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Title Page

Pitch Pine Stands Recover, Adapt, and Persist in the Absence of Fire Under the Influence of Elevation and Topographic Factors

Authors and affiliations:

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Key words

Pinus rigida, Pitch pine, Mount Desert Island, fire, elevation, resilience, adaptivity, chemical, geography

ABSTRACT

Globally rare pitch pine (*Pinus rigida*) is thought to depend on intermittent fire, which encourages reproduction and niche preservation. At Mt. Desert island in Acadia National Park (ME, USA) a stand-replacing conflagration enveloped a portion of the island in 1947. However, there has been no recurrence of fire. Other populations on the island have been unaffected by fire disturbance for over one hundred years. Fire history is shown to influence plant form and functioning, yet these impacts are not well quantified for pitch pine in relation to factors such as elevation and topography, which are also known to impact traits of this species. We studied the impact of fire history on traits of pitch pine individuals across elevation (9.5 to 404 m) and topographic (flat, ledge and cliff) gradients at Mt. Desert Island. Traits included growth, stand density, photosynthetic water use efficiency, and foliar nutrients. We also measured site data such as soil nutrients, soil water retention, elevation, slope, and aspect. Elevation was found to be a greater driver of persistence than fire history and there was little interaction between elevation and fire history. Our data indicates that fire return intervals were likely too infrequent to support selection for recovery capacity traits; instead, persistence capacity traits increased in response to low intensity disturbances. Trees at upper elevations were smaller, narrower, and less canopied

57 than those at lower elevations and had greater water use efficiency, indicating a preference for
 58 stress resistance overgrowth at harsher, high elevation sites. At modest elevation trees exhibited
 59 greater capacity for growth and a reduction in stress tolerance traits due to more favorable
 60 conditions, including greater soil moisture retention. Our data provide criteria for management of
 61 pitch pine survival where persistence capacity is greatest at flat and cliff locations in both burned
 62 and unburned populations.

64 INTRODUCTION

65 On Mt. Desert Island (MDI) in Maine USA, globally threatened pitch pine (*Pinus rigida*
 66 Miller) dwell at the edge of their northeastern range. Some fire ecologists in the Northeast USA
 67 suggest that wildfire is required every six to twenty-five years to perpetuate and rejuvenate pitch
 68 pines (Jordan *et al* 2003) such as these. Yet, on MDI, pitch pine survives despite fire suppression
 69 (Miller *et al* 2017), which has persisted in the aftermath of the infamous 1947 conflagration
 70 (Figure 1). It is not entirely clear what factors contribute to recovery and persistence of pitch
 71 pine in the absence of fire (Patterson Saunders and Horton 1983; Parshall *et al* 2003). In coastal
 72 Atlantic states further south, there is less concern since natural fire (Foereid *et al* 2015) and
 73 anthropogenic controlled burns (Carlo *et al* 2016) comprise a system where there is reduced fuel,
 74 removal of evergreen competition and opening of canopies (Neill *et al* 2007).

75 At MDI, trees in low-lying undisturbed (non-1947 fire) areas (Figure 2) appear to engage,
 76 in more seedling recruitment than trees in the upper elevation fire zone. Indeed, reaction to fire
 77 absence manifests as physiological and morphological adjustments over many years (Little
 78 1953). On the island, cone serotiny (Givnish 1981), thick bark, and epicormic re-sprouting
 79 (Renninger *et al* 2013) have disappeared in formerly fire-prone pitch pine ecosystems (Jordan *et*
 80 *al* 2003). Suppression makes it likely that such former fire adaptive mechanisms are no longer
 81 required for stand sustenance and are unnecessary investments which reduce competition with
 82 other evergreens (Buma *et al* 2013). Critically, it is not clear if, in combination with a long
 83 period without fire, recovery accelerates the disappearance of adaptive traits (Heuss 2018) or if
 84 this is a result of extrinsic responses to other, low intensity disturbances. Previous studies (e.g.,
 85 Ibáñez *et al* 2019) have framed resilience as an artifact of recovery (Charpentier 2020)
 86 specifically in the absence of further fire disturbance and adaptation to climate change (Swanston
 87 *et al* 2018). We attempt to distinguish between recovery and persistence capacity through a new

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110 qualitative model which explains pitch pine responses to fire history and non-fire environmental
 111 constraints as a function of elevation and topography (Dunne *et al* 2004) (Figure 3). The model
 112 is informed by earlier resilience theories (Jordan Patterson and Windisch 2003; Howard and
 113 Stelacio 2011; Ibáñez *et al* 2019). Here, we hypothesize that pitch pine populations exhibit non-
 114 mutually exclusive responses: (1) **recovery capacity** (*REC_C*) as a measure of plant performance
 115 (Ibáñez *et al* 2019) long after fire disturbance (Patterson Saunders and Horton 1983) and (2)
 116 **persistence capacity** (*PER_C*) that reflects responses in the absence of disturbance (Brand and Jax
 117 2007).
 118 Each capacity metric reflects physical responses, such as the tradeoffs between growth
 119 and stress avoidance and colony retreat and expansion (Swanston *et al* 2018), as a function of
 120 stand density (Churchill *et al* 2012) and as an ‘ecologically stable strategy’ (Day and Greenwood
 121 2011). *REC_C* is the better understood of the two pathways given the extensive literature covering
 122 resilience (Ibáñez *et al* 2019) and tree health (Fuller and Quine 2016). *PER_C* on the other hand,
 123 explains a trend where shade-intolerant pitch pine out-compete other evergreens, such as red
 124 spruce (*Picea rubens*), hemlock (*Tsuga canadensis*) and balsam fir (*Abies balsamea*), thus
 125 expanding into new, mostly uninhabited territory. There is a scarcity of the biogeochemical,
 126 elevation, and topographical data at MDI needed to inform the functionalities within this model.
 127 To remedy this, we consider soil and plant nutrition including carbon (C), nitrogen (N), and
 128 stable isotope analysis to determine how intrinsic water use efficiency ($iWUE_{\delta^{13}C}$), soil moisture
 129 retention, growth and stand density are affected by fire history and topography.
 130 Fire history is revealed by subsurface charcoal remnants found in previous fire zones.
 131 Charcoal pyrogenic carbon (PyC) is abundant in selected areas of the north side of Cadillac
 132 Mountain (Patterson Edwards and Maguire 1987) and downslope pockets along the Park Loop
 133 Road at Gorham cliffs. These deposits suggest the possibility of recalcitrant soil C and high
 134 mineral holding capacity long after a fire event (Pingree and DeLuca 2017). Both fire history
 135 artifacts like charcoal (Licht *et al* 2017) and increasing elevation have been shown to increase
 136 water use efficiency (Wang *et al* 2017). Given the difference in fire histories between
 137 populations, this provides a nearly ideal testbed to better clarify aspects of chemical geography
 138 (Verma and Jayakumar 2012) and address a number of key questions with regard to leaf traits,
 139 tree growth, and stand dynamics.

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Our foremost aim is to examine a proposed model through an analysis of four key pitch pine populations according to the *interactive* influence of fire *and* elevation. Given previous studies of fire involvement and post-fire photosynthetic response (Chen Wang and Jia 2017), we hypothesize *that* pitch pine growth and population expansion is greater at *non-fire sites* with low elevation *due to* *higher* soil C, *higher* foliar C (Butak 2014), more negative $\delta^{13}\text{C}$ (Licht and Smith 2020), and greater soil water retention (positive indicators of *PERC*). We further theorize *that* trees at low elevations display a greater propensity for growth in height, *canopy*, and DBH through more competitive resource conservation (Stambaugh *et al* 2015). *Additionally*, we *hypothesize that* ubiquitous contours (Howard and Stelacio 2011) at upper ledge elevations, which limit clustering (stand density) elsewhere, will be less stressful for colonization (Lafon *et al* 2014) and expansion on lower elevation flat and cliff surfaces. *We* predict *this* will increase pioneering efforts at gentler slopes and more southerly aspect.

METHODS

Study Extraction Sites

We investigated fifteen pitch pine specimens at each of four sites at MDI (Table 1), factorially crossed in a fire history (Miller *et al* 2014) by elevation design: (1) Wonderland trail between 9 and 25 m elevation (low elevation, outside the footprint of the 1947 fire), (2) Gorham cliffs between 24 and 36 m (low elevation, within the footprint), (3) St. Sauveur trail between 134 and 198 m (high elevation, outside the footprint) and (4) South Cadillac trail between 188 and 417 m (high elevation within the footprint).

Allometry

We measure individual tree height (m), canopy spread (m), and stem diameter at breast height (DBH; cm). Tree height was estimated using nested, 2 m calibrated, aluminum rods (Garelick, St. Paul, MN, USA). Canopy spread was measured using the span between the same calibrated aluminum rods fixed with two landscape flags as a ground truth reference. DBH was measured at 1.06 m using a ProSkit electronic digital caliper (Amelia, VA, USA).

Clustering

Mean distances were calculated between sampled trees ($N = 167$) and up to five of their nearest, reproductively mature, conspecific neighbors (within 5 m) in the same clump (Churchill

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et al. 2012). Mean neighbor distance is a surrogate, but inverse, measure for stand density (Mosseler Rajora and Major 2004).

Topographic Features

We used a Kodak Trimble Juno 3B unit to obtain horizontal resolution of data plotted using 5-7 satellite telecommunication vehicles to maintain a maximum position dilution of precision. These data were differentially corrected and have estimated accuracies in the horizontal and vertical direction of 2 m, while selective availability is set to zero. We also used multiple satellite-configured GPS data (USGS 2m LIDAR 2010) to determine coordinates for individual trees (Lubinski Hop and Gawler 2003) as well as slope and aspect attributes using ArcGIS (version 10). Mapping of this type of data has been used in the past to compare physiography and recalcitrant chemical biogeography, particularly in fire prone contexts (Szpakowski and Jensen 2019).

Isotopic Analysis

We obtained C isotopic data ($\delta^{13}\text{C}$) and N isotopic data ($\delta^{15}\text{N}$) of fully expanded leaves (needle cluster) for 15 individual pitch pines at each site. Sample fascicles were separated and dried for two days at 60 °C, ground in a SPEX ball mill (Metuchen, NJ, USA), weighed to 2 mg for leaf tissue and 5 mg for soil using a micro analytic balance (Cole-Palmer, Vernon Hills, IL, USA), and rolled in 5 x 9 mm tin capsules (Costech, Valencia, CA, USA). Combustion gasses were separated on a gas chromatograph column, passed through a diluter and reference gas box, and introduced into the spectrometer (Thermo Delta V+ IR-MS, Waltham, MA, USA). $\delta^{13}\text{C}$ was used to indicate water use efficiency (iWUE $\delta^{13}\text{C}$) (Farquhar et al. 1989).

Foliar Tissue Analysis

Leaf tissue was obtained from excision of basal fascicle bundles at 1.06 m height. 50 mL samples of needles were separated, cut and dried for two days at 60 °C. Then they were ground in a SPEX ball mill (Metuchen, NJ, USA), sieved to <10 mm, and <2 mL were fed to a Leco C/N-2000 Carbon-Nitrogen Analyzer (Leco Corp., St. Joseph, MI) coupled with the spectrometer to determine C and N concentrations. 35 mL aliquots were submitted for standard plant tissue nutrient analysis using a TJA Model 975 AtomComp ICP-AES (Thermo Jarrell-Ash Corp., Franklin, MA). The method comprised submersion in a 5 mL trace-metal-grade HNO₃ treatment, then refluxed on hot block at 80 °C for two hours and diluted to 25 mL with 0.4 micron PTFE syringe filters to access extractable macro and micro inorganics.

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289 Soil Analysis

290 Soils (porous and acidic hornblende granite or Ellsworth schist) were uniformly shallow,
291 homogeneous, low fertility (varying between .7-2.5 cm) and overlain with rapidly drying needle
292 duff (Day *et al* 2005). All sites were excavated similarly by hand trowel and soil probe
293 (Accuproducts, Saline, MI, USA). Aliquots were extracted from O_a-A_b horizon soil pockets of
294 organic and mineral deposits within 50 cm of the tree base. 250 mL soil samples were sieved
295 (#10) and measured in 2019. Drying was performed in an oven at 100°C for two days. Analysis
296 was performed using a modified Mehlich method using inductively coupled plasma
297 spectroscopy, pH measurement via proton activity of a 1:1 slurry and effective soil cation
298 exchange capacity (CEC) via formic acid extraction. These methods are described more fully
299 elsewhere (Licht and Smith 2018). Soil C and N were calculated using elemental analysis in a
300 similar fashion to method above for foliar samples.

301 Soil Water Retention (SWR)

302 70 mL soil samples were extracted at 15 tree locations at each of four sites, from <7.5 cm
303 (O_a-A_b) horizon above bedrock. In a laboratory, 50 g H₂O were added to each aliquot to assess
304 net water retention as a subset of soil moisture evaporation (ψ_g) to determine net evaporative loss
305 or adsorption to surfaces. Soil water retention analysis was conducted according to the Fields
306 method (Licht and Smith 2018). Retention effects of gravitational and evaporation forces was
307 made on a wet basis where $W_m = g \text{ H}_2\text{O} \bullet (g \text{ moist soil})^{-1}$ (Jingfang and Wenwei 2018).

308 Statistical Analysis

309 All data were analyzed using a similar linear model structure with elevation (high or low)
310 and presence of the 1947 fire (yes or no) as categorical fixed factors. The interaction between
311 elevation and presence of the 1947 fire was also included in each model. In total, 27 models were
312 fit with the following dependent variables: tree height (m), canopy spread (m), DBH (cm), mean
313 distance between neighbors (m), foliar: carbon (C, %), nitrogen (N, %), carbon/nitrogen (C/N,
314 unitless), $\delta^{13}\text{C}$ (‰), $\delta^{15}\text{N}$ (‰), calcium (Ca^{2+} , g g⁻¹), phosphorus (P, g g⁻¹), potassium (K^+ , g g⁻¹),
315 magnesium (Mg^{2+} , g g⁻¹), aluminum (Al^+ , g g⁻¹), zinc (Zn, g g⁻¹), soil: C (g g⁻¹), N (g g⁻¹), C/N
316 (unitless), Ca^{2+} (g g⁻¹), P (g g⁻¹), K^+ (g g⁻¹), Mg^{2+} (g g⁻¹), Al^+ (g g⁻¹), Zn (g g⁻¹), water retention
317 (%), pH (unitless), and CEC (cmol_c kg⁻¹). Tree height, canopy spread, DBH, foliar P, foliar K,
318 foliar Zn, soil P, soil Al, soil Zn, and soil C/N were log transformed to meet model assumptions

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of normality and heterogeneity of variances. Soil water retention was arcsin square root transformed to meet model assumptions.

All linear models were fit using the 'lm' function in R (R Core Team 2019). Significance tests for each fixed factor was performed using the 'anova' function in R (R Core Team 2019). Post-hoc Tukey's tests were done to examine significant interactions between elevation and the presence of the 1947 fire using the 'emmeans' package in R (Lenth 2018). Because aspect data is circular in nature, we analyzed aspect data using a Watson's Two-Sample Test of Homogeneity as implemented in the R package 'circular' (Agostinelli and Lund 2017). Specifically, one-to-one comparisons were done between each site in all six possible combinations.

All analyses were performed with R version 3.5.1 (R Core Team 2019).

RESULTS

Aspect

Watson's two sample t-tests indicated that the aspects of all sites differed with respect to one another except for the two sites that experienced the 1947 fire (Gorham Cliffs and South Cadillac Trail), which had similar aspects (Table 2 and Figure 4).

Allometry and Stand Density

There was a significant interaction between fire and elevation on tree height ($P < 0.01$; Figure 5A and Table 3) and DBH ($P < 0.05$; Figure 5C and Table 3), with trees at higher elevation that experienced the 1947 fire being shorter than those at low elevation that did not experience the fire and having a smaller DBH than all other sites. Canopy spread tended to be reduced at high elevation ($P < 0.01$, Figure 5B and Table 3), although Tukey's HSD tests revealed no difference between sites at $\alpha = 0.05$. Distance between neighbors was greater at high elevation sites, particularly the one that experienced the 1947 fire ($P < 0.01$, Figure 5D and Table 3).

$\delta^{13}\text{C}$

Trees at higher elevations experienced less negative $\delta^{13}\text{C}$ ($P < 0.01$, Figure 6A and Table 4), reflecting greater water use efficiency, regardless of fire history. There were no significant differences between tree populations for $\delta^{15}\text{N}$ ($P > 0.05$, Figure 6B and Table 4).

Foliar Organics

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On average, foliar C was greater at higher elevations, however the results were not statistically significant ($P > 0.05$, Figure 7A and Table 5); nor was there a difference in C/N between sites ($P > 0.05$, Figure 7C and Table 4). Our linear model suggested that fire accounted for a significant influence on foliar N ($P < 0.05$, Table 5), however post-hoc Tukey's tests found no difference between sites at $\alpha = 0.05$ (Figure 7B).

Foliar Macronutrients

Foliar Ca^{+2} was negatively impacted by increasing elevation ($P < 0.001$, Figure 8A and Table 6). Our linear model suggested that foliar P was significantly higher at fire-involved sites ($P < 0.01$, Table 6), although this was not confirmed by post-hoc Tukey's tests (Figure 8B). Foliar K^{+} was reduced in the high elevation site that experienced fire as compared to the other sites (elevation x fire; $P < 0.05$, Figure 8C and Table 6). Neither foliar Al^{+} nor Mg^{2+} differed by site ($P > 0.05$ in both cases; Figure 8C and Table 6). Foliar Zn concentrations were 9% lower in the high elevation sites than on the low elevation sites ($P < 0.01$, Figure 8F and Table 6), due to a particularly strong reduction at the high elevation site that experienced fire.

Soil Organics

Soil C concentrations were greater at lower elevations ($P < 0.05$) and sites that did not experience the 1947 fire ($P < 0.05$, Figure 9A and Table 7). Soil N did not vary between sites ($P > 0.05$, Figure 9B and Table 7). Soil C/N was 15% lower at high elevation sites ($P < 0.05$, Figure 9C and Table 7), but we found no significant disparity in C/N when either fire history or fire history by elevation interactions were examined ($P > 0.05$ in both cases).

Soil Macronutrients

Soil Ca^{+2} decreased with elevation ($P < 0.05$, Figure 10A and Table 8). P, Mg^{2+} , and Zn were not significantly different across sites (Table 8). However, fire accounted for a 48% reduction in K^{+} at sites with fire history ($P < 0.01$, Figure 10C and Table 8). There was an interaction between elevation and fire history for Al^{+} ($P < 0.01$, Figure 10E and Table 8), which indicated...

Soil Water Retention, CEC, and pH

There was an interaction between elevation and fire history on SWR ($P < 0.01$, Figure 11A and Table 9), with markedly higher values at Gorham cliffs, the low elevation site that experienced fire, as compared to other sites. Soil pH was not different between sites ($P > 0.05$, Table 9). Our linear model indicated that CEC was higher at the high elevation sites ($P < 0.05$,

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Table 9), but this was not confirmed by our post-hoc Tukey's tests, which indicated no difference between sites (Figure 11C).

DISCUSSION

Elevation, as opposed to fire, was the dominant driver of the plant and ecosystem processes we measured, which indicated that persistence capacity (PER_C) was more important than recovery capacity (REC_C) at MDI, at least over the last one hundred years according to twenty-four statistically significant response variable data. Our findings underscore differences between REC_C and PER_C pathways and provide an explanation to resolve an enigma of persistence in fire absence and the dominant influence of elevation.

Elevation played a role in several meaningful ways. We confirmed that increased elevation tends to improve efficiency (increased $iWUE_{\delta^{13}C}$ over growth (Wang *et al* 2017; Chen, Wang and Jia 2017). Further, we found distance between neighbors at higher elevation was greater compared to lower elevation sites, thus generating sparser tree numbers aggregated within REC_C compared to PER_C . At the highest elevation, South Cadillac trail, we expected to find the steepest slopes, but they were far less steep than those at Gorham cliffs, a low elevation site. We anticipated that low elevation (<50 m) populations would feature a greater number of conspecific neighbors as a function of no fire history, flat or cliff orientation, evidenced by a gentle slope (<10°), and tendency towards a southerly aspect ($\mu = 180^\circ$). In fact, this theory was found correct, as Wonderland, which was by far the flattest terrain, trees achieved the widest distribution with the greatest distance between trees over the widest contiguous area as a function of REC_C . There was sufficient variability in some of the data, like stand density, to produce valuable information about differences between flat, cliff and ledge communities, even if at a small spatial scale.

Fire history was less important than elevation in the response variables we measured, even at high elevation ledge communities. We found little compelling empirical evidence that fire is a necessary ingredient in perpetuation at MDI. Fire return intervals have lengthened at MDI to the point where they are quite likely to be too intermittent to perpetuate previous fire resistance traits. A shift back to fire, accompanied by a re-introduction of serotinous characteristics, is not impossible in the future; however, current climate projections advise against this occurrence. Despite the absence of fire, there is the presence of fire remnants. The

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972 current study builds on previous work (Licht and Smith 2020) to determine how an obvious post-
 973 fire effect—anthropogenic fire charcoal (PyC)—changes according to elevation and topography
 974 in association with greater (more negative) $\delta^{13}\text{C}$, negligible consumption of Ca^{2+} , K^{+} and
 975 Mg^{2+} and increased soil moisture holding capacity. In this study we hypothesized that $\delta^{13}\text{C}$
 976 stored plant C and soil water retention would change significantly as a result of fire history.
 977 However, besides an increase in soil water retention with fire at the low elevation site, this
 978 hypothesis was not supported. Instead, we found lower $\delta^{13}\text{C}$ at high elevations regardless of
 979 fire history, consistent with reported outcomes for non-glaciated populations in flat, sand plain
 980 New Jersey Pine Barrens (Mikita-Barbato *et al* 2015; Schafer and Bohrer 2016). We also found
 981 congruence between low elevation outcomes in the present study and those reported ($\mu = 33\text{m}$
 982 above sea level) in the New Jersey pine barrens (Carlo *et al* 2016). However, we could not draw
 983 any other useful comparisons between the studies due to a lack of data concerning clustering
 984 (stand density), slope, or aspect factors. There is evidence from previous investigations that post-
 985 fire PyC remnants, which endure in the soil layer (DeBano 1981), increase alkali cations (Kolden
 986 *et al* 2017), and solubilized minerals (Caldwell and Richards 1989) and are likely linked to
 987 thermal exfoliation (Shakesby and Doerr 2006). From the standpoint of reproduction, the
 988 absence of fire at locations such as PERC-oriented Wonderland trail (Butak 2014), does not
 989 appear to be slowing down expansion in that flat-sloped region nor in other cliff locations that
 990 we and others studied (Howard 2010).
 991 Developing further insights into the ecological stoichiometry of pitch pine at MDI is a
 992 worthwhile goal given earlier discoveries by Fernandez (2008). Our nutrient analysis derived
 993 from burned and unburned trees was similar to a methodology in a New Jersey study (Renninger
 994 *et al* 2013) and produced some similar results. Since elevation is a key factor, we noted foliar Zn
 995 was higher at lower elevations at MDI; this was consistent with findings by others in another
 996 New Jersey investigation (Kolker *et al* 2013). In both Maine and New Jersey, it is possible PERC
 997 may be enhanced by higher concentrations of foliar Ca^{2+} , K^{+} , Mg^{2+} , P, Al^{+} and Zn (Mg^{2+} foliar
 998 availability was not significant in this study). We were particularly interested in P, a limiting
 999 factor (Verma and Jayakumar 2012); it is sometimes found to co-occur with pools of greater C
 1000 (Preston and Schmidt 2006). Scientists elsewhere assert that fire-induced sedimentary charcoal
 1001 produces soil C enrichment (Patel *et al* 2016) as measured in soil columns (Hart Horn and
 1002 Grissino-Mayer 2008). One could argue that charcoal remnants likely play a role in REC at

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1071 burned-over Cadillac Brook (below the heights of South Cadillac trail), but it is not known to
 1072 what extent these benefit the larger ecosystem. We conjecture that soil C persistence since the
 1073 1947 fire at burned-over areas such as South Cadillac trail reflects a Jack of pyrogenic carbon
 1074 removal (Doerr *et al* 2018), though elsewhere lower C availability is attributable to greater
 1075 consumption by fungi (Luo *et al* 2017). P concentration at upper elevations at MDI contrasted
 1076 with more modest availability at other, low-lying pinelands at MDI and in New Jersey
 1077 (Renninger *et al* 2013; Alkaniiz *et al* 2018). One explanation for substantial soil P availability is
 1078 that it derives from charcoal remnants; however, lacking mycorrhizal studies we were unable to
 1079 confirm the extent of P liberated from the charcoal in the two 1947 fire precincts.
 1080 Climate is likely the final arbiter of decline rather than stand-replacing fire disturbance in
 1081 the case of long-term pitch pine livelihood. Recent climate change models anticipate negative
 1082 impact on future vegetative status at MDI (Fernandez *et al* 2015), but these do not specifically
 1083 address the adaptability of pitch pine nor the extent to which plasticity (Day *et al* 2014) is
 1084 shaping tendency towards *PERC* or *REC*. What has been clear for at least two decades is the
 1085 effect of global climate change on ecophysiology traits. Day, Greenwood and White (2001)
 1086 found that an uptick in annual temperatures signaled increased leaf-air vapor pressure deficits
 1087 which negatively impacted pitch pine stomata response and limited gas exchange. In a related
 1088 report, scientists found that warming trends (Kunkel *et al* 2013) increased pitch pine difficulties
 1089 in reproduction (Ledig Smouse and Hom 2015). This includes weather-related effects such as
 1090 episodic drought, harsh winds, and salt spray (Schmitt 2015; Fernandez *et al* 2015), as well as
 1091 conditions that increased cold intolerance (Berang and Steiner 1985). Increases in annual winter
 1092 temperatures (Lesk *et al* 2017) coupled with an absence of fire cause concern about a quite
 1093 different disturbance—potential invasion within the next decade of an herbivore, Southern Pine
 1094 Beetle (*Dendroctonus frontalis* or ‘SPB’). Although deer and rodent damage (Ledig *et al* 2013)
 1095 historically impeded tree survival in pine barrens, SPB has already paid a deadly visit to Long
 1096 Island, NY (Dodds *et al* 2018). Unless its progress is deterred by other insect predators like
 1097 Dubious Checkered Beetle, (*Thanasimus dubius*; Coulson and Klepzig 2011), it is possible that
 1098 pitch pines along with understory plants, butterflies and moth members of the Acadia ecosystem
 1099 will suffer the same fate experienced in more southerly locations (Lesk *et al* 2017). According to
 1100 several authors (Day *et al* 2005; Lee *et al* 2019) warming climate impacts the suitability of
 1101 habitat and pitch pine tendencies to consolidate, regenerate or migrate may be in jeopardy. These

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1118 effects are likely to eventually limit aspects of PER_C such as niche expansion, if they have not
1119 already, through a combination of diminished open space capacity, loss of enriched substrates,
1120 and elimination of 'safe sites.'

1121 Pitch pine is considered an important guardian of underlying heath communities at MDI;
1122 it is foundational as a necessary ecosystem component in a stressed environment. Despite
1123 increasing climate pressures, trees retreating into ever more sparse conditions reinforces their
1124 facilitator status (Connell and Slatyer 1977). This species explicitly maintains the livelihood of
1125 underlying flora through a sharing and distribution of ecoservices. Nevertheless, competitive
1126 advantages enjoyed currently may even give way to 'mesophication'—negative feedback for
1127 shade intolerant trees like pitch pine (Nowacki and Abrams 2008), perhaps more widespread at
1128 the confluence of fire suppression, overabundance of deer, and climate change.

1129 The model we proposed is not built on a quantitative framework nor is it intended as a
1130 predictive model, *per se*, yet results attached to this model are useful in several ways. First, these
1131 metrics provide a context for describing recovery or persistence in mathematical relationships
1132 along an adaptivity curve. Second, our method operationalizes recovery and persistence
1133 mechanisms fit to an ecological framework (Brand and Jax 2007). Finally, our model may be
1134 used to better understand how pitch pine in other ecosystems outside of the Northeast U.S.,
1135 discriminate between REC_C and PER_C at a given elevation and within certain topographic
1136 parameters. The data presented here provides a fuller understanding of current regeneration and
1137 expansion concepts which are essential to an appreciation of influences on persistence in the
1138 absence of forest or prescribed fire.

1139 CONCLUSION

1141 Here, we present an explanatory model of pitch pine post-fire recovery and persistence
1142 capacities to analyze population status as a function of fire and topography. We found adaptivity
1143 effects (growth, expansion into greater stand density) account for greater growth and stand
1144 density on more hospitable terrain, with little impact from fire history. This is likely due to the
1145 fact that fire return intervals are so infrequent as to reduce recovery features found elsewhere
1146 (e.g., cone serotiny). Flat and ledge pitch pine populations exhibited greater buoyancy than trees
1147 in more strenuous cliff situations. We also identified a selective preference for either growth at
1148 low elevations or stress tolerance at high elevations using multiple plant and ecosystem metrics.

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1188 Our findings unravel an enigma about persistence in a post-fire milieu during a critical phase of
1189 the Anthropocene age (Crutzen and Stoermer 2000). At lower elevations, which represent the
1190 vast majority of pitch pine populations in the Northeast US, we predict newly pioneered
1191 locations reflect a continuation of *PERC* signaled by significant differences in density, slope, and
1192 aspect. At a time when continued climate change may tip the scale away from survival, our
1193 findings encourage the use of a model by forest managers to better understand the imposition of
1194 fire absence on flat and ledge communities.

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1195 **Data Availability Statement**

1196 Data used in this article can be found at the following repository:

1197 https://github.com/SmithEcophysLab/mtDesertIsland_Pinusrigida

1198 (DOI:10.5281/zenodo.4663255).

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1201 **Author Contributions**

1202 JL and NS conceived the work, contributed substantially to the interpretation of the data
1203 and to drafting the manuscript, gave final approval of the version submitted, and agreed to be
1204 accountable for all aspects of the work. Questions related to the accuracy or integrity of any part
1205 of the work are appropriately investigated and resolved. JL carried out sample collection and
1206 field measurements, conducted soil water retention tests and prepared samples for EA-IRMS
1207 analysis. NS performed C/N foliar analysis, conducting statistical analyses and formulating
1208 figures and tables.

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1217 prior to submission.

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1230 Department of Interior.

1231

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Again, more abbreviations are more confusing. I recommend just referring to recovery capacity and persistence capacity to reduce the number of acronyms

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Do you mean that each capacity metric reflects an ecologically stable strategy?

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Recovery capacity needs a better explanation here. This paragraph would be a great spot to clearly link recovery capacity to fire history and persistence capacity to elevation so that it's very obvious why you chose those as independent variables for the analysis

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Elevation is an aspect of topography, right?

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NGS to take a further look at this explanation

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Are they all significant? I count only 20 response variables with significant relationships

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You measured distance between neighbors, not number of neighbors. So, would you expect a lower mean distance between neighbors at low elevations?

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Wonderland has the lowest mean distance between neighbors, which I think means the trees are denser. Not sure how this relates to cliff orientation or aspect. Also- not sure if you can claim that this is a function of recovery capacity?

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Since we used mean distance between neighbors in the analysis, not stand density, it's worth it to be careful about how you reference stand density in the results/discussion.

Also, you state that there is valuable information about differences between flat, cliff, and ledge communities but then you don't elaborate.

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Climate projections advise against resuming prescribed fire or they don't believe natural fires will return? Is there a citation for this?

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This is already said above (without the citations)

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μ is used previously for aspect in degrees

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Is this correct? You associate Wonderland with recovery capacity in the previous paragraph.
If each site typically uses a different pathway, it would be worth explaining that at the beginning of the discussion as well as the evidence supporting why.

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Foliar or soil? A limiting factor to what?

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