

Pre-fire forest remnants affect post-fire plant community structure and composition



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ABSTRACT

The vegetation of jack pine (*Pinus banksiana* Lamb.)-dominated ecosystems in northern Lower Michigan is maintained by large, frequent, stand-replacing fires that often leave unburned forest strips (hereafter called “stringers”) which may persist for decades on the post-fire landscape. Regional fire suppression practices have altered the fire regime, however, and structural variability has been further disrupted by extensive plantations designed to provide habitat for the federally-endangered Kirtland's warbler (*Setophaga kirtlandii* Baird). Jack pine plantations lack stringers and other structural heterogeneity found in fire-regenerated forests, and older live trees that comprise stringers are often harvested for timber. However, ecological effects of stringers on adjacent vegetation patterns and processes are poorly understood. We hypothesized that stringers act as post-fire refugia for plant species and provide a prolonged jack pine seed source for reseeding the burned landscape, and thus should be considered for inclusion in ecosystem-based management plans. We sampled data from four post-fire areas of different times-since-fire to investigate effects of stringers on post-fire plant community composition and stand structure. We evaluated plant community composition and compared stand density and age distributions at increasing distances from stringers to determine stringer effects on post-fire regeneration. In several burned areas, ground cover plant communities farthest from stringers differed from those both adjacent to and within stringers; areas burned relatively recently (12 and 32 years post-fire) showed the most pronounced differences. Structurally, several burned areas displayed broader sapling age distributions closer to stringers, suggesting that mature trees in stringers act as a prolonged seed source to the adjacent burned area. Thus, stringers not only influence immediate post-fire heterogeneity by retaining living trees on the burned landscape, but they also continue to provide inputs to the regenerating post-fire forest. Because the Kirtland's warbler population has recovered, and the warbler's delisting from endangered status is imminent, our results may be useful for guiding future ecosystem-based, adaptive forest management practices and, more broadly, retention patterns in stand-replacing fire-prone areas.

1. 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 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). Such 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 (> 1000 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, Simard et al., 1983), 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 larger than the original management objective proposed by the Kirtland’s Warbler Recovery Team (MDNR, 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., 2010). 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, 2015).

This study examines the potential of stringers to affect post-fire jack pine 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.

2. Methods

2.1. Study area

The study area lies within the Grayling Outwash Plain (sub-sub-section VII.2.2), in the Highplains subsection (VII.2) of the Northern Lacustrine-Influenced Lower Michigan Section (VII) of Region II (NLM; 44°30'N, 84°30'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 punila* L.), and Pennsylvania sedge (*Carex pennsylvanica* Lam.) among other species of woody plants, forbs, and grasses (Kashian et al., 2003). 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 (Fig. 1): 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.

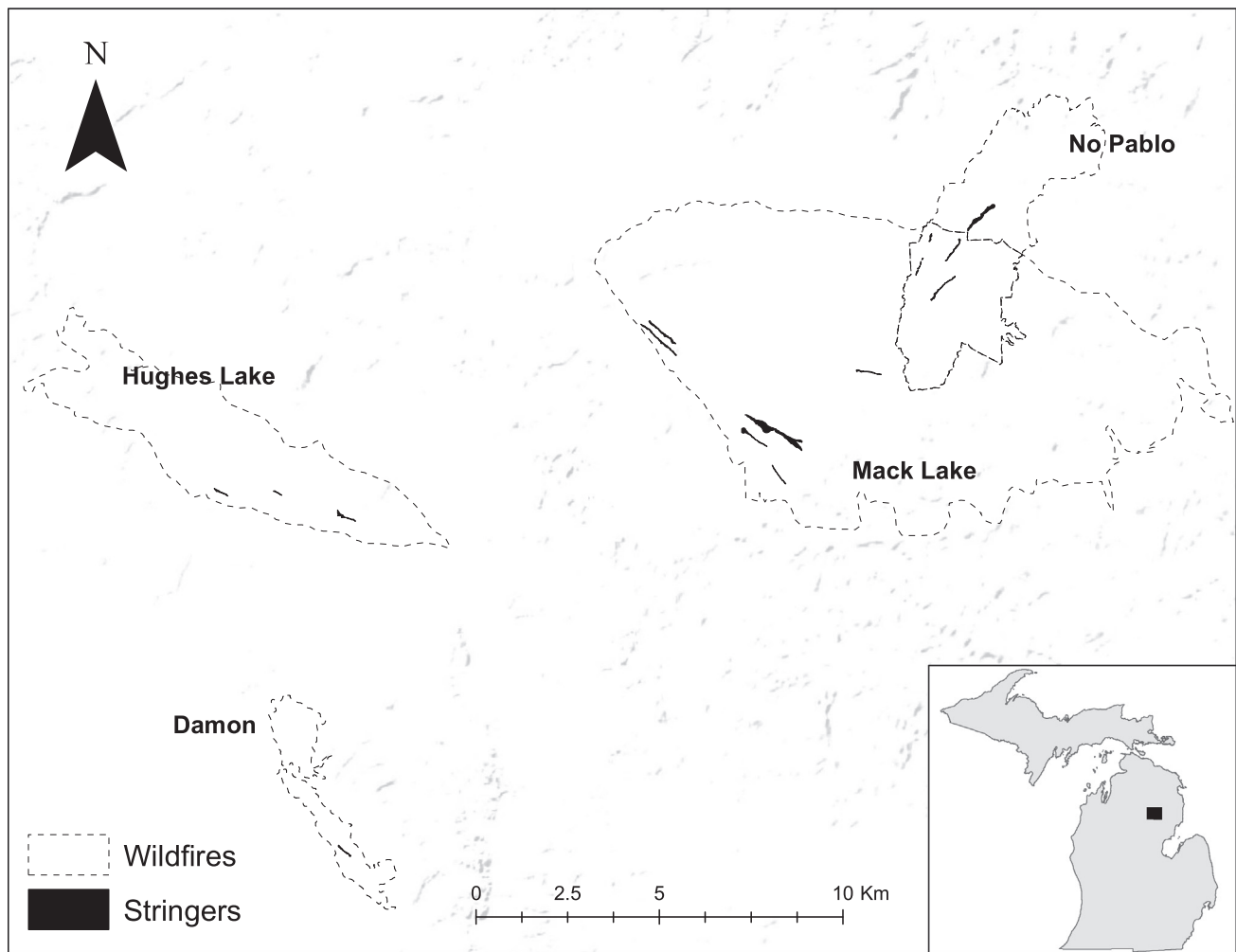


Fig. 1. The 4 sampled burns and 15 sampled stringers in the study area in northern Lower Michigan, USA.

2.2. Field methods

The experimental unit for the study was the individual stringer, sampled with three replicate transects per stringer. Along each transect we sampled 9–100 m² plots that consisted of a single plot in the center of the stringer and 4 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 (Fig. 2). 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 m² plot we counted overstory (> 9.0 cm diameter at breast height, DBH) and understorey (1.5–9.0 cm DBH) jack pines to calculate tree density (stems/ha). Overstorey trees were not included for the plots that fell within the stringer to provide an appropriate comparison to the regenerating forest within the surrounding burned area. We used a basal area prism (basal area factor = 10 ft²/acre, 2.3 m²/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 m² 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.

2.3. Data analysis

To determine the extent that stringers affect post-fire plant community composition, differences in community composition between plots nearest to stringers (0.5× and 1× the tree height of mature trees in the stringer) and farthest plots (2× and 3×) 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

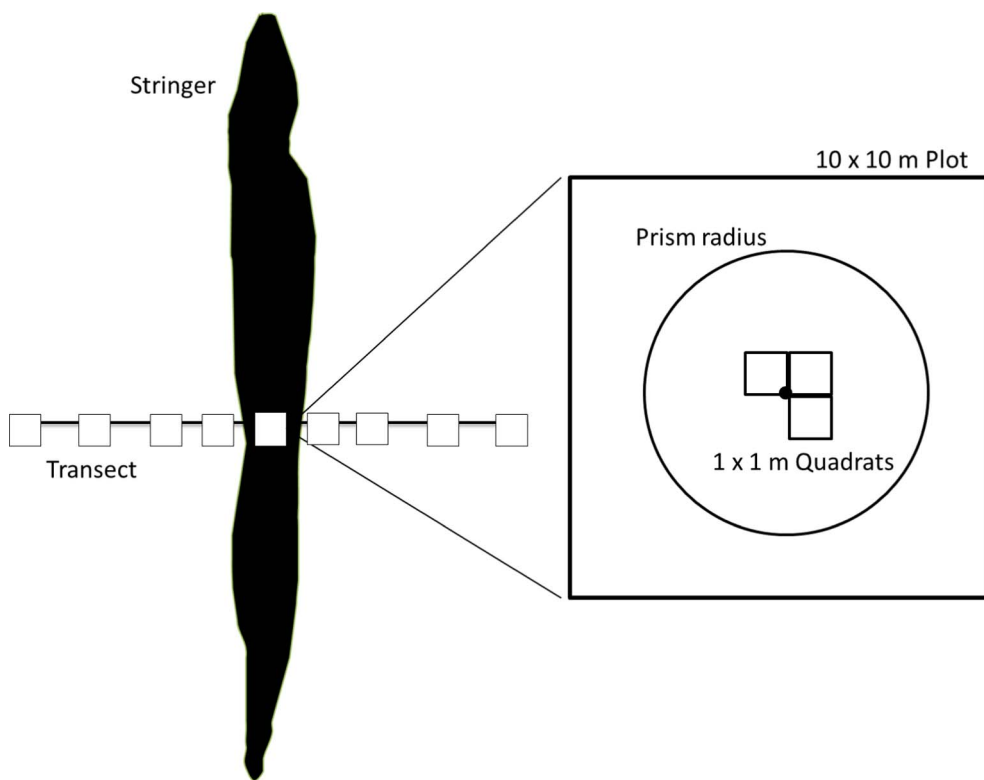


Fig. 2. Schematic of sampling protocol used in the field. Plots along transects were sampled for density and over/understory composition, while quadrats within plots were sampled for aerial cover class of groundcover plant composition. Trees within the basal area prism radius were sampled for age (increment 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.

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 ($0.5\times$ and $1\times$) and the farthest plots ($2\times$ and $3\times$), 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 (*fd*) 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 ($0.5\times$ and $3\times$ 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 and 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 because 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.

3. Results

3.1. Community composition

NMDS ordinations of the individual burns qualitatively showed dissimilarity of community composition between plots nearest to (0.5x and 1x) and farthest from (2x and 3x) the stringers in some of the burns. Dissimilarity of the nearest and farthest plots from the center stringer plots was 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 (Fig. 3). 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 ($F_{(2)} = 2.028, p < .05, R^2 = 0.403$); 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.

Table 1

Results of percent similarity analyses (SIMPER) showing the three species most responsible for contributing to differences in plant communities between the nearest plots (0.5x and 1x) and farthest plots (2x and 3x). No Pablo had only 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	<i>Lycopodium</i> spp.	11.25	5.25	27.5
Damon	<i>Vaccinium angustifolium</i>	4.25	6.00	11.3
Damon	<i>Pteridium aquilinum</i>	3.75	1.50	7.9
Mack Lake*	Bryophyte	16.25	40.29	35.4
Mack Lake*	<i>Vaccinium angustifolium</i>	26.00	14.29	11.8
Mack Lake*	<i>Pteridium aquilinum</i>	14.83	14.54	10.2
JP Mack Lake**	Bryophyte	9.17	34.92	31.4
JP Mack Lake**	<i>Vaccinium angustifolium</i>	20.17	17.17	17.6
JP Mack Lake**	<i>Quercus ellipsoidalis</i>	8.08	10.50	4.7
No Pablo*	<i>Vaccinium angustifolium</i>	17.73	12.25	40.7
No Pablo*	<i>Comptonia perigrina</i>	3.65	3.18	7.0
Hughes Lake	<i>Carex pensylvanica</i>	14.83	4.75	20.5
Hughes Lake	<i>Deschampsia flexuosa</i>	7.33	5.50	14.6
Hughes Lake	<i>Vaccinium myrtilloides</i>	6.92	3.75	11.6

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 1). At Mack Lake and JP

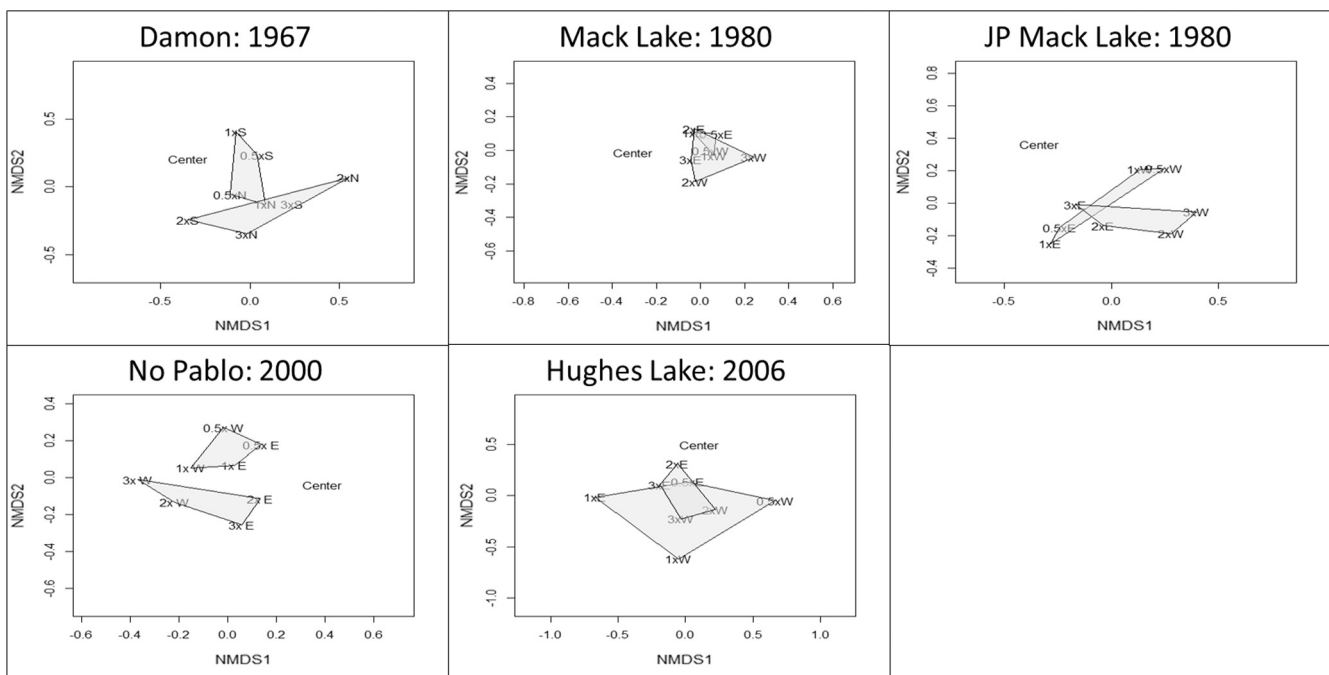


Fig. 3. Non-metric multidimensional scaling using the Bray-Curtis dissimilarities of plant communities at each burn. Plots nearest the stringers (0.5x and 1x) and farthest from the stringers (2x and 3x) in both directions, center points within stringers are separate. JP Mack Lake shows only the stringers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

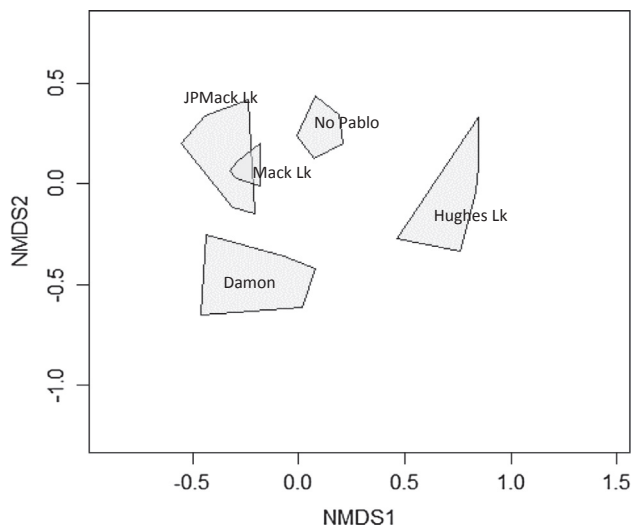


Fig. 4. Non-metric multidimensional scaling using Bray-Curtis dissimilarities of plant communities of all burns combined. Hulls are drawn around individual burns. JP Mack Lk shows only the stringers at Mack Lake that were dominated by jack pine.

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 aquilinum* (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 (Fig. 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.

3.2. 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 2). However, regeneration density along transects was not significantly affected by the sustained seed source (Table 2). 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 2). 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.

3.3. Microclimate

Temperature and light intensity were both significantly reduced by

Table 2

Structural metrics of burned areas. “Nearest” refers to plots $0.5 \times$ the height of stringer trees, “farthest” refers to $3 \times$ 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 ($p < 0.05$).

	Anderson-Darling statistic: T.AD	Mean age: years (SE)	Range: years	Mean density: stems/ha (SE)
Hughes Lake	29.37**			
Nearest		6.9 (0.2) ^{a,**}	6	122 (53)
Farthest		7.8 (0.2) ^{b,**}	6	100 (53)
Stringer		34.5 (1.3)	40	11 (75)
No Pablo	18.39**			
Nearest		12.9 (0.1) ^{a,**}	9	3510 (719) ^{b,**}
Farthest		13.9 (0.1) ^{b,**}	7	3513 (719) ^{b,**}
Stringer		30.4 (0.2)	11	107 (1018) ^{a,**}
JP Mack Lake	3.658*			
Nearest		26.1 (0.7)	12	1000 (186)
Farthest		27.7 (0.7)	17	1325 (186)
Stringer		61.6 (0.8)	24	717 (251)
Mack Lake (all)	0.9652			
Nearest		28.2 (0.5)	15	1381 (119) ^{b,**}
Farthest		29.0 (0.5)	19	1494 (119) ^{b,**}
Stringer		56.3 (0.7)	56	761 (168) ^{a,**}
Damon	-0.5723			
Nearest		38.1 (1.1)	16	1517 (268) ^{b,*}
Farthest		38.5 (1.0)	26	1000 (268)
Stringer		63.0 (2.67)	52	500 (380) ^{a,*}

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 (Fig. 5).

4. 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 (Fig. 4). 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 (Fig. 3). 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

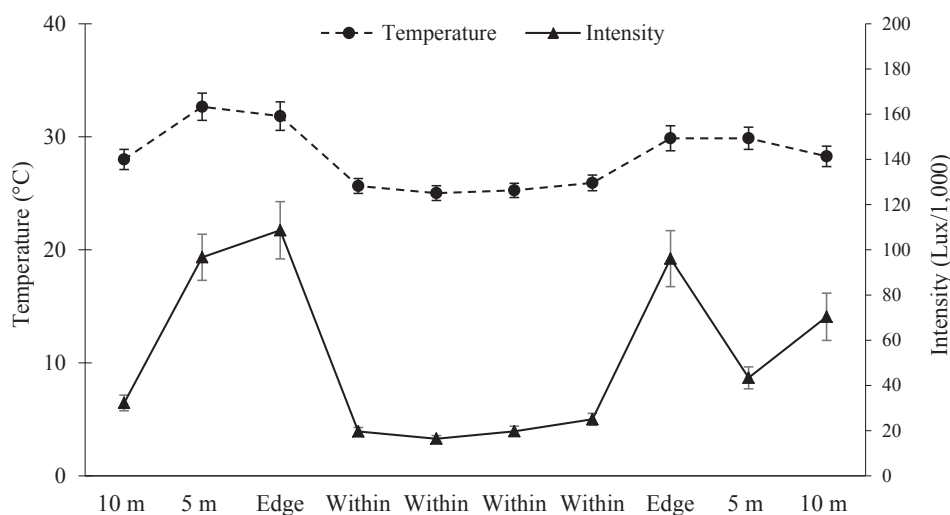


Fig. 5. Average temperature and light intensity at 16:00 during the month of August 2011 as sampled by HOBO sampling devices. Plots are labeled along transects from 10 m and 5 m outside a stringer, at the edge of and within a stringer, and again outside the other side of the stringer. Data were sampled using stringers at No Pablo. Error bars represent standard error.

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 and 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 1). 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 (Fig. 5) 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 (Fig. 5), 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 Brosfoske 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 2), 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 2). In addition, plant community composition was dissimilar between plots near and far from the stringer (Fig. 3) 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 Department of Natural Resources, the USDA Forest Service, and the US Fish and Wildlife Service collectively have an annual objective to produce more than 1500 ha for breeding habitat (MDNR, 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, 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.

5. 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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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2017.10.038>.

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