of the landscape. I calculated the number of patches, percentage of landscape, mean patch size, and percent like adjacencies for the pine barrens fuel type (which correlates to the cover type) at year 200 for each of the climate scenarios and statistically compared them using ANOVA or Welch's test, followed by post-hoc comparisons (Tukey or Games-Howell). In the same way I compared the extent of the barrens fuel type at year 200 on output maps of the various scenarios to determine how climate might affect the amount of barrens found on the landscapes. All statistical analyses were performed using SPSS (v. 25; IBM Corp. 2017), alpha = 0.05.

Results

Wildfire severity and barrens abundance

The proportion of wildfires in the historical scenario that produced barrens in the following timestep varied by fire severity. The severity class with the highest proportion of fires that produced barrens was class 4 - 83.3 % of fires in that severity class produced barrens in the subsequent timestep, closely followed by class 5, which produced barrens 82.5% of the time. Class 1 produced barrens just 4.0% of the time (Figure 13). Percent barrens cover differed significantly across the five fire severity classes ($F_{(4,\ 4.011)} = 922.392$, $p < 0.001$). Post-hoc tests showed that class 1 produced significantly fewer barrens than all other classes ($p < 0.02$ for all comparisons). Classes 4 and 5 produced significantly more barrens than both classes 1 and 2 ($p \leq 0.001$). The proportion of fires that produced barrens in the following timestep also differed significantly across climate scenarios ($F_{(7,\ 45.446)} = 11.290$, $p < 0.001$). Fires in the historical scenario produced barrens at the highest rate across severity classes (53.0%), significantly higher than both the CanESM 8.5 (6.5%) and CCSM 8.5 (13.7%) scenarios ($p < 0.01$ in all cases; Figure 13).

Mean severity was significantly different between the scenarios ($F_{(7,18227)} = 956.519$, $p < 0.001$), and was markedly higher in both rcp 8.5 scenarios than any other (Figure 14). Although the median severity was consistent among all groups except the rcp 8.5 scenarios, the variability of fire severity was higher in the projected climate scenarios compared to the historical and current scenarios (CanESM and CCSM; Figure 15). The average percent cover of barrens was significantly different among climate scenarios ($F_{(7, 16)} = 2.966$, $p < 0.05$). The scenario with the greatest barrens coverage after 200 years of simulations was the current climate scenario (10.0% barrens overall), which was significantly higher than all other scenarios ($p < 0.01$). The CanESM 8.5 scenario had the least barrens coverage at 6.6% (Figure 6; $p < 0.01$). The historical scenario had a mean coverage of 8.1%.

Stand age

The average stand age of jack pine-dominated stands in the climate scenarios were overall statistically different ($F_{(7, 16)} = 5.511$, $p < 0.01$, Figure 17). Average stand-age ranged from 58.2 years in the current scenario to 66.2 years in the CanESM 8.5 scenario. The historical mean stand-age was 60.7 years. The CanESM 8.5 scenario was significantly older than all other scenarios except CCSM 4.5 ($p < 0.05$).

Fire rotation and number of fires

Fire rotations were statistically different between several scenarios (Figure 18). The shortest rotation was produced by the CanESM rcp 8.5 scenario (63.1 years) and the longest rotation was produced by the CanESM rcp 4.5 scenario (87.3 years). Overall, the projected climate scenarios were shorter than the historical and the current climate scenarios except for the CanESM rcp 4.5. The average number of fires per timestep was significantly different ($F_{(7, 201.938)} = 22.362$, $p < 0.001$) and differences between scenarios were most pronounced in the business-as-usual, rcp 8.5 scenarios (Figure 19).

Landscape metrics

Landscape metrics suggest differing landscape composition and configuration among scenarios (Table 8). The number of patches representing barrens varied across the scenarios, with the fewest patches in the historical scenario and the most patches in the CanESM 2.6 scenario. Mean patch sizes also varied, from 1.7 ha in the CanESM 8.5 scenario to 3.3 ha in the current climate scenario. Percent cover of the landscape represented by barrens varied slightly between 2.1% in CanESM 8.5 and 4.2% in the current climate scenario. Barrens were much more aggregated in the historical scenario than any other (33.3%) and were most disaggregated in the CanESM 8.5 scenario (8.1%). Thus, the current climate scenario produced the highest coverage of barrens, which were the largest produced by the scenarios and among the most aggregated across the landscape. In contrast, the most extreme climate scenarios (rcp 8.5) produced the lowest coverage of barrens that were the smallest in area and least aggregated (Table 8).

Discussion

Climate change is expected to have profound effects on terrestrial ecosystems, and this study suggests that those effects may also be manifest in landscape structure in northern Lower Michigan. This study demonstrates effects of climate change on fire severity, post-fire barrens creation, and potential for future changes in tree establishment altogether. Overall, climate change may play a role in wide-ranging alterations to the region.

Climate-wildfire-barrens interactions

Changes in climate can have direct effects on wildfire severity through increased temperatures and/or precipitation, and my simulations showed evidence of these effects in the highest emissions scenarios. Mean severity was higher and variability in fire severity was greater in the 8.5 rcp scenarios than in all other scenarios. The total coverage of barrens on the historical landscape in the study area was not necessarily affected by the severity of wildfires however, as the scenarios with the shortest fire rotations (CCSM 2.6 and CanESM 8.5) did not have the greatest extent of barrens coverage (Figures 16 and 18). Furthermore, the scenarios with the highest average fire severity and greatest number of fires (both rcp 8.5 scenarios) did not have large amounts of barrens coverage (Figures 14, 15, and 19). Higher fire severity did produce barrens coverage at a higher rate than lower severity fires, but those interactions were not maintained in the more extreme scenarios, and barrens coverage was low in both rcp 8.5 scenarios (Figure 13). These results suggest that other factors are at least as important as fire severity in barrens establishment.

Fire rotation is likely as important as severity of individual fires, as repeated fires in close succession would likely lead to jack pine regeneration failure and subsequent barrens establishment. Fire rotations were qualitatively shorter on all projected scenarios except CanESM 4.5, where they were significantly longer (Figure 18). The variability of the historical and current scenarios likely precluded finding significant differences, but a trend toward shorter rotations in several scenarios might suggest increased barrens coverage under those scenarios (CCSM 2.6, CCSM 8.5, and CanESM 8.5). That increased coverage of barrens was not associated with these scenarios, and in fact CanESM 8.5 had significantly lower coverage of barrens than the other scenarios suggest that fire rotation alone may also not be as closely associated with barrens creation as expected, at least when considering impacts of climate change.

Successful post-fire establishment (or lack thereof) is a critical factor in barrens creation, and local, short-term weather as well as longer-term climate are presumably important influences. My original conceptual model (Figure 11) described potential effects and feedbacks among climate, wildfires, and barrens distribution. I hypothesized that changes in climate (specifically increased temperature and precipitation) could reduce barrens coverage via increases in plant establishment. Many researchers have concluded that changes in species establishment and abundance will be caused by changes in climate (Iverson and Prasad 2001; Duveneck et al. 2014), and my data support those results. The significant reduction in barrens coverage described in Figure 3 suggests that barrens may convert to other cover types. Furthermore, jack pine stands in the CCSM 8.5 scenario were significantly older than all others except CCSM 4.5 (Figure 17), which may indicate reduced establishment of jack pines post-fire, especially considering the same scenario had a significantly short fire rotation (Figure 18). This shows that although fires burned more frequently jack pines did not regenerate enough to keep the stand age within bounds of the other scenarios. Further work is needed to investigate this interaction, but the occurrence of jack pine in the region, already at the southern limit of the range for the species, has been predicted to contract with climate change (Iverson et al. 2008), and closely-associated barrens cover types would likely be reduced in such conditions.

I conversely suggested that increased temperatures could result in more frequent and higher severity fires that could increase barrens coverage. Simulations showed that the scenarios with the highest average fire severity and short fire rotations (CanESM 8.5 and CCSM 8.5; Figures 15, 16, and 18) had more barrens than the historical scenario but they were smaller, more disaggregated, and comprised less of the overall landscape (Table 8). Therefore, effects of climate may have mixed effects on barrens distribution on the landscape. In the more extreme rcp 8.5 scenarios there appears to be a shift away from historically-consistent barrens arrangement. Furthermore, the percentage of fires that produce barrens were drastically reduced in these highest emissions scenarios, suggesting that under projected climate parameters the region could exhibit a tendency toward a reduction in overall extent and variability of barrens.

Are jack pine barrens transient ecosystems?

There is evidence that barrens may be transient in nature (Grossmann and Mladenoff 2007), appearing and disappearing from specific locations on the landscape over time. Consistent with this evidence, the model in this study simulated many barrens that persisted for only a few decades before infilling with trees. This transience is an important aspect of the landscape overall, as the frequent, high-severity fire regime creates a shifting mosaic of dense stands and open barrens and is an important consideration for land management in the region. Kirtland's warblers' extensive use of the region for nesting habitat emphasizes this as a long-term, historical characteristic of the landscape. Since warblers require young stands of jack pine < 25 years old for their nesting habitat, their presence reinforces the idea that the landscape was historically disturbed at least frequently enough to produce those stands. As forest management practitioners aim toward a sustainable solution to Kirtland's warbler management, changes in climate may inhibit or alter the regions' characteristic variability.

In contrast to the dynamic nature of barrens on this landscape, anecdotal evidence suggests that small glacial ice-block depressions on the landscape may maintain more stable barrens that persist for several decades. Frosts late in the growing season are most prominent in low-lying areas where cold air settles at night (Kashian and Barnes 2000; Kashian et al. 2003a; Walker et al. 2003), and establishment of tree species in these areas is reduced (Albert 1995; Kashian and Barnes 2000). Many inhibitory effects of frost pockets on tree establishment could be lessened given predictions of future warming temperatures, although it is possible that frost pockets may act as refugia for some species and cover types in the face of a warming climate. Despite the potential importance of frost pockets for barren persistence, detailed data to describe the processes in these small-scaled phenomena do not exist, and as such LANDIS-II cannot accurately them. Further data collection and investigation are necessary to determine what effects changes in climate may have on regeneration failure in these low-lying, persistent barrens areas.

Caveats and limitations

Landscape modeling allows examination of landscape changes in the context of projected climate scenarios and offers insights into future forest conditions, but some limitations of this approach are evident. In contrast to the size-based fire distribution approach I used to model fires in this study, a duration-based distribution for simulations is available within the Dynamic Fire and Fuels LANDIS-II extension. Although I calibrated the size-based option to approximate historical records of fire sizes (Comer et al. 1995), the duration-based technique allows for a more dynamic, fuels-based fire regime within the model. This study more simply describes changes in fire severity due to climatic changes (temperature and precipitation), provides a platform from which investigation of the duration-based simulations may proceed, and details effects of climate on fire severity and barrens distributions at a fundamental level. Future work using the duration-based calibrations will allow me to investigate ways these climate parameters affect fuels more specifically, and the interactions therein with subsequent fires. Furthermore, simulations using other LANDIS-II extensions may provide more insight into the interactions between fire, barrens, and climate change. For example, the Biomass Succession extension (Scheller and Mladenoff 2004) provides estimates of above-ground biomass, which likely provides a more complete description of barrens coverage. Uncertainties regarding the potential for replacement of jack pine-dominated areas by other species at the high rcp scenarios may be improved by incorporating species predicted to move into the region (see Iverson et al. 2008) into the model.

Overall, jack pine barrens are an important structural component of the landscape in northern Lower Michigan, but they have been reduced largely due to forest management designed to provide Kirtland’s warbler habitat. This study has shown that climate change may further reduce natural barrens creation, particularly in more severe, fossil-fuel intensive climate scenarios. If barrens are to remain a part of the landscape moving forward, conditions may require careful planning to recreate historical structure or otherwise conform and adapt to changing conditions such as those described in this study.

Table 5. Parameters utilized for the multiple climate scenarios including historical (PRISM data), current (RAWS data), and 3 RCP scenarios for both the Canadian Centre for Climate Modelling and Analysis (CanESM2), and the Community Climate System (CCSM4) models. The RCPs represent the value of radiative forcing associated with greenhouse gas emissions; higher RCP values depict higher emissions scenarios (see methods for full description). Values in parentheses represent standard error of the mean.

Scenario	**Mean Minimum Temperature (C)**	**Mean Maximum Temperature (C)**	**Mean Monthly Precipitation (cm)**
Historical	-0.5 (3.0)	11.8 (3.4)	6.6 (0.9)
Current	0.3 (2.7)	12.8 (3.2)	5.7 (0.7)
CanESM2 – rcp2.6	3.7 (2.4)	15.0 (3.1)	7.7 (1.4)
CanESM2 – rcp4.5	3.5 (2.6)	15.6 (3.6)	7.4 (1.1)
CanESM2 – rcp8.5	5.9 (2.7)	18.6 (3.7)	8.5 (1.4)
CCSM4 – rcp2.6	1.5 (2.3)	14.0 (3.1)	5.9 (0.8)
CCSM4 – rcp4.5	2.2 (2.5)	15.3 (3.6)	6.7 (0.7)
CCSM4 – rcp8.5	5.5 (2.2)	19.0 (3.2)	6.7 (0.8)

Table 6. Species life history parameters used for LANDIS-II simulations (Burns and Honkala 1990; Fire Effects Information System database).

Species	Longevity (yr)	Maturity (yr)	Tolerance		Seed Dispersal (m)	
			Shade	Fire	Effective	Maximum
Sugar maple	300	40	5	1	100	200
American beech	250	40	5	1	30	3,000
Paper birch	100	30	2	2	200	5,000
Jack pine	120	8	1	3	20	100
Red pine	200	40	2	4	12	275
E. white pine	400	40	3	3	60	210
Bigtooth aspen	90	15	1	1	500	5,000
N. pin oak [1]	90	35	2	3	30	3,000
Red oak	250	25	3	2	30	3,000
N. white-cedar	300	30	5	1	45	60
Gram - barrens pseudospecies	15	1	1	1	universal	5,000

[1] Parameterized as scarlet oak (*Quercus coccinea)* due to scarcity of records for N. pin oak.

Table 7. Classification of ecoregions and communities used to create initial communities for the LANDIS-II simulations.

Ecoregions	**Description**	**Dominant Species/Communities**[1]
Moraines	Sandy, well-drained soils; more nutrient-rich than the other glacial landforms	aspen/birch; jack pine; red/jack pine
Ice-contact	Steep hills; well-drained sand; low nutrient	white/red pine; red/jack pine; oak and jack pine barrens
Outwash	Flat topography perched at high elevation (320-400 m); excessively-drained sand and gravel; very low nutrient	white/red pine; red/jack pine; jack pine
Low elevation outwash	Flat topography at lower elevation (below 200 m); excessively-drained sand and gravel; very low nutrient	white/red pine; jack pine; hemlock/wh pine
Lowland wet	Lacustrine or till-deposited clay-loam; somewhat poorly drained; nutrients status varies	lowland conifers

[1] Communities based upon GLO notes (Comer et al. 1995; Maclean and Cleland 2003)

Table 8. Landscape metrics of jack pine barrens calculated for the climate scenarios. "Number of patches" is the number of discernable barrens in the study area; "% Cover Barrens" is the proportion of the study area occupied by barrens; "Mean patch size" is the average size of barrens; and "Percent Like Adjacencies" is a measure of the degree of aggregation of barrens, with higher values representing higher aggregation.

Scenario	**Number of Patches**	**% Cover Barrens**	**Mean Patch Size (ha)**	**Percent Like Adjacencies**
Historical	26,147	3.3	2.6	33.3
Current	42,423	4.2	3.3	26.9
CanESM2 - 2.6	55,935	4.0	3.1	18.2
CanESM2 - 4.5	45,055	3.4	2.7	20.2
CanESM2 - 8.5	47,352	2.1	1.7	8.1
CCSM4 – 2.6	50,999	3.2	2.5	16.1
CCSM4 – 4.5	44,086	3.5	2.8	21.7
CCSM4 – 8.5	52,130	2.8	2.2	12.2

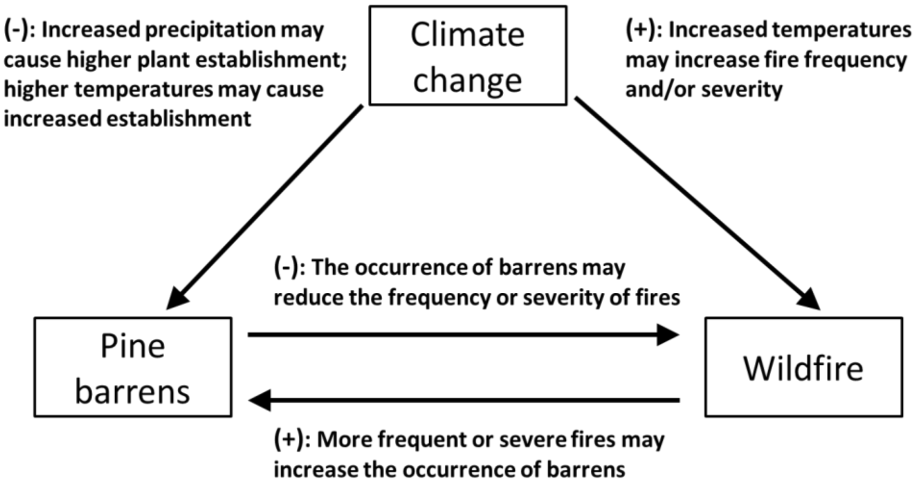


Figure 11. Conceptual diagram to describe the feedbacks between wildfire, climate change, and barrens distributions.

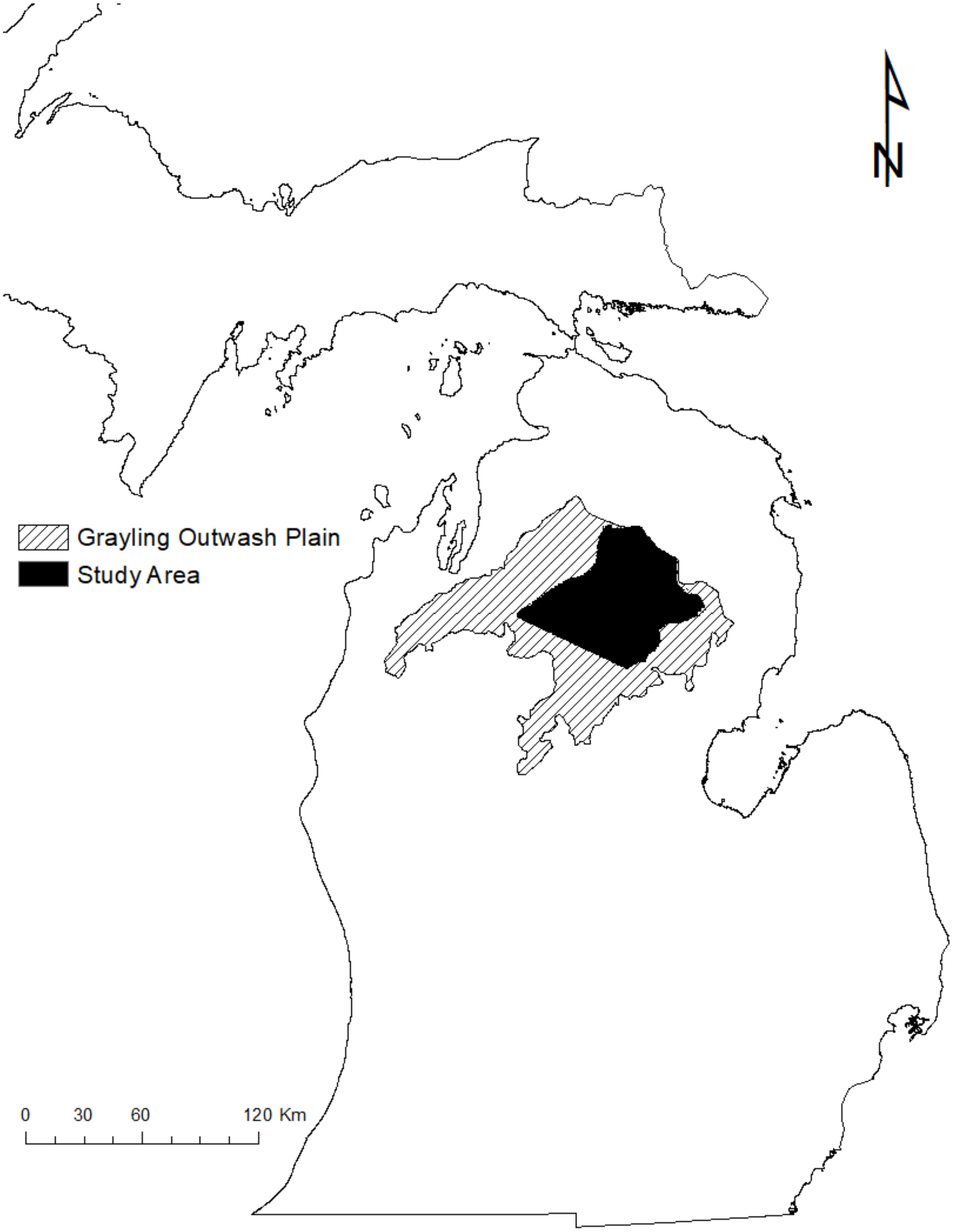


Figure 12. The study area in northern Lower Michigan, U.S.A. encompasses over 370,000 ha within the Grayling Outwash Plain and is dominated by jack pine stands and open barrens.

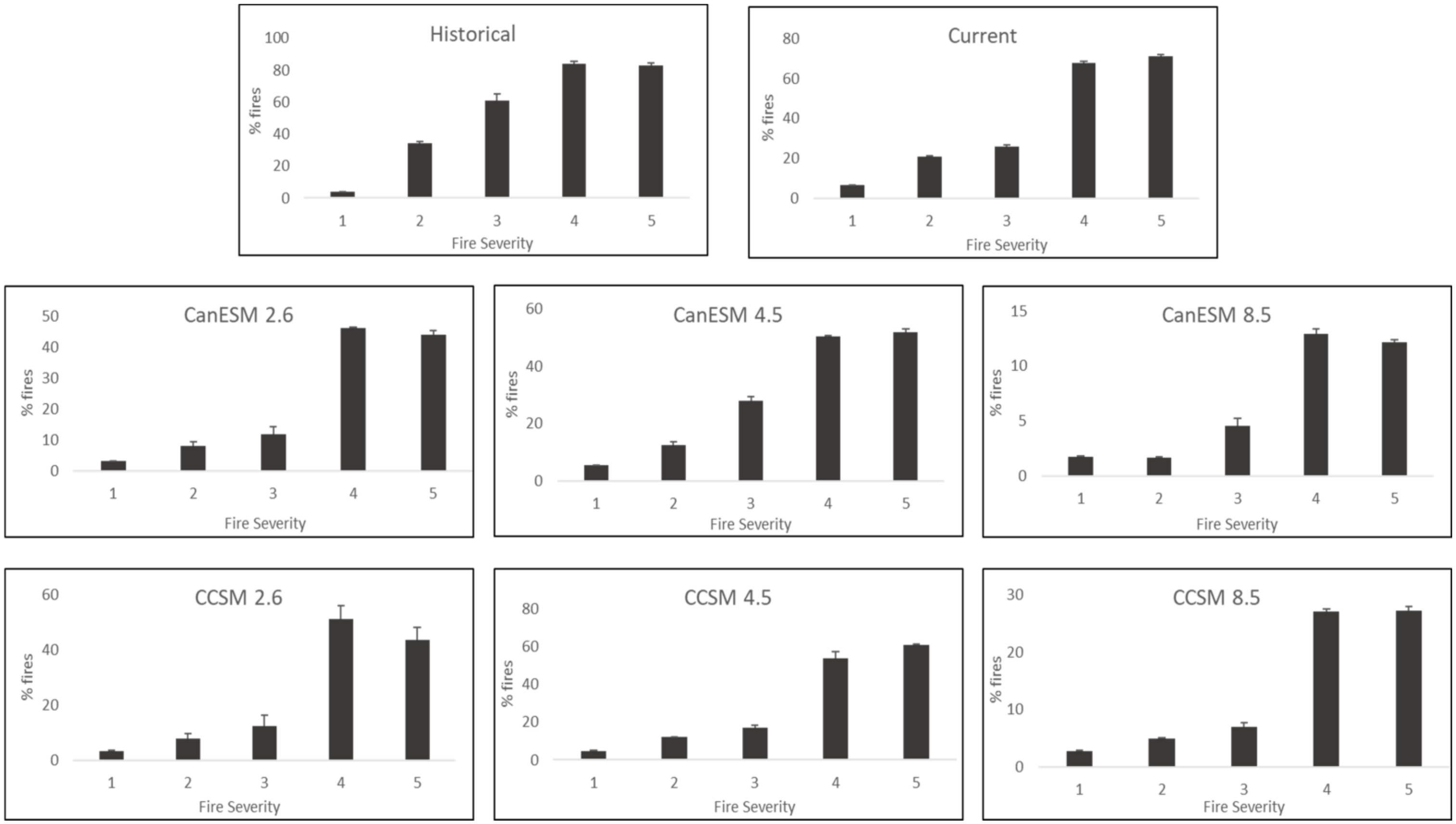


Figure 13. Percentage of fires that produced barrens in the following timestep, categorized by severity class. Classes are: 1: burned but no cohorts damaged; 2: ≤ 20% of cohorts killed; 3: ≤ 50% of cohorts killed; 4: ≤ 85% of cohorts killed; 5: all cohorts of all species killed. Both 8.5 rcp scenarios had significantly fewer barrens produced after fires than the historical scenario ($p < 0.005$). Note the different y-axes.

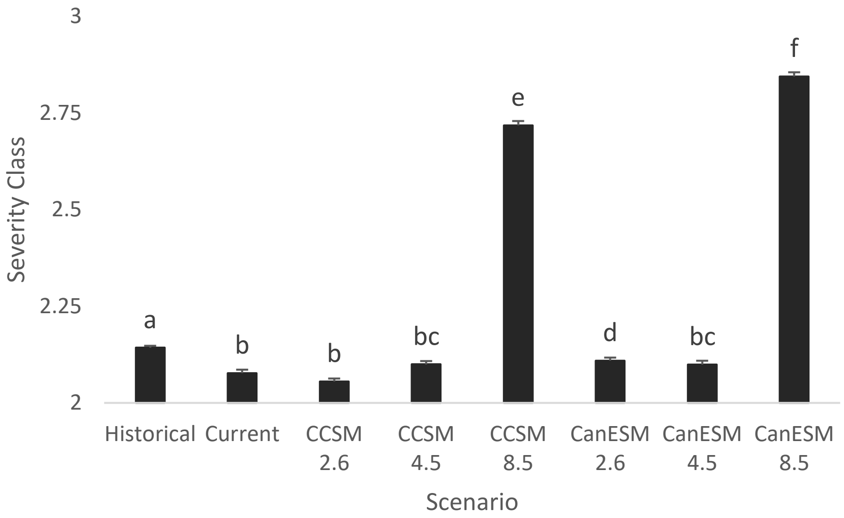


Figure 14. Mean fire severity by scenario. Bars with different letters indicate significant differences at $p < 0.05$. Fire severity was notably higher in the rcp 8.5 scenarios than any other climate scenario.

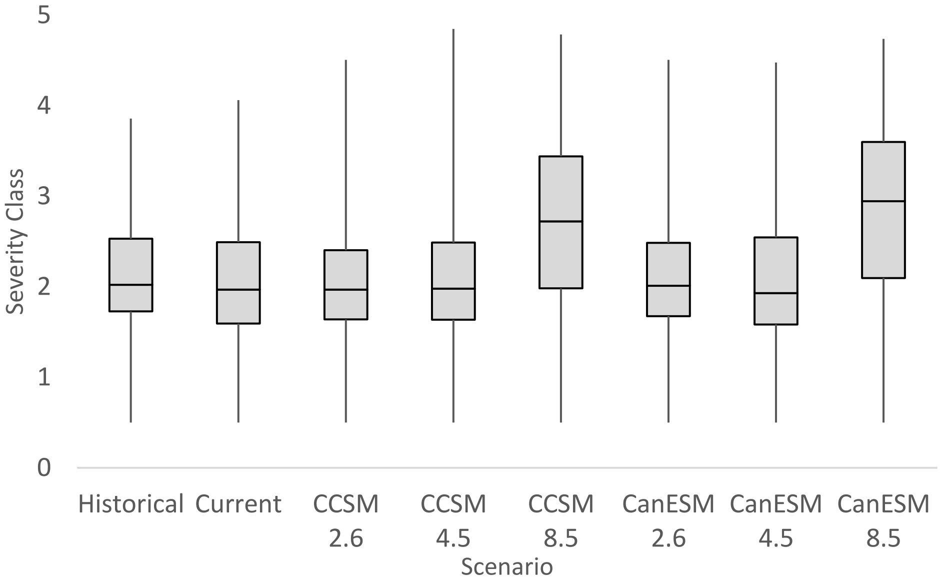


Figure 15. Median, maximum, and minimum severity of fires in each climate scenario. Fire severity was more variable in projected climate scenarios than in the historical and current climate scenarios.

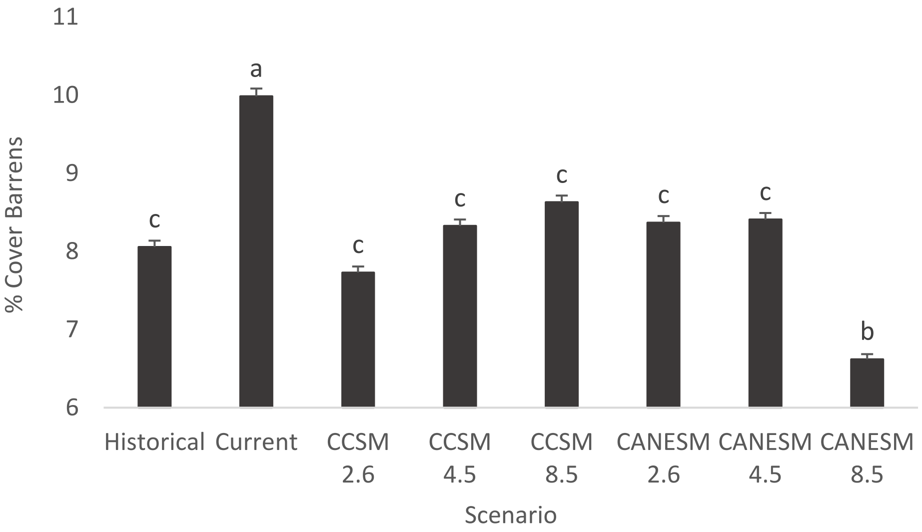


Figure 16. Percent cover of barrens simulated on landscapes modeled using the different scenarios. The CanESM 8.5 scenario produced the lowest coverage of barrens, and the current climate scenario the highest. Different letters represent significant differences ($p < 0.05$).

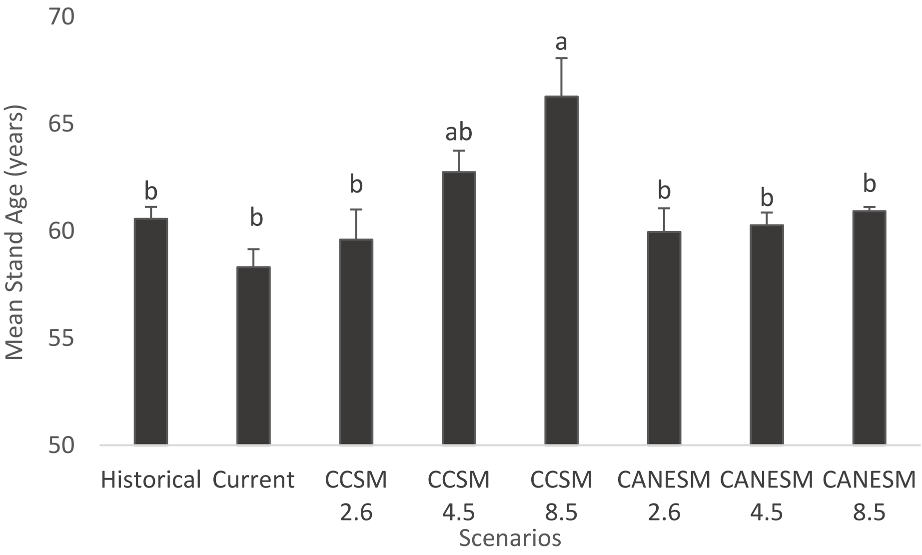


Figure 17. The mean age of jack pine stands in each climate scenario after 200 years of simulations. Only the CCSM 8.5 scenario differed significantly ($p < 0.05$) from the historical stand age. Different letters indicate significant differences.

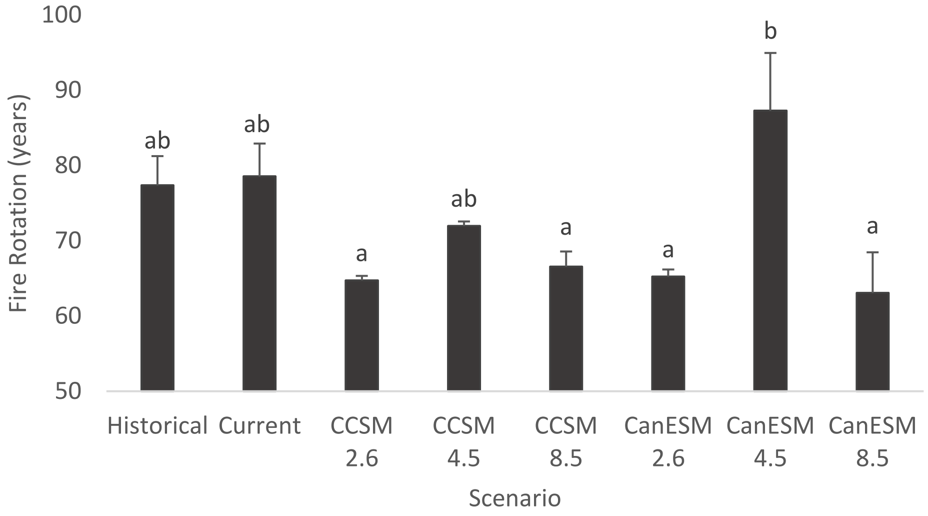


Figure 18. Fire rotation in years for each climate scenario. Bars with different letters are significantly different ($p < 0.05$). Several projected climate scenarios predicted a shorter fire rotation compared to the current or historical climate scenario except for CanESM 4.5.

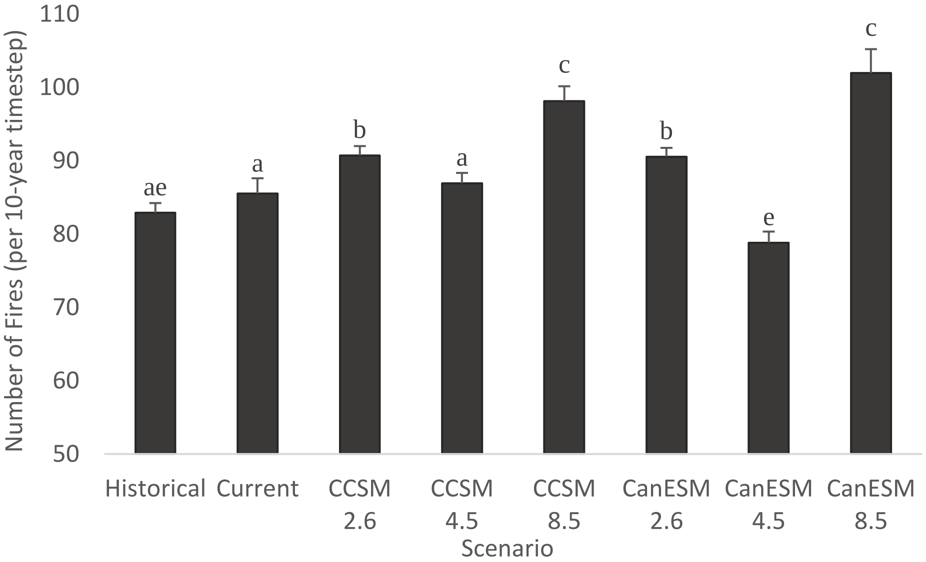


Figure 19. The average number of fires per 10-year timestep. Significant differences ($p < 0.05$) are indicated by bars with different letters. The average number of fires per timestep was highest in the rcp 8.5 scenarios, and lowest in the CanESM 4.5 scenario.

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ABSTRACT

EFFECTS OF DISTURBANCE ON JACK PINE (*Pinus banksiana* Lamb.) DOMINATED ECOSYSTEMS IN NORTHERN LOWER MICHIGAN: FOREST MANAGEMENT, WILDFIRES, AND CLIMATE CHANGE

by

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Jack pine-dominated forests in northern Lower Michigan were historically characterized by a frequent, severe fire regime that produced a patchwork of dense stands interspersed with open barrens. This structure also provided breeding habitat for Kirtland's warblers, a migratory songbird. Fire suppression management caused forests to become older and reduced Kirtland's warbler habitat, resulting in severe population losses. Kirtland's warblers were designated as endangered, and subsequent habitat management has produced homogeneous forests that lack historical structural and compositional diversity. Moreover, future climate may increasingly complicate forest and fire management moving forward. In a landscape defined by disturbance, novel disturbances or changes to the established regime may cause profound change.

To investigate effects of disturbance attributable to forest management we interpolated historical survey data to determine the age structure of forests prior to significant Euro-American settlement. We compared current and historical age distributions and found that Kirtland's warbler habitat management has significantly altered the age structure of the forests, resulting in younger, more homogeneous stands.

Naturally-produced structural variability has also been affected by Kirtland's warbler management. Living forest remnants (stringers) are common following wildfires but are often harvested for timber, and their effects on post-fire plant community composition and structure have not been examined. Our field-based project found that stingers affect post-fire landscape structure, plant community composition, and sapling age distributions, and as such should be preserved or emulated in landscape management.

Populated fire-prone areas must adapt wildfire management to future fire regimes considering global climate change. Jack pine barrens were historically common on the landscape but have been drastically reduced due in large part to Kirtland's warbler habitat management. We used LANDIS-II to model fire severity and barrens distributions under various predictions of future climate. We found that climate change caused increased fire severity and number, but reduced cover of barrens. Further, our model predicted large-scale losses of currently dominant species, perhaps signaling the development of novel ecosystems under extreme climate scenarios. As a whole, these projects provide context for applying historical variability and structure to future management decisions to maintain the unique character of this highly managed landscape.

AUTOBIOGRAPHICAL STATEMENT

I earned a Bachelor of Sciences form Wayne State University in May 2011 with a major in Environmental Sciences and a Geology minor. I then started as a Master of Sciences student in the Biological Sciences department in September 2011, and subsequently transferred to the Ph.D. program in 2013. During my time in graduate school I have given 6 talks at conferences, 3 talks at forest management meetings, 3 invited talks for local management teams and/or community groups, and 1 talk at a departmental retreat. I have also presented posters at conferences or meetings 7 times. I was awarded a Graduate Research Innovation Award from the Joint Fire Science Program and a Michigan Garden Club, Inc. scholarship in 2014, won a NASA-MSU professional enhancement award in 2017, won best student paper from the Natural History section at the Ecological Society of America annual meeting in 2016, and was awarded best student poster twice in 2014. Within the Biological Sciences Department, I have been recognized for exceptional service in teaching 3 times, for research once, and I also received the Stanley Ellis, Ph.D. Endowed Memorial Graduate Research Award in 2018. I have published 2 first-authored papers (2016, 2018) and was a co-author on a third (2017).

Throughout my time in grad school, I have worked hard to balance research and teaching with my responsibilities to my family, with varying levels of success. But between my two kids I have managed preschool through high school while working on my Ph.D. I have attended countless soccer games, karate lessons and tests, theatre performances, football games, wrestling tournaments, orchestra concerts, and innumerable other things that I can’t recall, often while working on the sidelines. I feel this has made me a more determined, although admittedly slower, scientist than I would have been without these complications. But I look forward to continuing to pursue both quality science and a full schedule of extracurricular events in the future.