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Variability and persistence of post-fire biological legacies in jack pine-dominated ecosystems of northern Lower Michigan

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ABSTRACT

On the dry, flat, jack pine (*Pinus banksiana* Lamb.)-dominated ecosystems of the northern Lake States and eastern Canada, wildfire behavior often produces narrow, remnant strips of unburned trees that provide heterogeneity on a landscape historically shaped by stand-replacing wildfires. We used landscape metrics to analyze a chronosequence of aerial imagery to examine these "stringers" of mature trees within historical wildfires in northern Lower Michigan. Our major objective was to describe the natural range of variability of stringer patterns and their persistence and change during the fire-free interval. Field studies were then used to examine stringer composition and structural variability. Stringers were found to occur in all fires >1000 ha, in about one-third of wildfires >80 ha, but never in fires <80 ha, likely because of the lack of fire intensity on smaller fires that is necessary for stringers to be formed. Stringers were typically composed of many small, well-aggregated patches that represented 3–14% of the area within the burn perimeter, and stringer formation was relatively independent of pre-fire forest structure or composition. Stringer patterns changed mostly in the first decade after the fire that created them and then stabilized. Major changes that occurred in stringer patterns after this period were most often due to human activities, highlighting their natural persistence through the fire-free interval. The historical persistence and importance of these features also highlights their importance on modern fire-prone landscapes, particularly in northern Lower Michigan where a high proportion of land management is focused on jack pine plantations for breeding habitat for Kirtland's warbler (*Dendroica kirtlandii* Baird), an endangered species.

1. Introduction

Biological legacies are well documented as being important for forest ecosystem recovery following stand-replacing disturbances (Franklin et al., 2000). Post-disturbance legacies in forests are often considered to be small components of the prior vegetation, such as green trees, surviving plant parts (including propagules), dead wood, organic soil, and other surviving organisms (Harmon et al., 1986; Maser et al., 1988). Entire patches of mature forests that survive a disturbance are common on many landscapes and may be thought of as ecosystem-level biological legacies that provide refugia and allow persistence of many species while the surrounding landscape recovers from the disturbance (Perry and Amaranthus, 1997). Such patches are critical for the continuity they provide between the pre-disturbance and post-disturbance ecosystems, and play important roles as seed sources (White and Mladenoff, 1994), species habitat (Carey and Johnson, 1995), and in ecosystem function (Franklin et al., 1981; Spies, 1997). Biological legacies in general have important implications for the conservation of biological diversity where forest landscapes are heavily disturbed (Lindenmayer and Franklin, 2002).

Biological legacies are often explicitly addressed in ecological forestry, which emphasizes a wide range of ecological values – such as forest biodiversity and ecosystem processes – as well as timber production (Seymour and Hunter, 1999). Ecosystem-level biological legacies represent important contributions to structural complexity and heterogeneity on landscapes where silvicultural practices are geared toward mimicking natural disturbance regimes (Franklin et al., 1997; Hunter, 1999). This type of legacy is particularly important on landscapes characterized by stand-replacing wildfires, where individual surviving trees within the fire perimeter are uncommon.

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Stand-replacing wildfires have historically shaped the structure of dry, sandy, jack pine (*Pinus banksiana* Lamb.)-dominated ecosystems of the northern Lake States and eastern Canada (Whitney, 1987). Forest composition in this region is dominated by jack pine where fire interval is relatively short (30–50 years) and fire severity is stand-replacing (Whitney, 1987; Simard and Blank, 1982; Frelich, 2002). Fire behavior during large wildfire events on these flat outwash plains has been documented to preserve long, narrow strips of unburned trees arranged parallel to the direction of fire spread (Fig. 1; Haines, 1982; Foster, 1983; Simard et al., 1983; Arseneault, 2001). The mechanisms behind the creation of these unburned strings of trees (also called "tree crown streets" (Haines, 1982); hereafter termed "stringers" for brevity) is unclear. Physical laboratory experiments (Haines and Smith, 1983) and field observations during fire events (Haines, 1982; Simard et al., 1983) have attributed stringer formation to horizontal-roll vortices that develop in a parallel orientation to the wind direction (Haines and Smith, 1983). These horizontal roll vortices create a strong downward draft that effectively "blows out" the flames along their length, protecting trees at the base of the downward movement from lethal heat. The stringers are often (although not always) formed near the successive flanks of the fire as it spreads, and thus can mark the fire perimeter as the fire develops (Arseneault, 2001). Horizontal roll vortices (and associated stringers) have been also documented in other regions and ecosystem types where stand-replacing fires occur, including general boreal forests (Foster, 1983), ponderosa pine (*P. ponderosa* Douglas ex C. Lawson) forests in Arizona, pinyon pine (*P. edulis* Engelm., *P. monophylla* Torr. & Frém., *P. quadrifolia* Parl. ex Sudw.) forests in California (Haines and Smith, 1983), pocosin and pond pine (*P. serotina* Michx.) in North Carolina (Wade and Ward, 1973), and in sawgrass (*Cladium* spp.)-dominated ecosystems in the Everglades (Klukas, 1972). Another potential explanation for stringer formation is that the flanks of spot fires ahead of the main fire front under burn the surface beneath live trees, protecting them from consumption when the main fire front burns over the spot fire area (P. Huber, pers. obs.). Despite the prevalence of stringers in many regions and ecosystem types, their natural range of variability in frequency, size, shape, composition, and longevity after formation has thus far never been examined, making it difficult to incorporate these biological legacies into silvicultural prescriptions for jack pine-dominated ecosystems within an ecological forestry context (e.g., Corace et al., 2009).

The jack pine-dominated ecosystems of Michigan, Wisconsin, and Ontario constitute the breeding grounds for the federally endangered Kirtland's warbler (*Dendroicus kirtlandii* Baird). Kirtland's warblers nest exclusively under young, dense, patchy stands of jack pine historically created by wildfires (Whitney, 1987; Comer et al., 1995; Probst et al., 2003) for only a short window of time before abandoning them due to successional changes in stand structure (Probst, 1986). Given the effectiveness of fire suppression in the region, the Kirtland's Warbler Recovery Plan (Byelich et al., 1976) encouraged the creation and management of jack pine plantations to ensure a continuous supply of suitable habitat on a rotational basis (Probst and Weinrich, 1993; Kepler et al., 1996). This multi-agency management of jack pine plantations has increased warbler populations from about 400 birds in 1971 to nearly 3600 birds today (unpublished annual census data).

Kirtland's warbler breeding habitat management presents an informative case study for the occurrence and importance of post-wildfire biological legacies and their inclusion into intensive and extensive silvicultural prescriptions (Corace and Goebel, 2010). In most jack pine plantations created for warbler habitat, trees are specially arranged in an "opposing wave" pattern to incorporate grassy openings (∼0.1 ha) that mimic wildfire-generated tree patterns to a degree (Byelich et al., 1976; Probst, 1988). The Strategy for Kirtland's Warbler Management (USDA Forest Service, 2001) and other research (Probst, 1988; Corace et al., 2010a) recommends the maintenance of biological legacies such as snags and even stringers within warbler plantations; these legacies are increasingly recognized as important for structural and biological diversity and thus use of these lands by species other than Kirtland's warbler (Byelich et al., 1976; Probst, 1988; Corace

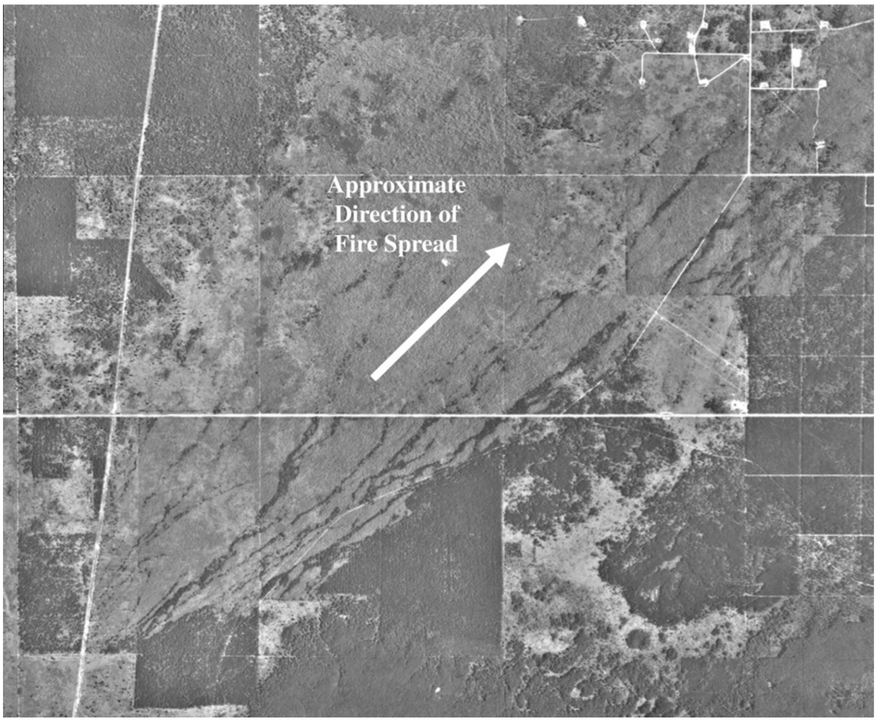

Fig. 1. Stringers (darker bands within lighter burned area) located within the perimeter of a portion of the 1968 Fletcher Fire in Kalkaska County, Michigan (photo date 1973). Note that stringers are oriented parallel to the direction of fire spread and are composed of variable-sized patches of unburned trees that are arranged into long strips.

et al., 2010b). However, no systematic survey or description of stringers exists that can guide managers in managing mature patches of trees in plantations within a natural or historical range of variability. We examined the occurrence of stringers following stand-replacing wildfires in northern Lower Michigan using a chronosequence of aerial imagery and field studies to address (1) the natural range of variability in stringer size, shape, and occurrence for wildfires in this region over the last 40 years; (2) how stringers change over time and how long they persist on the landscape; and (3) composition and structural variability of stringers.

2. Methods

2.1. Study area

We examined stringers within 54 wildfire perimeters in the core breeding range of Kirtland's warbler in northern Lower Michigan (44°30′N, 84°30′W). Forty-three of the 54 sites (80%) were located in the Highplains Subsection (VII.2) of the Northern Lacustrine-Influenced Lower Michigan Section (VII) of Region II (northern Lower Michigan) as described by Albert (1995); the remaining 11 sites were located in the adjacent Arenac (VII.1) and Presque Isle (VII.6) Subsections of Section VII and Region II. The Highplains Subsection has the most severe climate in Lower Michigan due to its inland location, northern latitude, and high elevation relative to the surrounding area (Albert, 1995). Late-spring freezes are common, with a mean annual temperature of 6.7 °C, and average temperature during the growing season of 16.9 °C. The physiography of the region results from a broad, sandy outwash plain dominated by excessively-drained sands of the Grayling series (Typic Udipsamments) (Werlein, 1998). The vegetation of the study area is dominated by jack pine and, to a lesser degree, northern pin oak (*Quercus ellipsoidalis* E.J. Hill) and red pine (*P. resinosa* Aiton). Stand-replacing fire historically maintained jack pine forests prior to European settlement (Albert, 1995; Comer et al., 1995) at a fire-return interval estimated in the literature to range between 30 years (Simard and Blank, 1982) to 59 years (Cleland et al., 2004).

2.2. Analysis of historical photography

We conducted a survey for stringers within wildfire perimeters viewable on aerial photography dating between 1973 and 2009. Digital imagery was obtained from the USDA Natural Resource Conservation Service in East Lansing, Michigan and the Aerial Imagery Archive at Michigan State University, and online from the Michigan Center for Geographic Information. Ten major wildfires in the region that occurred prior to 1980 were located based on personal communication with land managers and examined for stringers. The remaining wildfires examined in this study ($n = 44$) burned since 1981 and were located using spatial fire databases obtained from the Michigan Department of Natural Resources and the Huron-Manistee National Forests. An initial photo reconnaissance of 48 additional fires <80 ha in size that had burned since 1981 revealed no stringers, and thus the 44 wildfires examined for stringers in this study were above a minimum fire size of 80 ha (about 200 ac). Fires were examined using imagery as near to the date of the fire as possible based on the availability of historical photos. Because aerial photography of the region is less frequent prior to 1973 and stringers become more difficult to detect with increasing time since fire, our survey is biased towards wildfires that have burned in the last 30 years.

From the population of 54 wildfire perimeters, we identified stringers by their general shape and orientation within a burn perimeter in 11 wildfires that burned between 1967 and 2006. Next, polygons representing stringers were generated across the full chronosequence of imagery available for each burn using ArcMap 10 (ESRI, 2011) (Table 1). We defined a stringer on an aerial photograph as contiguous areas of mature trees within a burn perimeter with gaps of no more than two tree crowns. The boundaries of a stringer therefore represented the edge of contiguous tree crowns; boundaries were drawn at the unburned forest edge when the stringer intersected the burn perimeter. Roads were not considered breaks in the stringer if the feature was consistent on each side of the road (Haines and Smith, 1983). Stringers for a given burn and a given year of photography were analyzed using FRAGSTATS (McGarigal et al., 2002). FRAGSTATS was used to calculate the area within the burn perimeter as well as the total number and area of the stringer patches, and the patch size distribution including the largest, smallest, and average patch size. Less intuitive metrics were also calculated in FRAGSTATS (Table 2), including the number of patches per unit area (patch density), the aggregation of the stringers across each burn (landscape shape index), and the connectedness of the stringers within the burn perimeter (patch cohesion index). The correlation of these metrics to fire size was tested using Pearson correlations.

2.3. Field sampling and analyses

A subset of 7 of the 11 mapped wildfires were selected to represent a chronosequence of fires that formed stringers between 1967 and 2006, and were sampled in the field during the summer of 2011. Stringers were selected at random from the most recent available aerial imagery and sampled using three variable-radius plots established 30 m apart along a transect run along the long axis of the stringer. Transects were established at a minimum of 50 m from the intersection of the stringer with roads so as to minimize edge effects on measured tree variables. At each plot, overstory tree species composition was noted, and the width of the stringer was measured. A 20 BAF prism was used to select trees at each plot center for measurement; species and diameter at breast height (DBH) was measured for each selected tree to calculate basal area, quadratic mean diameter, and species relative dominance. Height to the base of the live crown was measured for four dominant overstory trees nearest the plot center. Finally, the distance, DBH, and species of the four closest trees to the plot center were measured to calculate tree density using the quarter point method (Elzinga et al., 1998). Species composition was categorized in an *ad hoc* manner into an overstory dominated by red pine vs. jack pine, and differences in basal area, tree density, and height to crown base was compared among stringers dominated by either red or jack pine using analysis of variance (ANOVA). Assumptions of normality and heteroscasticity were tested and met, except for tree density which was log-transformed.

3. Results

3.1. Aerial imagery and mapping

Stringers were located in a wide range of wildfires >80 ha in northern Lower Michigan (Table 1), and showed only a weak relationship between stringer presence and fire size. We discerned stringers on 18 of the 54 (33%) wildfires we examined in this study (Fig. 2). Although the small sample size precludes statistical analysis of this data set, approximately 67% of the stringers were located in wildfires <500 ha in area, while the remaining 33% of the stringers were found in larger fires (particularly those >1000 ha). All wildfires >1000 ha ($n = 5$) were found to have stringers in them (Fig. 1). Specifically, 29% of wildfires <500 ha were

Table 1
Locations, fire size, event year, and imagery used to map stringers in 11 wildfires in northern Lower Michigan. Stringers in fires denoted with * were also visited in the field.

Fire	County	Size (ha)	Year	Imagery
Damon*	Ogemaw	481	1967	1978, 1992, 1998, 2005, 2009
Artillery Range	Crawford	382	1967	1981, 1992, 1998, 2005, 2009
St. Helen*	Roscommon	331	1967	1978, 1992, 1998, 2005, 2009
Fletcher	Kalkaska	1087	1968	1973, 1981, 1986, 1992, 1998, 2001, 2005, 2009
Hale	Iosco	196	1972	1979, 1992, 1998, 2005, 2009
Bald Hill*	Crawford	774	1975	1981, 1992, 1998, 2005, 2009
Mack Lake*	Oscoda	9825	1980	1982, 1998, 2005, 2009
Stephan Bridge Road	Crawford	2394	1990	1992, 1998, 2005, 2009
ATV*	Oscoda	340	1999	2005, 2009
No Pablo*	Oscoda	2104	2000	2005, 2009
Hughes Lake*	Oscoda	2345	2006	2009

Table 2
Description of landscape metrics used to describe and compare stringers in 11 wildfires in northern Lower Michigan.

Metric	Code	Description
Number of patches	NP	Total number of discernable stringer patches within the burn perimeter
Patch density	PD	Number of stringer patches per 100 ha
Percent of landscape	PLAND	Percent of the area within the burn perimeter occupied by stringers
Landscape shape index	LSI	Measures the aggregation of stringer patches using the total length of stringer patch edge; patches are more aggregated as metric decreases towards 1
Patch cohesion index	COHESION	Measures the connectedness of the stringer patches across the landscape; connectedness increases as metric approaches 100

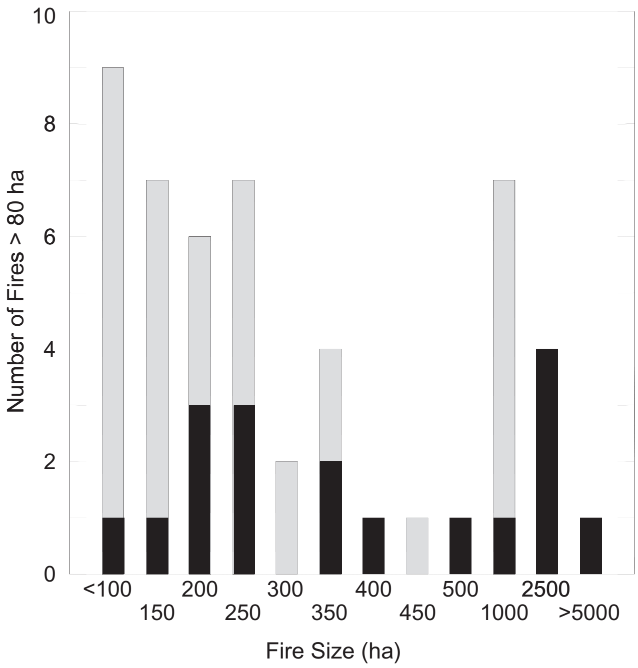

Fig. 2. Frequency diagram for fires >80 ha that burned in northern Lower Michigan. Black bars represent wildfires that contained stringers discernable from digital aerial imagery. Note that *x*-axis labels refer to the upper bound of each size class.

found to have stringers, while 50% of fires >500 ha had stringers (Fig. 2). Notably, no stringers were located in the 48 wildfires <80 ha found in the spatial fire databases obtained from the Michigan Department of Natural Resources and the Huron-Manistee National Forests.

Landscape metrics calculated over a chronosequence of imagery for each wildfire revealed substantial variation in stringer patterns across the 11 wildfires examined. Stringers occupied 3–14% of the landscape in the first decade after the fire. Stringers were generally small (mean patch size 0.5–3.1 ha), with patches well aggregated (LSI range 3.1–20.4) and arranged across the burned landscape in a manner that resulted in very high connectivity (COHESION range 93–100; Table 3). Patch size distributions of stringers exhibited dominance by many small patches rather than fewer larger patches for most wildfires, with large patch sizes (>10 ha) more common in the largest wildfires (Fig. 3). High patch density in most wildfires also suggests that stringers most often consisted of long, linear arrangements of many small patches of unburned trees rather than large, contiguous strips of trees. The No Pablo Fire, in particular, was dominated by many small patches, with extremely high patch density (PD = 2129/100 ha), very small patch size (mean patch area = 0.1 ha), and low aggregation of patches (LSI = 66.1; Fig. 4), although this pattern may have been related to the relatively young age of the pre-fire forest (20 years). An exception to this generalization were stringers at Mack Lake, which were large (mean patch area = 8 ha) and well dispersed (PD = 12.5/100 ha); metrics revealed the Artillery Range to also have large, well dispersed stringers, but this entire wildfire contains only one or two large patches (Fig. 3 and Table 3).

Landscape metrics identified changes over time in stringer patterns for only 5 of the 11 (45%) wildfires mapped. Five of the 11 wildfires exhibited no changes in the metrics calculated in this study: Hale 1972 (over 30 years of available imagery), Artillery Range 1967 (28 years), Stephan Bridge Road 1990 (17 years), ATV 1999 (4 years), and No Pablo 2000 (4 years) (Table 3). Only one year of imagery was available for a sixth recently-burned fire (Hughes Lake 2006) that precluded analysis of change in this burn. Where stringers exhibited changes over time (Fletcher, Mack Lake, Bald Hill, Damon, and St. Helen), changes in stringer patterns varied significantly across the wildfires (Fig. 5a–e):

3.1.1. Fletcher 1968

Fletcher exhibited a steady decrease in PLAND, PD, and LSI (more aggregated), and an increase in mean patch area, while COHESION remained largely unchanged over the 36 years of available imagery. The largest degree of change occurred between 2001 and 2005, with sharp decreases in PLAND, LSI, and mean patch area and a sharp increase in PD that likely correspond to harvesting activities during that time (Fig. 5a–d).

3.1.2. Mack Lake 1980

Mack Lake experienced a decrease in PLAND, mean patch area, and COHESION and an increase in LSI and PD over the 27 years between 1982 and 2009 (Fig. 5a–e). The rate of change in each of these five metrics was greatest in the first decade after the fire between 1982 and 1998 that correspond to salvage logging and tree

Table 3
Landscape metrics calculated for stringers mapped in 11 wildfires in northern Lower Michigan. Stringers in wildfires denoted with * showed no change over the duration of the available imagery. Metrics presented were calculated using the earliest imagery available after a given fire event; changes in metrics are presented in Fig. 5.

Fire	Years of observation	% of Landscape	Patch density (# per 100 ha)	LSI	Mean patch area (ha)	Patch cohesion
Fletcher	1973	9.8	80.0	20.4	1.2	95.5
Mack Lake	1982	5.7	12.5	18.3	8.0	98.2
Bald Hill	1981	4.9	55.2	10.1	1.8	96.2
Damon	1978	8.1	72.0	11.2	1.4	97.3
St. Helen	1978	14.1	32.1	8.5	3.1	97.9
Hale*	1979–2009	6.0	204.4	8.4	0.5	92.9
Artillery Range*	1981–2009	6.0	4.4	3.1	22.9	100
Stephan Bridge Road*	1992–2009	3.3	48.3	9.2	2.1	96.0
ATV*	2005–2009	6.7	66.1	8.1	1.5	96.4
No Pablo*	2005–2009	5.0	2128.6	60.9	0.1	62.5
Hughes Lake	2009	5.8	80.2	12.0	1.2	95.4

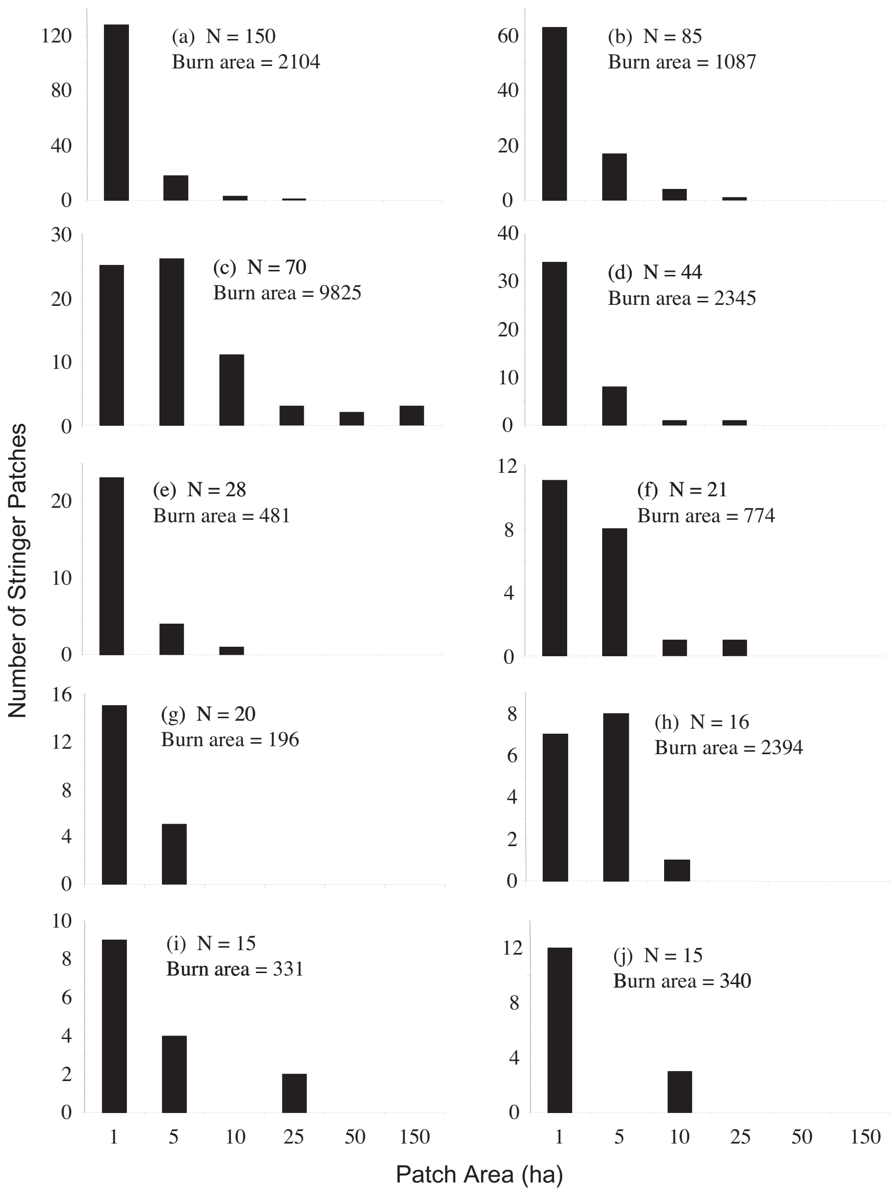

Fig. 3. Patch size distributions for stringers in 11 wildfires in northern Lower Michigan: (a) No Pablo 2000; (b) Fletcher 1968; (c) Mack Lake 1980; (d) Hughes Lake 2006; (e) Damon 1967; (f) Bald Hill; (g) Hale 1972; (h) Stephan Bridge Road 1992; (i) St. Helen 1967; (j) ATV 1999. Burn area values are in hectares. Note that the scale of the *Y* axis differs among graphs.

mortality. Several stringers were also lost when the 2000 No Pablo Fire burned the far eastern portion of this wildfire area. As such, the initial large, continuous patches that characterized the stringers at Mack Lake were fragmented into smaller (decrease in mean

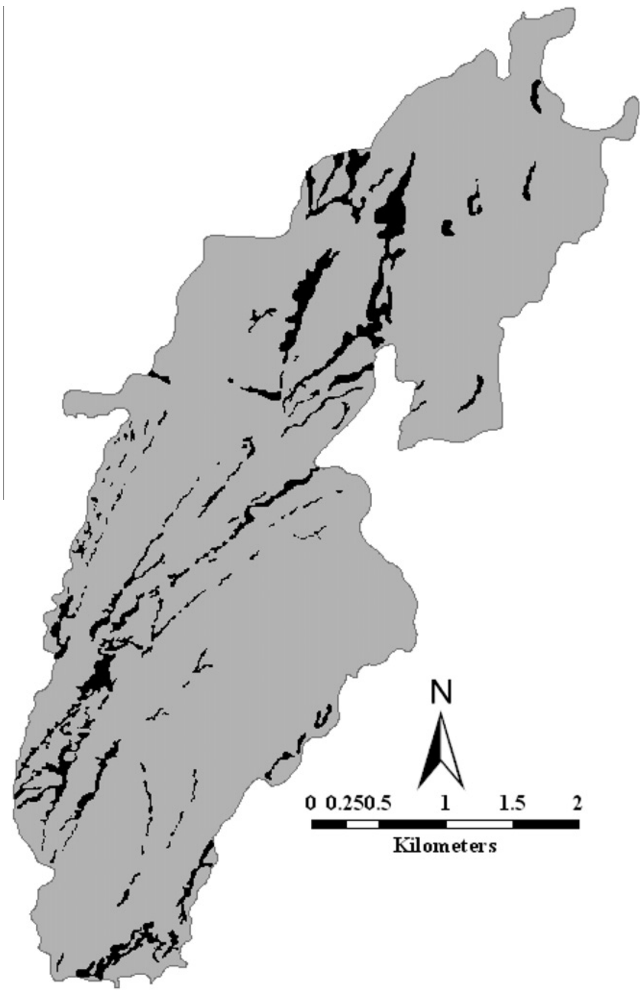

Fig. 4. Stringers (shown in black) within the fire perimeter of the 2000 No Pablo Fire in Oscoda County, Michigan (mapped from 2005 imagery). Stringers are dominated by many small patches.

patch size), more numerous (increase in PD), less aggregated (increase in LSI) patches across the landscape that changed relatively little afterwards (Fig. 6).

3.1.3. Bald Hill

Similar to Mack Lake, Bald Hill experienced a sharp decrease in PLAND and PD in the first decade after the fire and little change afterwards. In contrast, LSI decreased and mean patch area increased sharply, suggesting the complete loss of small, isolated stringer patches across the landscape between 1981 and 1992 (Fig. 5a–d).

3.1.4. Damon

Major changes in stringers at Damon occurred several decades after the fire rather than soon after the event. PLAND, PD, and LSI decreased steadily and mean patch size increased beginning in 1978 until 2005, when PLAND, LSI, mean patch size, and COHESION quickly decreased while PD sharply increased (Fig. 5a–e). Such changes suggest one or more major harvesting events by 2005 that reduced the number of stringers on the landscape and fragmented those remaining.

3.1.5. St. Helen

Stringers at St. Helen exhibited changes similar to those at Mack Lake, with a marked decrease in PLAND, mean patch size, and COHESION early in the chronosequence between 1978 and 1992, followed by a steady decrease thereafter; PD and LSI showed a sharp increase prior to 1992 (Fig. 5a–e). St. Helen was subjected to harvesting of stringers that reduced the size and increased the number of stringer patches across the landscape, though the remaining patches were increasingly aggregated.

Of the landscape metrics calculated in this study, PLAND and mean patch area were significantly correlated to the size of the wildfire, but PD, LSI, and COHESION were not. The proportion of the landscape occupied by stringers decreased with increasing fire size (Pearson correlation $r = -0.836$, $p = 0.01$) while mean patch area increased ($r = 0.82$, $p = 0.013$).

3.2. Field sampling

Field data showed very high variation in species composition and structural features that provide little predictive ability across the region. Species composition within the stringers was either red pine or jack pine, with a minor component of northern pin oak. Current stringer species composition was reflective of pre-fire composition, but older fires tended to have higher dominance of red pine (ANOVA: $F = 7.272$, $p = 0.012$), often the remnants of pre-fire plantations (Table 4). Red pine was dominant in 64% of the fires sampled >30 years after the fire, and represented 100% of the trees in 25% of those stringers. In contrast, jack pine dominated in all other fires, sampled <11 years after the event (Table 4). Basal area was higher when the stringer was dominated by red pine ($F = 6.172$, $p = 0.019$), and height to base of the crown was higher for red pine compared to jack pine-dominated stringers ($F = 18.592$, $p < 0.001$). Density was highly variable within the stringers, ranging from about 350 trees/ha in a stringer composed of red pine and northern pin oak to 11,400 trees/ha in a stringer composed of young jack pine, but did not differ between stringers dominated by one species or the other ($F = 3.761$, $p = 0.063$; Table 4).

4. Discussion

Efforts to understand and define the limits or natural range of variability of ecosystem structure and function depends on the use of historical knowledge in the management of ecosystems (Landres et al., 1998). Defining this range of variability for post-fire biological legacies, therefore, is critical for understanding the dynamic nature of landscapes characterized by stand-replacing fires and to assess processes associated with contemporary patterns that occur on them (Swetnam et al., 1999). Changes that occur on landscapes resulting from land management must be constrained by this range of variability not only as an attempt to mimic ecological patterns such that the appearance of human impact is reduced, but also because ecosystems have functional and evolutionary limits that cannot be exceeded in a sustainable way (Christensen et al., 1996). In northern Lower Michigan and much of northeastern North America, land managers have begun to acknowledge the importance of maintaining biological legacies on fire-prone landscapes, but have little baseline data that define or describe the occurrence and persistence of these features over time. For jack-pine dominated ecosystems, this is the first study that provides data that may be used to guide and constrain resource management actions where stringers are an important feature of the landscape.

Stringers are common features in large wildfires (>80 ha) in northern Lower Michigan, and were found in every fire >1000 ha ($n = 5$) that we sampled. In contrast, stringers were absent from all small fires (<80 ha) we examined ($n = 48$) that had burned in the region since 1981. The absence of stringers in small fires

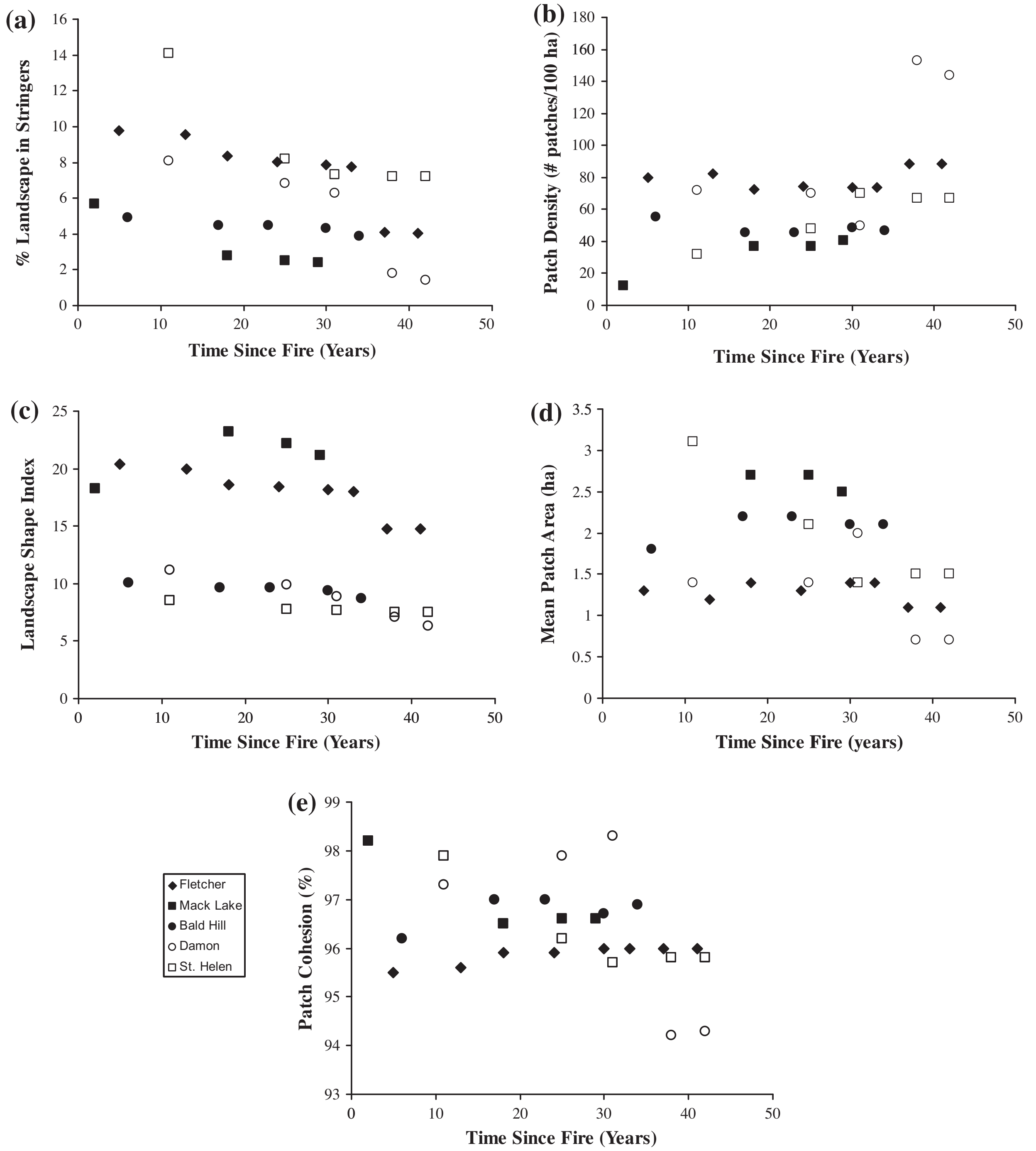

Fig. 5. Changes in landscape metrics measured for stringers along a photosequence for five wildfires in northern Lower Michigan: (a) proportion of the burned landscape occupied by stringers; (b) patch density; (c) landscape shape index; (d) mean patch area; (e) patch cohesion.

compared to larger fires likely results from the lack of sufficient intensity in small fires required to develop the atmospheric conditions necessary for horizontal roll vortices to form, or to generate sufficient energy for crown fire and spotting conditions. Even large wildfire events apparently do not always exhibit fire behavior necessary for the formation of stringers, however, as we found these features only in approximately one-third of fires >80 ha examined in this study.

Our data suggest that stringer formation is relatively independent of pre-fire forest structure or species composition. For example, we noted in the field the formation of stringers from 40 to 60 year old red pine plantations at the time of the Mack Lake Fire in 1980, as well as stringers formed from dense 20–25 year old jack pine plantations at the Hughes Lake Fire in 2006. Stringer formation therefore is more likely driven mainly by fire behavior during large events compared to pre-fire forest structure. Moreover, we found no evidence in the field that topography was related to the formation of stringers, which we located at the tops of low ridges, in shallow valleys and depressions, and in flat areas with no evident topography. The smallest fire we noted that had stringers was a 91 ha fire in Otsego County, and the largest without stringers was a 773 ha fire in Otsego County. Despite detailed experiments with the formation of horizontal roll vortices in the laboratory (Haines and Smith, 1983), the ambiguity of the physical drivers

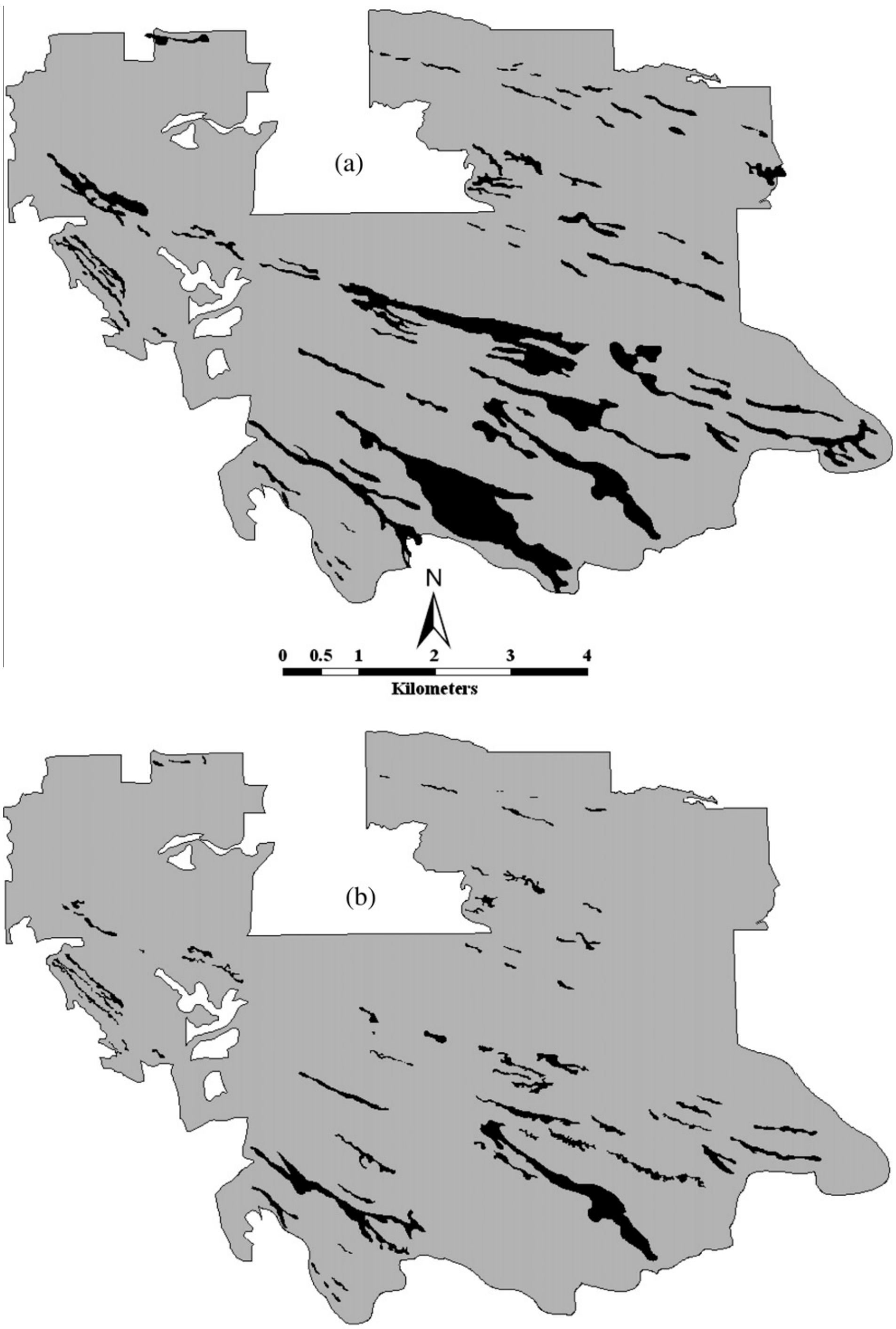

Fig. 6. Changes in stringers (shown in black) across the 1980 Mack Lake Burn in northern Lower Michigan between (a) 1982 and (b) 2009. Stringers at Mack Lake were initially large and continuous, but became increasingly smaller, more numerous, and less aggregated over time.

of the fire behavior necessary to create this phenomenon in wildfire events of different ecological context and size warrants further research, as does the possibility that stringer formation results from fire spotting rather than horizontal roll vortices.

When present, stringers typically represent 3–14% of the burned landscape and are most often composed of many small, discrete patches oriented into linear features rather than large, contiguous strips of unburned trees. Such a pattern may be in part an artifact of scale and the methodology of how patches were mapped within a GIS environment. However, the discontinuous nature of stringers was supported anecdotally during our field research; stringers at the Hughes Lake Fire and ATV Fire, for example, were particularly discontinuous and were often separated by 20–50 m of burned forest. The No Pablo Fire and Hale Fire best exemplify this pattern in the wildfires we examined, but they contrast markedly from the large, contiguous stringers found at the Mack Lake Fire (Table 3). Notably, the Mack Lake Fire was historic in its intensity and extent (Simard et al., 1983), and our data suggest a negative correlation of PLAND and a positive correlation of mean patch area with increasing fire size. Thus, while very large wildfires may have a lower proportion of area in stringers based on the sheer size of the burns alone, the stringers that form tend to be larger and

Table 4
Field data collected in 29 stringers from 7 wildfires in northern Lower Michigan. JP = jack pine, RP = red pine, NPO = northern pin oak.

Fire and Year	Stringer #	Tree species composition	Basal area (m^2)	Quadratic mean diameter (cm)	Jack pine relative dominance (%)	Red pine relative dominance (%)	Tree density (trees/ha)	Height to crown base (m)
Damon 1967	1	JP, RP	126.7	22.2	63.5	36.5	1405	7.5
St. Helen 1967	1	JP	126.7	15.0	88.9	0.0	1250	5.3
	2	JP, RP	153.3	19.4	32.4	67.6	1199	6.8
Bald Hill (East) 1975	1	JP, RP	93.3	12.8	85.9	14.1	2601	5.5
Mack Lake 1980	1	RP, NPO, JP	140.0	27.5	0.0	100.0	1100	6.9
	2	RP	120.0	39.3	0.0	100.0	416	9.3
	3	RP	193.3	27.1	0.0	100.0	1723	6.9
	4	RP, JP	173.3	12.7	20.0	66.7	637	7.9
	5	JP, RP	146.7	15.5	68.8	23.3	1590	3.9
	6	RP	166.7	25.2	0.0	83.8	784	9.2
	7	RP, NPO	126.7	27.5	0.0	79.0	346	10.3
	8	JP, RP, NPO	140.0	16.7	48.9	51.1	6307	6.8
	9	JP	120.0	19.4	25.4	74.6	2543	7.5
	10	JP	80.0	10.4	100.0	0.0	1851	2.5
ATV 1999	1	JP, RP, NPO	40.0	12.8	4.8	62.7	496	4.1
	2	JP, RP, NPO	63.3	19.4	40.7	32.6	475	5.2
No Pablo 2000	1	JP	60.0	8.8	82.2	0.0	1866	4.2
	2	JP	133.3	10.3	100.0	0.0	11394	3.6
	3	JP	53.3	22.1	100.0	0.0	395	5.8
	4	JP	120.0	11.6	100.0	0.0	2028	5.0
	5	JP	126.7	11.2	72.2	0.0	1967	4.0
	6	JP, NPO	120.0	9.0	100.0	0.0	3655	4.1
	7	JP	106.7	9.2	93.3	0.0	4013	5.5
	8	JP	80.0	12.5	100.0	0.0	1156	3.3
	9	JP	133.3	9.9	100.0	0.0	3880	4.6
Hughes Lake 2006	1	JP	100.0	9.7	73.3	0.0	3705	3.4
	2	JP	126.7	9.0	100.0	0.0	5303	3.9
	3	JP	106.7	18.9	100.0	0.0	737	4.6
	4	JP, RP, NPO	106.7	24.5	58.9	41.1	397	7.7

more continuous. High wind speeds present during the Mack Lake Fire (Simard et al., 1983) may have caused more distant spotting that allowed the flanks of the surface spot fires more time to spread laterally before they were reached by the main fire, thus creating wider stringers. Horizontal roll vortices at Mack Lake in 1980 (Simard et al., 1983) may have been a driver of stringer formation and likely their subsequent patterns across the landscape.

Once formed, successional changes that occur in stringers are most notable soon after the fire event, followed by a longer period of relatively little change in their pattern. We noted a lack of any change in stringers (discernable from aerial imagery) in more than half of the wildfires in which we examined stringers in detail; a lack of change was found over approximately 30 years of imagery for 2 of the fires (Table 3). For those wildfires where changes in stringers did occur, major changes featured the loss of smaller, more isolated patches of unburned trees and some shrinkage of larger stringer patches near their margins. These changes typically occurred in the first decade after the fire, however, after which changes in stringer pattern for most of the fires were relatively minor (Fig. 5). This relative lack of change suggests that stringers persist – at least for the 30–40 year photo record we were able to obtain for this study – in the absence of human activity or subsequent fires that burn them. Harvesting for the establishment of plantations has been the major source of change for most of the stringers we studied, evident from sudden changes in landscape metrics several decades after the fire event (Fig. 5) as well as photographic evidence of harvesting and planting. Subsequent wildfires were a factor in stringer loss for only one of the five fires where changes in stringers were evident (Mack Lake, due to the No Pablo Fire in 2000). We found little evidence for wind or insect damage that significantly altered the shape or arrangement of stringers between fire events. Though speculative, these trends imply that stringers that formed in the region prior to European settlement often persisted at least through the fire interval, though it remains unclear how often stingers formed during this period.

Despite its apparent lack of importance for stringer formation, the forest species composition and structure of stringers may have implications for stringer persistence and future management. In particular, the longer stability of a red pine – dominated overstory compared to jack pine may allow stringers dominated by red pine to persist for a longer duration, in part because exposed jack pine is more susceptible to wind throw compared to red pine (Whitney, 1986). We noted red pine to be more dominant in older wildfire areas, but it is difficult to discern whether stringers composed of jack pine were lost to wind or whether red pine was simply more common on the pre-fire landscape of those areas. Stringers composed of young jack pine such as those at the No Pablo Fire (30 year old fire-regenerated jack pine) and the Hughes Lake Fire (20–25 year old jack pine plantation) are less likely to persist, especially because the unburned trees are small and susceptible to wind throw. If true, the conversion of much of the landscape of the region to young jack pine plantations for Kirtland's warbler habitat (and thus the removal and replacement of red pine) may have important implications for the persistence of these biological legacies following future fires. When stringers were composed of red pine, crown height was significantly greater than when stringers were composed of jack pine. If the vegetation surrounding stringers are short enough to prevent damage to the stringer overstory during a stand-replacing fire, stringers composed of red pine may be more likely to survive the fire compared to those composed of jack pine because their foliage is located further from the ground due to self-pruning and their bark is more resistant to fire. The survival of stringers over multiple fires clearly depends on fire intensity, but the structure of stringers likely has implications for their persistence and is an important area of future research.

The occurrence and persistence of stringers have important implications for land management, particularly with regard to habitat management for the Kirtland's warbler. The current high population level of Kirtland's warblers presents an opportunity for a broadening focus on biological legacies within the natural range of variability compared to past decades when the warbler population was low and these features were not emphasized. The inclusion of "leave strips" of live jack pine or red pine in a pattern that mimics stringers should increase heterogeneity within warbler plantations to better emulate natural structure found after wildfires (Spaulding and Rothstein, 2009). Likewise, we suggest the retention of wildfire-created stringers regardless of whether natural regeneration of the burned area is managed as warbler habitat or the area is converted to a warbler plantation. Stringer occurrence in primarily large wildfires should not deter their inclusion in land management prescriptions for Kirtland's warbler, since contemporary prescriptions strive for large, contiguous plantations that approach the size of many large wildfires. We documented a wide natural range of variability in stringer size, composition, and structure which suggests that land managers have a great deal of flexibility in "designing" stringers to include within plantations, with only a few general characteristics useful in mimicking stringers created naturally by wildfires. When stringers are included in plantations, long, thin strips of mature trees better mimic the pattern of stringers created by wildfires than do short, wide strips. Wide, contiguous stringers are common only in very large wildfires and are unnecessary in plantations <500 ha. Stringers should be oriented along the longest axis of the planted area, and red pine should be retained as stringers where possible because it is commonly found in stringers, is longer-lived than jack pine, and is most likely to survive a future wildfire.

Although well beyond the scope of this study, we speculate that the structural heterogeneity provided by stringers on jack pine-dominated landscapes may have significant ecological importance for biodiversity as they have in other forest types (e.g., Harmon et al., 1986; Carey and Johnson, 1995). For example, stringers may benefit wildlife species that require nesting or perching habitat containing legacy trees, snags, or other structural features (Corace et al., 2010b). Stringers also provide significant variability in vegetation structure that may result in more diverse or different insect communities (Franklin et al., 2000), or may provide habitat for small mammals (Carey and Johnson, 1995) that is not available within the adjacent recently burned or planted area. Moreover, vegetation within stringers is in a later successional stage than their immediate surroundings, and thus stringers may act as important sources of plant propagules to adjacent, early-successional forests (White and Mladenoff, 1994). Notably, the presence of stringers may also have negative implications for some species, for example, if they benefit unfavorable pathogens or competitors, or if their presence results in a population sink within the landscape. We suggest that stringers are a significant feature within the natural range of variability of jack pine-dominated ecosystems of this region, but their specific ecological relevance has yet to be determined from targeted field research.

5. Conclusions

We conclude that stringers are common in large wildfires in northern Lower Michigan and are important for creating heterogeneity in jack-pine dominated ecosystems. These stringers are naturally persistent throughout the fire interval in the region, although they currently are subjected to human activities that limit their shape, size, and longevity. This study provides baseline data on the occurrence, pattern, and persistence of stringers in jack-pine dominated ecosystems of northern Lower Michigan, but the implications of these data for biological diversity on these landscapes remains unknown. Subsequent research is necessary to ascertain, for example, the ecological importance for structural differences between stringers and between stringers and the adjacent forest; potential effects of stringers on the surrounding forest development (see Arseneault, 2001); how plant communities differ between stringers and the forest matrix and the implications of stringers for small mammal, bird, and/or insect populations and communities.

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