

ARTICLE

Forest resilience and regeneration dynamics following wildfire disturbance

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Abstract

Species that are adapted to specific disturbance regimes may be sensitive to changes such as severity, frequency, and extent of ecosystem perturbation. Along range margins, these sensitivities may be exacerbated by concurrent changes in climate resulting in loss of resilience and shifts to alternative ecosystem states. *Pinus banksiana* (jack pine) is a serotinous species dependent on fire disturbance to open cones, release seed, reduce understory competition, and expose mineral soil. The Altona Flat Rock in northern New York is a globally rare sandstone pine barrens, at the southern edge of jack pine's range. In the summer of 2018, a wildfire burned approximately 200 ha of the Flat Rock barrens, providing the opportunity to study post-disturbance jack pine and understory resilience. We aimed to establish if jack pine regeneration would occur, and if so, would it be influenced by fire severity, pre-fire stand characteristics, and competition. We predicted that higher seedling densities would be associated with higher burn severity, higher pre-fire jack pine stand density, and lesser understory competition. We collected seedling density and understory composition data annually from 2019 to 2022 across 45 plots spanning the disturbed and adjacent undisturbed barrens. In 2021 and 2022, seedling heights were also collected. Seedling densities following the disturbance ranged from 275,385 to 390,513 ha⁻¹; $\bar{x} = 357,821$ ha⁻¹. Jack pine seedling density was positively associated with fire severity and moss abundance for all years. Pre-fire stand density along with ericaceous shrub, grass, and duff abundance were also positively associated with seedling density in some years. Seedling height was positively associated with fire severity along with grass and blueberry abundance. These factors, for both establishment/survival and growth, point to the importance of seed supply, microsite conditions, and facilitation in jack pine regeneration success. At this point, it does not appear that the interaction of disturbance with changing climate has shifted enough to prevent the recovery of this ecosystem to its pre-disturbance jack

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pine-dominated state. However, ongoing climate change may still have an impact on seedlings/saplings as this forest continues to mature.

KEYWORDS

jack pine, *Pinus banksiana*, resilience debt, sandstone pavement pine barrens, seedling growth, seedling recruitment, understory community

INTRODUCTION

The ability of a forest to regenerate following disturbance is an essential component of ecosystem health and resilience and often relies on landscape-level variability (Koontz et al., 2020). Holling (1973) defines ecological resilience as an ecosystem's ability to reorganize without loss of function following perturbation. Donato et al. (2009) characterize resilience following a disturbance as maintaining community richness and a core suite of species with some additional ruderal species. Other researchers have evaluated forest resilience by characterizing vegetation into dominant (more common) and subordinate (less common) species and monitoring whether dominants maintain abundance or subordinates expand following disturbance (Baltzer et al., 2021).

Disturbance is one process associated with shaping and maintaining ecosystems, influencing composition, structure, and function (Seidl et al., 2014). Recurring disturbance results in the development of an ecological memory, which facilitates a more resilient ecosystem prepared for similar future disturbances (Johnstone et al., 2016). Ecological memory is the result of strong selection on life history traits that increase fitness following specific disturbance types, such as jack pine (*Pinus banksiana*) cone serotiny following stand-replacing fires (Johnstone et al., 2016). Stand-replacing fire not only opens serotinous cones but reduced understory competition has been shown to trigger rapid regeneration of a disproportionate abundance of seed (Lamont & Enright, 2000), which sets long-term dominance patterns.

Anthropogenic or climate-change-related alterations to disturbance type and regimes may disrupt this ecological memory and change forest resiliency, represented by alteration to forest composition and structure, or potentially more dramatically by shifting the system into an alternative state (i.e., unforested or compositionally different; Braziunas et al., 2018; Enright et al., 2015; Mcewan et al., 2011; Murray et al., 2012; Rooney et al., 2000; Seidl et al., 2017; Stevens-Rumann et al., 2018; Turner et al., 2022). This is especially critical for species at their range margins, as they are potentially already experiencing climatic conditions at the limits of their physiological tolerance, enhancing vulnerability to the

interactions between changing disturbance regimes and environmental conditions (Pelletier et al., 2022; Pelletier & de LaFontaine, 2023; Thomas, 2010).

Fire is one form of disturbance that drives ecosystem dynamics for many North American forests. Regular fire disturbance leads to communities of species that are adapted to or dependent on fire for reproduction, which limits biomass accumulation and eliminates competitors (Chrosiewicz, 1990; Stephens et al., 2018). In North American boreal forests, where jack pine (*Pinus banksiana*) is prevalent, fire regimes are dominated by relatively infrequent but high severity crown fires (de Groot et al., 2013). Jack pine is a fire-dependent species with predominantly serotinous cones, although levels of serotiny vary based on fire return interval and severity (Gauthier et al., 1996; Lamont et al., 2020).

Fire not only stimulates jack pine regeneration, but also creates conditions that may threaten survival, especially under climate warming. In addition to heat-opening cones and releasing seed (Pelletier & de LaFontaine, 2023), fire exposes bare mineral soil and reduces germination competition (Lamont et al., 2020). Jack pine regeneration following fire disturbance results in pure or mixed (Savva et al., 2007) even-aged stands (Arseneault, 2001; le Goff & Sirois, 2004), with the majority of seedlings establishing within the first year following disturbance (Greene et al., 2013). However, while fire is necessary to enable seed release and germination, it may also create issues for seedling survival following germination. Soil organic materials, with low thermal conductivities, are subject to extreme surface temperatures when exposed to direct solar radiation (Chrosiewicz, 1990). MacHattie and Norton (1963) performed a seeding experiment in a cleared forest along a microtopographic gradient of soil temperatures and found mortality of jack pine seedlings was positively correlated with June soil surface temperatures. This may lead to seedling mortality due to harsh surface temperatures, which cause high evapotranspiration rates (Strong & Grigal, 2011). Despite being one of the most shade-intolerant species within its native range, seedlings in drier sites often require some shade to persist (Benzie, 1977).

The Altona Flat Rock (hereafter referred to as the Flat Rock) sandstone pavement barrens in northeastern

New York is one of the largest jack pine barrens in the United States. Located at the southernmost extent of jack pine's range, individuals at this site may be particularly susceptible to changing climate and associated shifts in the disturbance regime (Pelletier et al., 2022). Mean annual temperature in the region has risen over the past century by 1.8°C (Stager et al., 2022). Further, since 1990, July and September local temperatures have significantly increased by over 2°C (Stager et al., 2022). Seedling stage individuals may be most susceptible to these changes due to their more restricted physiological niche (i.e., increasing temperature; Jackson et al., 2009). However, for disturbance-driven species, such as jack pine, a lack of recent disturbance (1957 was the last recorded wildfire) may limit our ability to determine whether environmental conditions have moved beyond the range of seedling tolerance and created a situation of potential resilience debt (Johnstone et al., 2016). Resilience debt results from a decoupling of life history traits essential for recovery from disturbance under changing environmental regimes (Frelich et al., 2020), which may not be evident among mature trees within the ecosystem, but may prove unsuitable for seedling and saplings with narrower physiological tolerances.

In July 2018, a fire burned just over 200 ha at the Flat Rock, creating an opportunity for us to study how the barrens ecosystem would recover from disturbance, especially considering ongoing climate change. Specifically, we were interested in whether jack pine regeneration would occur, or whether in fact the site was already in a state of resilience debt—where increasing temperatures had exceeded seedling germination and survival requirements. We evaluated forest resilience by determining whether the post-fire community returned to pre-fire jack pine domination characterized by similar stand densities, as well as similar understory species composition, richness, and diversity. Further, we sought to determine how jack pine regeneration was related to fire severity (a proxy for how much of the cone crop opened and released seed), pre-fire stand characteristics (i.e., stand density as a proxy of seed source), and competition that may limit germination and seedling survival. We hypothesized that regeneration would be higher in areas that: (1) experienced higher severity burn; (2) had higher pre-fire jack pine density; and (3) had less competition from understory species for light, nutrients, and water, along with having more exposed mineral soil. Areas with higher burn severity (Greene et al., 2007; Pinno & Errington, 2016) and stand density (partial seed tree retention) are characteristically associated with greater jack pine seed availability and release (Jayen et al., 2006).

METHODS

Study area

The Flat Rock sandstone pavement jack pine barrens is located in northeastern New York (Figure 1a) and was formed as the result of catastrophic flooding scouring the landscape down to the sandstone pavement bedrock approximately 13,000 years ago. With an extent of ~2000 ha, this unique habitat is aptly named the Flat Rock. The New York Natural Heritage Program has ranked this site at a S1G2 designation, which is defined as having less than five sites statewide and 6–20 globally (Reschke, 1990). Annual precipitation averages ~80 cm and mean monthly air temperatures range from –11°C in January to 20°C in July. Summer surface temperatures, however, especially on exposed bedrock, often exceed 38°C and can be attributed to some cone opening (Cave et al., 2021; Franzi & Adams, 1999).

The eolian processes that created these pavement barrens have resulted in shallow, infertile soils underlain by Potsdam Sandstone, which characterize the site (Franzi & Adams, 1999). The Flat Rock overstory is dominated by jack pine (*Pinus banksiana*) but includes a mosaic of low-abundance northern hardwood species such as red maple (*Acer rubrum*), red oak (*Quercus rubra*), gray birch (*Betula populifolia*), white pine (*Pinus strobus*), and red pine (*Pinus resinosa*). The heath-like understory is dominated by ericaceous shrubs such as huckleberry (*Gaylussacia baccata*) and blueberry (*Vaccinium augustifolium*), as well as sweet fern (*Comptonia peregrina*), moss (*Sphagnum* sp.), lichen (*Lichen* sp.), and grasses (*Poaceae* spp.). Overall however, the Flat Rock barrens has relatively low species diversity compared with surrounding hardwood-dominated forests, which reflects low seasonal water availability and shallow nutrient-poor soils (Cave et al., 2021, personal observation; Franzi & Adams, 1999; Straub & Schultz, 2015).

On July 12, 2018, a wildfire burned 225 ha within the Flat Rock (Figure 1). The fire burned for 7 days before it was completely extinguished on July 18, 2018. Within the fire extent, landscape heterogeneity (i.e., wetland areas, beaver ponds, rocky escarpments) resulted in a range of fire severity from unburned refugia to complete combustion of the canopy layer and death of all trees. In most jack pine-dominated areas of the fire, understory vegetation was completely removed, mineral soil was exposed, and serotinous jack pine cones were opened by the heat of the fire—all requirements for successful seedling regeneration (Rudolph & Laidly, 1990). However, almost all jack pine stems, although dead, remained initially standing.

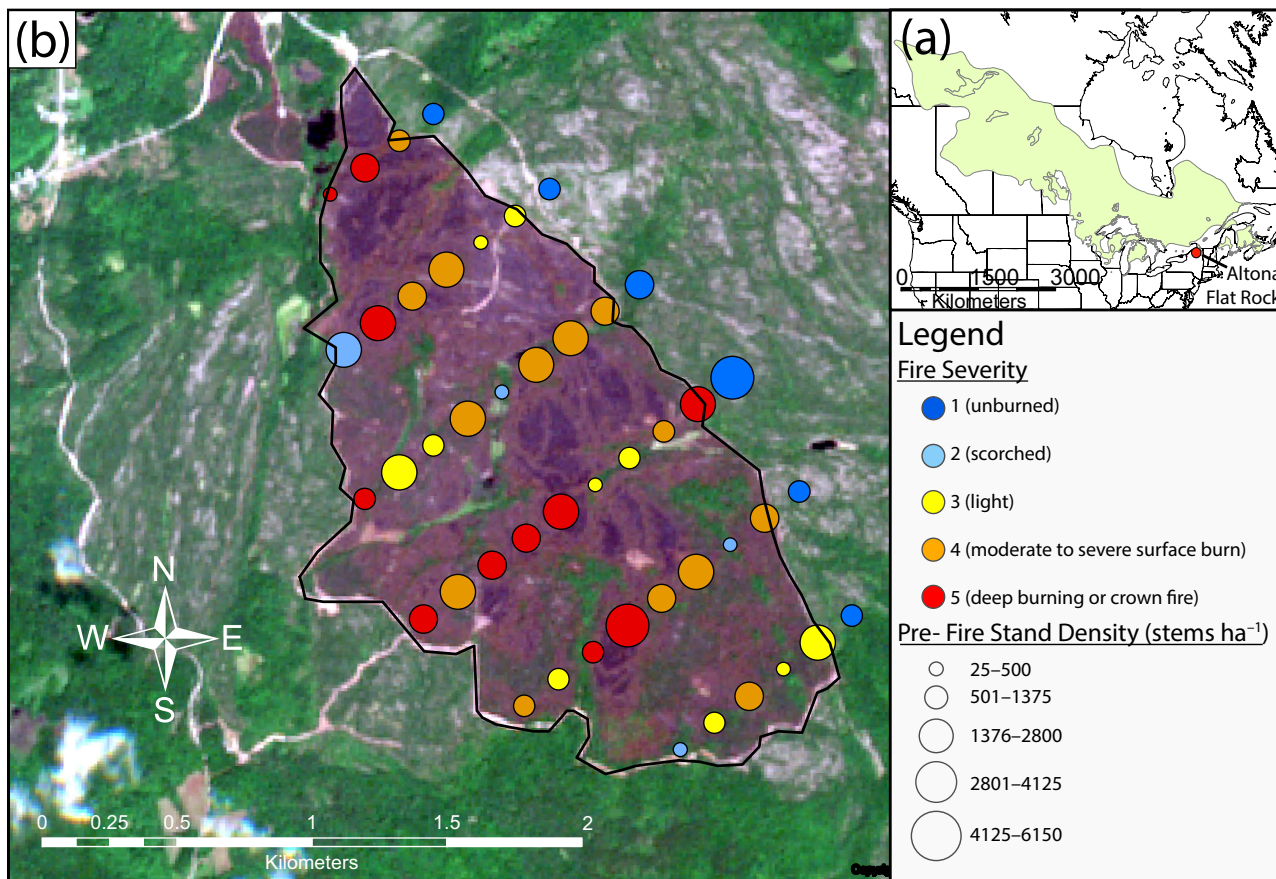


FIGURE 1 Map of 2018 disturbance study area. (a) Location of Altona Flat Rock in northern New York State. Shading shows the North American range of jack pine. (b) Black outline represents the 2018 wildfire extent. Plot locations are shown with filled circles. Symbol color and size represent fire severity and pre-fire stand density, respectively.

Field sampling

In spring 2019, 45 permanent plots were established traversing the 2018 wildfire and the adjacent unburned area (Figure 1). Plots were established every 200 m along six transects, each separated by 600 m. Plot location along a transect was dictated by the first disturbed plot along a transect being 25 m from the eastern edge of the burn. The other disturbed and undisturbed plots were then systematically distanced from that initial location (Figure 1). This unbiased sampling design maximized coverage of the disturbed area and incorporated gradients in topography, pre-fire forest structure and composition, and fire severity, while making sampling efforts feasible. At each 400-m² plot (20 × 20 m), we assessed burn severity based on a qualitative assessment adapted from a five-point scale (Keeley, 2009; Table 1).

Trees were tallied by species and classified as dead or alive to determine pre-fire stand density. At each plot, a soil sample was taken to assess soil moisture and organic carbon, and a densiometer was used to determine canopy cover. Lastly, within each plot, we subsampled three

1-m² plots to quantify understory cover (measured as percent abundance) and jack pine regeneration (measured as number of seedlings). Subplots were located 5 m from the plot center, with the first being directly north (0°) of the plot center and the second and third at 120° and 240°, respectively.

Following 2019 sampling, plots were monitored each subsequent spring (2020–2022) to track seedling density and understory changes. Additionally, beginning in 2021, as standing dead jack pine began to fall, we recorded coarse woody debris (CWD, all stems >7.6-cm diameter; Campbell et al., 2019) within a 5-m radius of the plot center. Also beginning in 2021, we measured heights of the 20 jack pine seedlings closest to a diagonal running from the northwest to southeast corner of each subplot.

Understory data analysis

We assessed understory composition (relative abundance) using nonmetric multidimensional scaling (NMDS) ordination in the “vegan” R package (Oksanen et al., 2019). This

TABLE 1 Qualitative fire-severity scale adapted from Keeley (2009), Ryan (2002), and Turner et al. (1994).

Fire severity	Description
1: Unburned	Plant parts green and unaltered, no direct effects from heat
2: Scorched	Unburned, but plants exhibit leaf loss from radiated heat
3: Light	Canopy trees with green needles although stems scorched; surface litter, mosses, and herbs charred or consumed; soil organic layer largely intact and charring limited to a few millimeters depth
4: Moderate or severe surface burn	Trees with some canopy cover killed, but needles not consumed; all understory plants charred or consumed; fine dead twigs on soil surface consumed and logs charred; prefire organic layer largely consumed
5: Deep burning or crown fire	Canopy trees killed and needles consumed; surface litter of all sizes and soil organic layer largely consumed; white ash deposition and charred organic matter to several centimeters depth

analysis allowed us to visualize differences in the understory community across time and fire severity. We also calculated understory species richness and transformed Shannon–Weiner diversity ($e^{H'}$) for the reference condition and each year. To further explore the relationship between understory richness and diversity in relation to time since disturbance and fire severity, we performed two-way repeated measures ANOVA to determine whether those effects were significant. For significant effects, we used Tukey’s honestly significant difference tests to determine significant differences between groups.

Jack pine regeneration analysis

We performed two-way repeated measures ANOVA to determine whether regeneration differed between years and fire severity. For significant effects, we used Tukey’s honest significance tests to determine significant differences between groups.

For each sampling period (2019–2022), we used a mixed-effects linear model to predict regeneration across the 39 disturbed plots. Prior to model fitting, regeneration density was checked for normality. We corrected for a right-skewed distribution by cubic-root transforming the seedling density and used the transformed variable in all

subsequent modeling. Fixed effects in the base model were (1) fire severity, (2) pre-fire stand composition and density—measures of seed source and availability—(3) understory species percent abundance—measure of competition—and (4) soil carbon and moisture—measures of site quality. All fixed-effect variables were standardized to facilitate direct comparison of effect sizes. We included subplots nested within plots as random effects in the model to account for fine-scale differences between and within sampling locations. All models were built using the “nlme” R package (Pinheiro et al., 2015). Base models, including all independent variables, were reduced using backward Akaike information criterion (“MASS” R package; Venables & Ripley, 2002). We checked models for issues of multicollinearity using the variance inflation factor (VIF) (“car” R package; Fox & Weisberg, 2019). Finally, models were checked to ensure that assumptions of residuals being normally distributed, linear, and having equal variance were met using q–q, observed versus predicted and residuals versus predicted plots (Appendix S1: Figure S1).

We modeled seedling height for 2021 and 2022 using the same suite of independent variables and modeling procedure. Seedling height was cubic-root transformed and models were checked using the same criteria as listed above (Appendix S1: Figure S2).

RESULTS

Pre-disturbance stand characteristics

The pre-fire average mature jack pine stand density across the disturbed area was 2046 trees ha^{-1} (Figure 1). Of those trees, 71% of them had been killed in the fire. Other tree species present across the site, prior to the disturbance (i.e., red maple, red oak, and white pine), contributed disproportionately less to overall density (437 trees ha^{-1}) and suffered 51% mortality in the fire. Average crown cover across the site was 43%. Stand characteristics across the six reference plots showed a slightly higher jack pine and other species density (2158 and 595 trees ha^{-1} , respectively), while canopy cover was the same compared with the disturbed plots.

Understory vegetation

Understory vegetation changed very little over time or between the reference condition and the disturbed plots (Figure 2; Appendix S2: Table S1). NMDS ordination (stress = 0.23) showed no differentiation of plots based on study year or plot type (Appendix S2: Figure S1). This

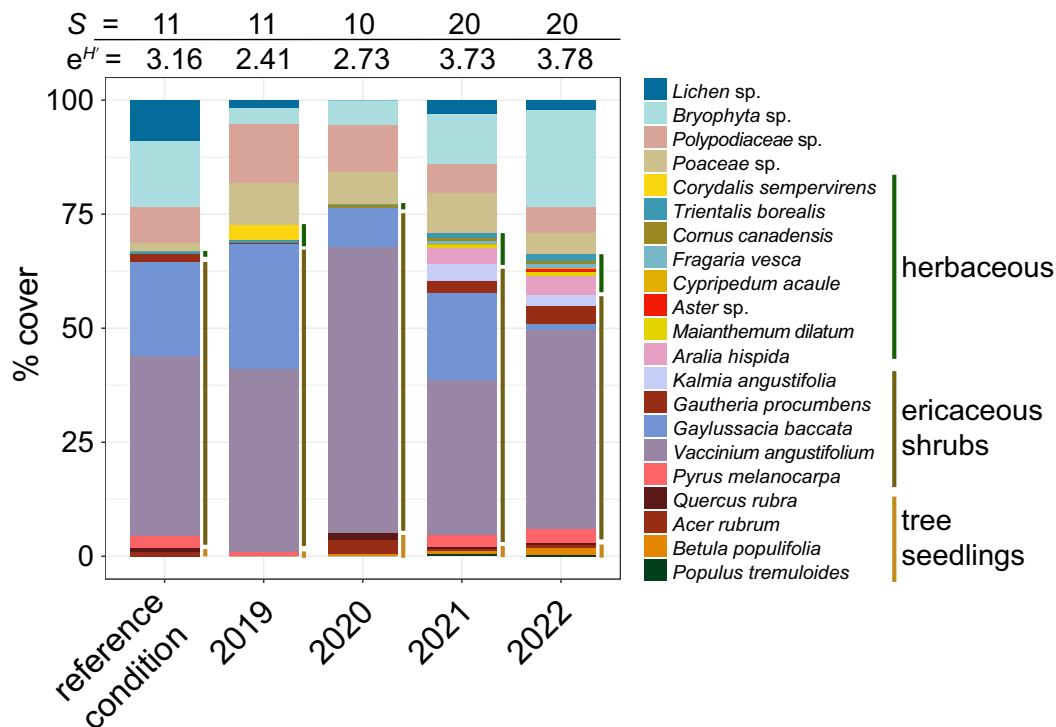


FIGURE 2 Average understory composition across the six unburned plots (data from 2019) and the 39 disturbance plots (sampled each year since the fire). Richness (S) and Shannon–Weiner transformed diversity (e^H) are given above each bar. Only species/groups that comprised $>1\%$ composition in at least one year of sampling were included (for composition details, see Appendix S2: Table S2).

lack of differentiation was driven by the immediate return in 2019 and then continued dominance of blueberry, huckleberry, mosses, ferns, and lichens following the disturbance, similar in composition to that of the reference condition community. Notable differences between the reference and disturbed plots were the continued higher proportions of grass in the disturbed plots, along with the herbaceous community (Figure 2). In particular, rock harlequin (*Corydalis sempervirens*) established immediately after the fire, but was absent from all other years and the reference plots (Figure 2). Other herbaceous species such as bristly sarsaparilla (*Aralia hispida*) and sheep laurel (*Kalmia angustifolia*) both appeared in the disturbed plots in 2021 and 2022, but were not present earlier, or in the reference plots. Finally, wintergreen (*Gautheria procumbens*) was not present in 2019 or 2020, but appeared in 2021 and 2022, similar to the reference plots (Figure 2). Increases in 2021 and 2022 of the number of herbaceous species were responsible for the greater diversity and richness seen in those years (Figures 2 and 3). However, in all cases, these species represent a very small percentage of the overall cover (Figure 2). Further, while understory diversity did significantly increase in 2021 and 2022 compared with earlier years and the reference condition (Figure 3; Appendix S2: Table S2), this effect was mediated by an

interaction with fire severity (Figure 3). From 2020 onward, there was a negative trend of fire severity on diversity, although these differences were only significant in 2020 and 2022 (Figure 3).

Regeneration patterns and models

In the spring of 2019, average regeneration across the disturbed area was 275,385 stems ha^{-1} (Figure 4). Density increased to 390,256 stems ha^{-1} in 2020, remained static in 2021 at 390,513 stems ha^{-1} , and declined in 2022 to 375,128 stems ha^{-1} (Figure 4). Differences between years were not significant (Figure 4; Appendix S2: Table S3). Jack pine seedling density was however significantly associated with fire severity, with higher fire severity resulting in overall higher seedling densities across all years (Figure 4; Appendix S2: Table S3). Variance in seedling density also increased with increasing fire severity (Figure 4). Compared with the pre-fire density of mature jack pine (2046 stems ha^{-1}), the post-disturbance area exceeded replacement density by $>370,000$ stems ha^{-1} . Tree seedling recruitment, besides jack pine, was low in all plots (Figure 2).

Final models for regeneration were all highly significant ($p < 0.0001$), with R^2 values ranging from 0.54 to

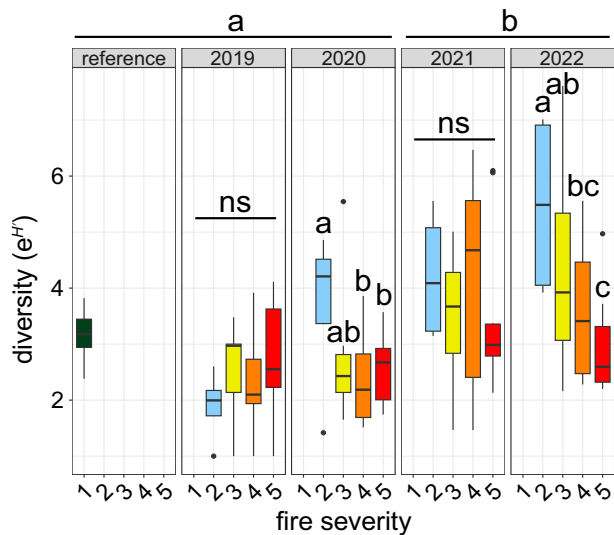


FIGURE 3 Understory diversity (transformed Shannon–Weiner index) as a function of year and fire severity. Reference values are based on 2019 sampling of the six unburned plots. Black lines within boxes represent the median seedling density. Boxes represent first and third quartiles, whiskers extend to the most extreme values within 1.5 times the interquartile range, and circles represent outliers. Different letters above boxes and above panels represent significant differences between fire severity within year and between years, respectively, at $p \leq 0.5$ based on repeated measures ANOVA and Tukey post hoc test results (Appendix S2: Table S2).

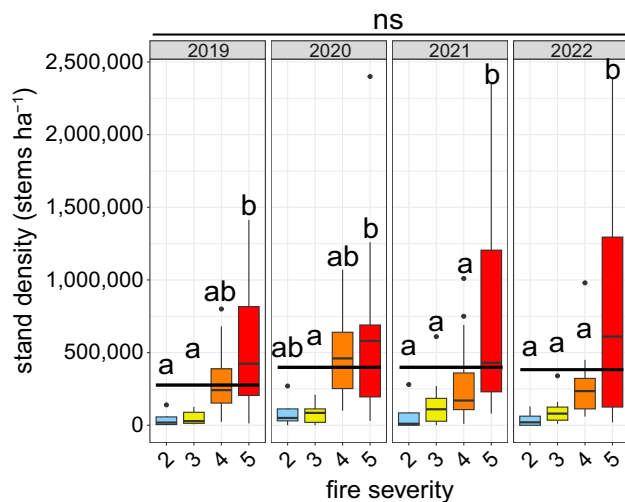


FIGURE 4 Post-disturbance seedling density by year and fire severity. Black lines within boxes represent the median seedling density. Boxes represent first and third quartiles, whiskers extend to the most extreme values within 1.5 times the interquartile range, and circles represent outliers. Different letters above boxes represent significant differences between fire severity within year at $p \leq 0.5$ based on repeated measures ANOVA and Tukey post hoc test results (Appendix S2: Table S3). The thick black line within each panel represents average seedling density across fire severity for each year (not significant).

0.68 in 2021 and 2019, respectively (Table 2). Fire severity was the most important driver of regeneration in 2019 and remained the most significant variable in regeneration each year thereafter (Table 2 and Figure 5). Moss was also positively associated with seedling density in all years (Table 2 and Figure 5). Pre-fire stand density was associated with higher seedling densities in 2019 and 2022, but not 2020 or 2021. Ericaceous shrubs were positively associated with seedling density in 2020 and 2021 respectively (Table 2 and Figure 5). Grass and duff were positively associated with seedling density in 2021 and 2022, respectively (Table 2).

Growth models

Final models of seedling height for 2021 and 2022 were highly significant ($p < 0.0001$) and had R^2 values of 0.45 and 0.35, respectively (Table 3). For both years, fire severity and % grass were positively associated with seedling height (Table 3 and Figure 6). Blueberry was also positively associated with seedling height in 2021 (Table 3 and Figure 6).

DISCUSSION

Forest resilience

Contrary to predictions from other studies (i.e., Miller & McGill, 2019; Stevens-Rumann et al., 2018; Vickers et al., 2019), our results suggest that climate change is not yet extreme enough to cause regeneration failure in this region. For populations located at an equatorial, or trailing, range margin, like jack pine at the Flat Rock, effects of climate change may be amplified, yet unobserved due to adult trees not yet suffering mortality (Jump et al., 2006). The persistence of adult trees, coupled with a lack of regeneration over the past 60 years due to a lack of stand-replacing fire disturbance prior to 2018 since 1957, limited our ability to determine whether the Flat Rock population was suffering from resilience debt (Johnstone et al., 2016; Jump et al., 2006). Our results, based on the 2018 disturbance, however, suggest that the jack pine forest is still highly resilient to fire disturbance. Our results agree with Hart et al. (2019) whose models showed jack pine forests as being highly resilient under a range of fire intervals and environmental conditions. Additionally, patterns of jack pine regeneration at the Flat Rock align with findings of other rear-edge boundary jack pine populations (Pelletier et al., 2022). Interestingly, regeneration not only occurred at the Flat Rock but exceeded density estimates of most other

TABLE 2 Final regression models for jack pine seedling densities by year.

Model	R ²	Fixed effects ^a	Coefficient ^b	SE	df	t	p	Random effects	SD
2019	0.68	Fire severity	0.4716	0.1041	35	4.53	<0.001	Plot	0.4826
		Pre-fire density	0.2788	0.1033	35	2.70	0.0106	Subplot	0.5101
		Moss	0.1556	0.0957	35	1.63	0.1131		
2020	0.61	Fire severity	0.5468	0.1034	35	5.29	<0.001	Plot	0.4287
		Moss	0.2581	0.0997	35	2.59	0.0140	Subplot	0.6125
		Huckleberry	0.1818	0.1054	35	1.73	0.0932		
2021	0.54	Fire severity	0.4714	0.1098	37	4.29	<0.001	Plot	0.5478
		Blueberry	0.1864	0.0824	75	2.26	0.0265	Subplot	0.5844
		Moss	0.1578	0.0713	75	2.21	0.0299		
		Grass	0.1357	0.0746	75	1.82	0.0727		
2022	0.61	Fire severity	0.4531	0.1052	36	4.31	<0.001	Plot	0.4528
		Pre-fire density	0.2543	0.1057	36	2.41	0.0214	Subplot	0.6002
		Moss	0.1614	0.0752	76	2.15	0.0350		
		Duff	0.1236	0.0729	76	1.69	0.0945		

Note: R² values are the marginal R² values for the fixed effects in the model.

^aVariables are listed on the order of effect magnitude.

^bAll coefficients are standardized.

post-disturbance jack pine studies (Chrosiewicz, 1988; Greene & Johnson, 1999; Pinno et al., 2013), suggesting that climatic tolerances for juveniles have not yet been exceeded (Jackson et al., 2009; Reyer et al., 2015). While much higher than many other studies, our regeneration densities of 375,128 seedlings ha⁻¹ do closely resemble those of de Groot et al. (2004), who also observed highly variable regeneration results ranging as high as 790,000 seedlings ha⁻¹.

Post-disturbance understory composition

Just as with the jack pine recovery, following disturbance, the understory community showed high resilience characterized by maintaining similar species richness and diversity (Day et al., 2017). Within one year, understory vegetation largely recovered back to the undisturbed condition with pre-fire dominant species such as blueberry, huckleberry, fern, and moss being the most abundant taxa in 2019. Blueberry, chokeberry (*Pyrus melanocarpa*), and ferns (*Polypodiaceae* sp.) are rhizomatous, a characteristic that allows for effective re-colonization of pre-established species following disturbance (Ahlgren & Ahlgren, 1960; Dawe et al., 2017; Engelmark, 1993; Hart & Chen, 2008; Scherer et al., 2018). Schimmel and Granström (1996) found that *vaccinium* returned to pre-disturbance conditions within 2–4 years, and we observed similar, if not more, accelerated results.

Disturbance events facilitate the establishment of otherwise inhibited understory species that are less competitive than the woody shrub-dominated understory of many mature forests, often resulting in higher species richness in the early years of recovery (Abella & Springer, 2015; Acker et al., 2017; Glitzenstein et al., 2012). Though we observed an almost immediate return to an understory compositionally similar to the undisturbed areas, there was a somewhat delayed response in increases in diversity and richness, which did not occur until three years post-disturbance, similar to what Day et al. (2017) found. Notable differences that led to this increase were first the ephemeral presence of sub-dominant graminoids and rock harlequin, classified as employing the evader strategy (Sirois, 1995) germinating from soil seed banks post-disturbance (Kershaw et al., 2002), and only present in the year immediately following the wildfire. By the third year, other herbaceous species not present in the reference plots (e.g., bristly sarsaparilla and wintergreen) emerged and may persist for some time until, for instance, light conditions from the maturing canopy alter the understory environment.

Patterns of regeneration and growth

Jack pine regeneration and growth was shown to be most strongly influenced by fire severity. This finding differs from other studies that report intermediate fire severity yielding highest regeneration rates (de Groot et al., 2004;

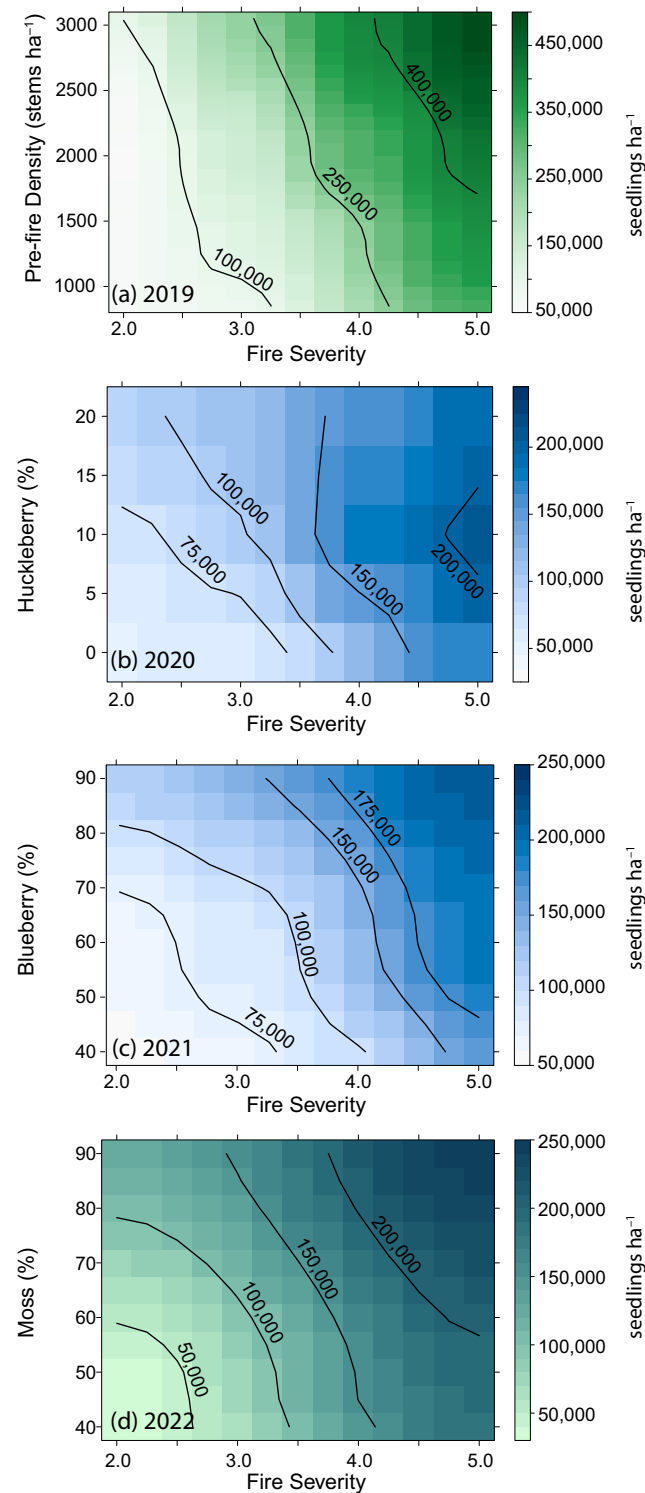


FIGURE 5 Variation in seedling density as a function of the two most influential predictor variables from each year's final regression model (with the exception of 2022 where the effect of moss is shown instead of prefire stand density as the second most influential variable). Seedling densities are shown across the full range of the predictor variables that were present in the disturbance. Darker shading indicates higher seedling densities, and isoclines indicate specific densities along the gradients.

Otto et al., 2010), but aligns with the findings of Jayen et al. (2006) who also observed that jack pine regeneration was most abundant in areas that experienced high fire severity. Discrepancies in how fire severity is related to regeneration success may be due to differences in rates of fire spread, head fire severity, and flame residence time—all of which impact the degree to which cones are opened and release viable seed, compared with being consumed by the fire (de Groot et al., 2004). Variation in these results could also be due to unstandardized fire-severity measurements. We determined fire severity based on Keeley (2009), while other metrics focus more specifically on average depth of burn in soil substrate (Whittle et al., 1997), degree of fuel consumption in the understory or canopy (Otto et al., 2010), or total effect of fire on an ecosystem (Jayen et al., 2006).

Our results indicate that pre-fire stand density, a proxy for seed rain, was a highly significant factor relating to seedling establishment in the first year of regeneration. Because it takes only one year for 90% of jack pine seeds to disperse (Greene et al., 2013), the absence of further recruitment after two years following disturbance suggests exhaustion of all viable seeds within the seed bed. The same relationship was observed by de Groot et al. (2004) in which regeneration numbers were primarily determined by total amount of seed rain within plots, but survival after the first year showed low correlation with seed rain. However, pre-fire stand density was also significant in our model for the fourth year, suggesting that the legacy effects of initial seedling density continue to be an important factor.

Contrary to the results of de Groot et al. (2004), our results show a positive association between duff and seedlings densities in the fourth year. Although seedlings rooted too deeply in duff are more susceptible to drought (Chrosiewicz, 1990), the sandstone pavement geology of the Flat Rock presents a unique environment, where the almost complete lack of soil and large areas of bare bedrock (Franzi & Adams, 1999) may make duff the more preferable rooting substrate.

Blueberry and huckleberry, the primary shrubs and groundcover at the Flat Rock, along with grass, positively affected both seedling densities and growth. This positive association may be a function of seedling survival and growth being facilitated by the shade and moisture retention these species provide. A similar nurse plant relationship between pine and *Vaccinium* sp. has been observed previously (Perkins, 2015), and grass may also be providing some shade or assisting with soil water retention (Holmgren et al., 1997). Grass may also be an indicator of higher quality microsites and thus be a proxy of favorable conditions for seedling growth (Graae et al., 2011). Further, blueberry may be facilitating jack pine seedling

TABLE 3 Final regression models for jack pine seedling heights by year.

Model	R ²	Fixed effects ^a	Coefficient ^b	SE	df	t	p	Random effects	SD
2021	0.45	Fire severity	0.3465	0.0983	37	3.52	0.001	Plot	0.3495
		Grass	0.1722	0.0868	76	1.98	0.0508	Subplot	0.7710
		Blueberry	0.1488	0.0889	76	1.67	0.0984		
2022	0.35	Fire severity	0.3851	0.0891	37	4.32	<0.001	Plot	0.1923
		Grass	0.1321	0.0852	77	1.55	0.125	Subplot	0.8500

^aVariables are listed on the order of effect magnitude.

^bAll coefficients are standardized.

success through belowground mycorrhizal interactions (Perkins, 2015). These findings support the idea that the positive effects of a facultative relationship can outweigh the negative effects of competition in environments with a paucity of soil and microsite differences, such as is found at the Flat Rock (Bertness & Callaway, 1994). Rowe (1983) noted similar post-fire regeneration patterns and attributed them to regeneration strategies (e.g., endurer, evader, invader, avoider). Ericaceous shrubs such as *Vaccinium angustifolium*, *Kalmia angustifolia*, *Gaylussacia baccata*, and *Pyrus melanocarpa* are characterized as endurers that persist as rhizomes following a fire disturbance (Rowe, 1983; Sirois, 1995; see Appendix S2: Table S1 for species regeneration classifications).

Finally, cryptogams can provide conifers with moist substrate favorable for early establishment and survival (Chrosiewicz, 1990). We observed high correlations between seedling densities and presence of moss in three of four years, which agrees with establishment patterns observed in jack pine stands in Quebec (Jayen et al., 2006) and with other pine species (Ahlgren & Ahlgren, 1960; Vanha-Majamaa et al., 2007). Turetsky et al. (2012) performed a meta-analysis on the important role for moss in maintaining ecosystem resilience because they aid in nutrient cycling (DeLuca et al., 2007), create microtopographic complexity (hummock and hollows; Titus et al., 1983), and can either facilitate or inhibit (allelochemicals; Steijlen et al., 1995) vascular plant germination. Field and laboratory studies from the fire-prone New Jersey pinelands determined that seedling germination is positively correlated with moss and negatively correlated with lichen, due to interference with ectomycorrhizal functioning (Sedia & Ehrenfeld, 2003). Similarly, Stuver et al. (2014) found that seedling germination can be facilitated by some mosses. However, crust-forming cryptogams have been shown to inhibit seedling germination in pine barrens soils (Gilbert & Corbin, 2019), which is a characteristic that is likely to increase with changing climate and is worthy of note in future studies at the Flat Rock. More specifically, warming temperatures and reduced rainfall patterns have

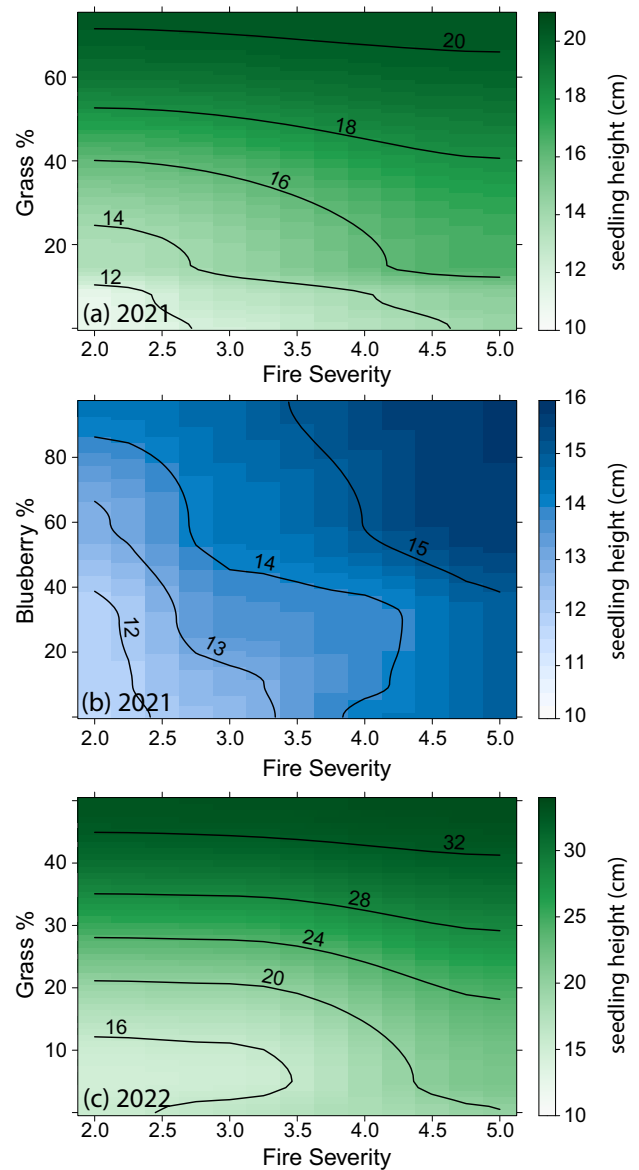


FIGURE 6 Seedling height as a function of (a) fire severity and grass relative abundance in 2021; (b) fire severity and blueberry relative abundance in 2021; and (c) fire severity and grass relative abundance in 2022. Seedling heights are shown across the full range of the predictor variables that were present in the disturbance. Darker shading indicates greater seedling height, and isoclines indicate specific heights along the gradients.

shifted moss-dominated biocrusts to lichen domination (Li et al., 2021), which may negate the nurse plant effect that many of the current understory plants are afforded when adjacent to mosses on the barrens.

Conclusions

The 2018 wildfire at the Altona Flat Rock gave us the opportunity to understand how jack pine resilience might have changed at its southern range margin in the time since the last disturbance (>60 years). We were able to document that the Flat Rock forest system not only appears to be free from resilience debt (Johnstone et al., 2016) or regeneration failure (Boucher et al., 2020), but also that regeneration exceeded most estimates. However, as climate continues to change, along with associated changes in the disturbance regime, long-term, fine-scale monitoring of vulnerable ecosystems, such as the Flat Rock, is essential. The short-term regeneration dynamics that we documented here may not be indicative of longer-term forest persistence and health, especially if fire rotation intervals become shorter (Braziunas et al., 2018) or climate conditions move beyond juvenile thresholds (Jackson et al., 2009).

AUTHOR CONTRIBUTIONS

Mark Lesser and Danielle Garneau conceived the idea and the experimental design for the study and conducted the field sampling from 2019 to 2022. Mark Lesser also conducted all statistical analysis. Harleigh Green conducted field sampling in 2019 and assisted in writing the first draft of the manuscript. Mikayla Osmer conducted field sampling in 2020–2021 and also contributed to writing early drafts of the manuscript. Devan Bushey conducted field sampling in 2020–2022 and wrote the final draft of the manuscript along with Danielle Garneau and Mark Lesser.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Lesser et al., 2023) are available from the Open Science Framework: <https://doi.org/10.17605/OSF.IO/6AB49>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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