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On The Edge: Pitch Pine Persistence in the Absence of Fire Under the Influence of Topographic Factors

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**ABSTRACT**

Globally rare pitch pine (*Pinus rigida* Miller) is thought to depend on intermittent fire, which encourages reproduction and niche preservation. At Mt. Desert Island in Acadia National Park (ME, USA) a major, stand-replacing conflagration enveloped a portion of the island in 1947 (Fig. 1); since then there has been no recurrence of fire. Other populations on the island have been unaffected by fire disturbance for over one hundred and twenty years. Fire history has been shown to influence plant form and functioning, yet these impacts are not well quantified for pitch pine in relation to other factors known to impact traits of this species. Thus we examined the influence of topography (including elevation, aspect and slope) along with fire history to better comprehend pitch pine resistance; this was achieved through an analysis of traits of individual trees in four separate stands. Significant differences were found in aspect, soil water retention, photosynthetic water use efficiency, foliar nutrients, growth and stand density. Topography, specifically elevation, was found to have a greater influence on soil, leaf and whole-plant traits. At lower elevation, trees exhibited greater capacity for stand density, expansion and colonization. Our insights provide a means to a better understanding of how to promote pitch pine persistence in communities, at varying elevation and topography, where fire is absent, across the northeastern and mid-Atlantic U.S.

**INTRODUCTION**

On Mt. Desert Island at Acadia National Park in Maine USA, pitch pine (*Pinus rigida* Miller), the most northerly member of the southern yellow pines (Plain, Kuser and Ledig 1987), dwell at the edge of their northeastern range (Fig. 1). Over millennia, fire is a constant disturbance in these pine barrens enabling persistence (defined as an ability to remain in a particular setting) through reduced competition, added pyrogenic carbon (C) by way of post-fire charcoal and long evolved adaptations like cone serotiny, thickened bark and epicormic growth. Serotinous cones (Little 1953) typically open only when fire engulfs the tree; in anticipation trees adopt thickened bark to withstand scorching and produce epicormic sprouting following fire to add photosynthetic capacity. These features were present on Mt. Desert, in 1947 (Fig. 1), when an intense fall fire started in a dump just west of Bar Harbor, on the east side of the island. Ferocious winds whipped the fire into a frenzy and, notwithstanding efforts to subdue it, persevered for nearly two weeks. Since that time, fire suppression is used to avoid a repetition of the tragic consequences seen long ago; during the fire aftermath tree pyrogenic adaptations undergo change. The undoing of cone serotiny began decades ago (Conkey, Keifer and Lloyd 1994), and becomes more widespread as time passes (Jordan, Patterson and Windisch 2003). As there is no longer a pressure to produce seeds which survive in the midst of a fire (Givnish 1981), neither is there the same need for thick bark or epicormic sprouting (tufts of needles on the bole and branches, Renninger *et al.* 2013), although there is epicormism in several of the populations we study. Instead tree defenses continue to adjust through phenotypic variation to warmer temperatures and increasing summer drought (Day *et al.* 2005) as well as ongoing competition with other evergreens ~~add to the decline of serotiny (Heuss 2018). Given the lack of a fire threat, pitch pine adaptation is more likely focused on more pressing needs including competition with other evergreens~~ Of at least seventeen pitch pine populations extant at Mt. Desert, all appear healthy despite fire absence. Their recent history is made more compelling based on a theory that fire (natural or proscribed) is likely a requirement every six to twenty-five years for pine barren well-being (Jordan, Patterson and Windisch 2003) based on a study on Long Island (NY). Crucially, if fire is truly a necessity to prolong longevity at Mt. Desert, investigators are tasked with understanding and interpreting factors, other than fire, which account for persistence.

Previously, pitch pine studies have emphasized the influence of natural fire (Foereid *et al.* 2015), anthropogenic controlled burns (Carlo *et al.* 2016) and opening of canopies (Neill *et al.* 2007). Here, in addition to fire history, we examine topography, which is known to be an important control over pitch pine populations (Parshall and Foster 2002; Fig. 2).

Pitch pine populations at Mt. Desert exist along topographical and fire history gradients, providing a testbedto untangle the influence of fire and topography on the species. Here, we use four populations (Fig. 3) to examine the effects of fire history and topography on pitch pine leaf, plant, and ecosystem (i.e., soil) traits. The four populations were chosen to represent a factorial combination of elevation (high or low) and fire history (having experienced the 1947 stand clearing fire or not). First, we characterize differences in topographical features of the four populations, including slope and aspect, given that these are likely important non-elevation topographical drivers of the traits examined. We then explore aspects of the soil environment, including soil carbon as well as macro and micro nutrient concentrations. Following previous studies, we expected to find greater soil carbon (DeBano 1981), alkali cations (Kolden *et al.* 2017), and solubilized minerals (Caldwell and Richards 1989) in soils that had experienced the 1947 fire. We also foresaw there would be greater soil carbon at low elevations due to thermal exfoliation (as explained by Shakesby and Doerr 2006) or a failure of fire to remove pyrogenic carbon (Doerr *et al.* 2018) in former fire zones. We also measured soil water retention, which we expected to be greater at sites that experienced the 1947 fire, as pyrogenic carbon is known to increase soil water retention (Licht and Smith, 2020). Beyond that, we anticipated higher soil water retention at low elevations due to flat terrain (alleviating erosion mechanics).

The authors hypothesized that topographical and fire history-driven changes to the growth environment would manifest in changes in leaf- and plant-level traits. We expected that stress induced by topographical features and low soil water retention at high elevation would lead to increased intrinsic water use efficiency (iWUE; Wang *et al.* 2017), as a stress tolerance response. The authors also anticipated a reduction in leaf nutrients at high elevation, mimicking likely reductions in the soil. In addition, there was the prospect that fire history might alleviate these stress indicators, as a result of increased soil nutrients and water retention. At the plant level, we predicted plants would attain reduced height, smaller DBH, narrower canopy, and sparser clustering (greater distance between conspecific neighbors) at high elevation, again as a result of the topography- and soil-induced stress. Investigators theorized smaller trees in areas that had experienced the 1947 fire due to age, but that the height difference would be less at high elevation due to stress-reducing effects of fire on the soil environment. A combination of hypothesis testing and data analysis facilitate an approach to pitch pine colony management at Mt. Desert along with other districts along the Eastern seaboard where natural fire and prescribed fire do not play a role in the lives of pine barrens.

**METHODS**

**Study Extraction Sites**

We investigate fifteen pitch pine specimens at each of four sites at Mt. Desert Island (Fig. 2, Tab. 1), factorially crossed in a fire history (Miller *et al*. 2017) by elevation design: (1) Wonderland trail at an average of 58.5 ft elevation (low elevation, outside the footprint of the 1947 fire), (2) Gorham cliffs at an average of101.5 ft (low elevation, within the footprint), (3) St. Sauveur trail at an average of563.5 ft (high elevation, outside the footprint) and (4) South Cadillac trailat an average of 912 ft (high elevation within the footprint). Elevation differences are more stark at higher elevations based on much longer trail transects. Soils at all four sites were overlain with rapidly drying needle duff (Day *et al.* 2005), porous and comprised of acidic hornblende granite or Ellsworth schist. In addition they were uniformly shallow, (varying between 0.7-2.5 cm) homogeneous, and low in fertility. In some cases, sampling was limited according to time, weather and site access.

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**Soil Elements and Water Retention (SWR)**

Soils were excavated by hand trowel and soil probe (Accuproducts, Saline, MI, USA); soil C, N and C/N were calculated from elemental analysis in a similar fashion to (foliar samples) the aforementioned method.

70 mL soil samples were extracted at fifteen tree locations at four sites, from <7.5 cm (Oa-Ab) horizon above bedrock. In a laboratory 50 g H2O were added to each aliquot to assess net water retention as a subset of soil moisture evaporation (*ψ*g) to determine net evaporative loss or adsorption to surfaces. Soil water retention analysis was conducted according to the Fields method (Lichtand Smith 2018). Retention effects of gravitational and evaporation forces was made on a wet basis where Wm=g H2O **●** (g moist soil)-1 (Qi, Jingfang and Wenwei 2018).

**Leaf Traits**

Maximizing seasonal data relative to active growth during the driest months of the summer was achieved by obtaining C isotopic data (δ13C) and N isotopic data (δ15N) of fully expanded leaves (needle cluster) of 15 individuals 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 Cole-Palmer (Vernon Hills, IL, USA) micro analytic balance and rolled in Costech (Valencia, CA, USA) 5 x 9 mm tin capsules. A Thermo Delta (Waltham, MA, USA) V+ IR-MS continuous flow isotope ratio mass spectrometer with a universal triple collector was used. Combustion gasses were separated on a gas chromatograph column, passed through a diluter and reference gas box, and introduced into the spectrometer. δ13C was used to indicate water use efficiency (iWUEδ13C) (Farquhar et al. 1989). Leaf tissue was obtained from excision of basal fascicle bundles at 1.06 m. 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 CN-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.

**Plant-level Traits**

Mean distances between sampled trees (*N* = 60) were calculated including up to five of their nearest, reproductively mature conspecific (within 5 m) neighbors (Churchill *et al.* 2012)—this method served as a surrogate, but inverse, measure for stand density (Mosseler, Rajora and Major 2004).

**Statistical Analysis**

All data were analyzed using a similar linear model structure with elevation (high or low) and presence of the 1947 fire (yes or no) as categorical fixed factors. The interaction between elevation and presence of the 1947 fire was also included in each model. In total, 27 models were fit with the following dependent variables: tree height (m), canopy spread (m), DBH (cm), mean distance between neighbors (m), foliar carbon (C, %), foliar nitrogen (N, %), foliar C/N (unitless), foliar δ13C (‰), foliar δ15N (‰), foliar calcium (Ca2+ %), foliar phosphorus (P, %), foliar potassium (K+, %), foliar magnesium (Mg2+, %), foliar aluminum (Al+, ppm), foliar zinc (Zn, ppm), soil C (%), soil N (%), soil C/N (unitless) and soil water retention (%). Tree height, canopy spread, DBH, foliar P, foliar K+, foliar Zn and soil C/N were log transformed to meet model assumptions 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 and 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**

*Topographical Features  
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 (Fig. 4 and Tab. 2).

*Soil Elements and Water Retention (SWR)*

Soil C concentrations were greater at lower elevations (*P* < 0.05) and sites that did not experience the 1947 fire (*P* < 0.05, Fig. 5A and Tab. 3). Soil N did not vary between sites (*P* > 0.05, Fig. 5B and Tab. 3). Soil C/N was 15% lower at high elevation sites (*P* < 0.05, Fig. 5C and Tab. 3), but we found no significant disparity in C/N when either fire history or fire history x elevation interactions were examined (*P* > 0.05 in both cases). There was an interaction between elevation and fire history on soil water retention (SWR; *P* < 0.01, Fig. 5D and Tab. 3), with markedly higher values at Gorham cliffs, the low elevation site that experienced fire, as compared to other sites.

*Leaf Traits*

Trees at higher elevations experienced less negative δ13C (*P* < 0.01, Fig. 6A and Tab. 4), reflecting greater water use efficiency, regardless of fire history. There were no significant differences between tree populations for δ15N (*P* > 0.05, Fig. 6B and Tab. 4)*.* On average, foliar C was greater at upper elevations, however the results were not statistically significant (*P* > 0.05, Fig. 7A and Tab. 4); nor was there a difference in C/N between sites (*P* > 0.05, Fig. 7C and Tab. 4). Our linear model suggested that fire accounted for a significant influence on foliar N (*P* < 0.05, Fig. 7B and Tab. 4), however post-hoc Tukey’s tests found no difference between sites at α = 0.05 (Fig. 7B).Foliar Ca2+ was negatively impacted by increasing elevation (*P* < 0.001, Fig. 8A and Tab. 5). Our linear model suggested that foliar P was significantly higher at fire-involved sites (*P* < 0.01, Fig. 8B and Tab. 5), although this was not confirmed by post-hoc Tukey’s tests (Fig. 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, Fig. 8C and Tab. 5). Neither foliar Al+ nor Mg2+ differed by site (*P* > 0.05 in both cases; Fig. 8D, Fig. 8E, and Tab. 5). Foliar Zn concentrations were 9% lower in the high elevation sites than on the low elevation sites (*P* < 0.01, Fig. 8F and Tab. 5), due to a particularly strong reduction at the high elevation site that experienced fire.

*Plant-level Traits*

There was a significant interaction between fire and elevation on tree height (*P* < 0.01, Fig. 9A, Tab. 6) and DBH (P < 0.05; Fig. 9C and Tab. 6), 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, Fig. 9B and Tab. 6), although Tukey’s tests revealed no difference between sites at α = 0.05. Distance between neighbors was greater at high elevation sites, particularly the one that experienced the 1947 fire (*P* < 0.01, Fig. 9D and Tab. 6).

**DISCUSSION**

*Topographic Traits*

Topography, specifically, elevation, is found to be a dominant driver of plant and ecosystem processes ~~we measured~~ during an extended fire absence interval. ~~This result that persistence capacity was more important than recovery capacity at Mt. Desert Island, at least over the last 100 years. Our findings underscore differences between recovery capacity and persistence capacity~~~~pathways and provide an explanation to resolve an enigma of persistence of pitch pine at Mt. Desert Island in the absence of fire.~~  We confirmed trees at lower elevations favored growth over stress tolerance consistent with findings by others with regard to intrinsic water use efficiency (Wang *et al.* 2017; Chen, Wang and Jia 2017). Further, we found trees at higher elevation, particularly those in the former 1947 fire district, persevered despite noteworthy challenges including less density and evidence of less reproduction—clearly there is an impetus to persist through stress avoidance. At the highest elevations on South Cadillac trail, we expected to find the steepest slopes but they were far less inclined than those at Gorham cliffs. Topography (slope) was found to be instrumental in shaping population expansion especially in combination with elevation exclusive of fire disturbance effects at lower elevation. In particular, we note the combination of a gentle 3° slope and low elevation, at Wonderland, accompanied by less soil moisture drainage (Howard and Stelacio 2011; Hanson, 2017), as more serendipitous to resilience than a free-flowing 31° slope at Gorham cliffs.

*Soil Traits*

Soil fertility and water retention vary, understandably, across those dimensions in the four colonies we observed. What seems apparent is the fact that fire history as much as topography plays a role in determining the extent to which trees derive enough support to persist despite fire absence, wind and other disturbances including competition from other evergreen trees. From a nutrition standpoint, there are reports of subsurface charcoal as a soil component in fire-exposed areas subsequent to 1947. One can argue that charcoal remnants probably play a role in recovery at burned-over Cadillac Brook (below the heights of South Cadillac trail) as reported earlier (Patterson, Edwards and Maguire 1987; Verma and Jayakumar 2012). To support this contention, there are previous findings which report post-fire pyrogenic C remnants endure in the soil layer (DeBano 1981) accompanied by increased alkali cations (Kolden *et al.* 2017) and solubilized minerals (Caldwell and Richards 1989). However, we found no obvious signs of charcoal particles at either South Cadillac or Gorham cliffs and it is doubtful that much pyrogenic carbon remains after such a long fire absence. Pertinently, we found greater C availability at Wonderland as compared to Gorham cliffs and South Cadillac, suggesting that topographic factors (slope for example) endow greater C retention based on the lack of fire to remove C (Doerr *et al.* 2018) as well as another mechanism, thermal exfoliation (as explained by Shakesby and Doerr 2006). Patel *et al.* (2018) studied soil N in several watersheds (drainages) below South Cadillac trail, at low to mid-elevation, to determine recalcitrant atmospheric deposition since the 1947 fire. Since fire is known to increase N losses there was an expectation of lower total nitrogen (TN) at sites closer to the most intense burns but differences did not materialize. These are consistent with our findings.

Our expectations for micronutrient concentrations at Mt. Desert are colored by a previous pine barren study which featured experiments with non-glaciated soils and very juvenile trees exposed to forest fire, anthropogenic fire and no fire treatments (Licht and Smith 2020). While pyrolysis (either natural or anthropogenic) is shown to increase SWR (Licht and Smith 2020), in that investigation, we hypothesize a combination of traits are responsible for heightened moisture availability at Mt. Desert—most apparent at low elevation and highest where a pyrolysis history exists from 1947. At Wonderland and even more at Gorham cliffs, the combination of flat terrain (alleviating erosion mechanics), negligible consumption of Ca2+, K+, and Mg2+ (Licht and Smith 2020) and greater soil C availability were deciding factors in greater SWR. Alternately, it is not difficult to conjur weaker SWR at upper ledge elevations where the previous factors do not obtain. Due to a winning combination of soil nutrient and SWR, we speculate greater opportunity at low lying forests where these (nutrient and SWR) traits together with open canopies enhance expansion, stand density and consolidation (Churchill *et al.* 2012; Lafon *et al*. 2014; Swanston *et al.* 2018).

*Leaf Traits*

Elevational gradients towards St. Sauveur and South Cadillac summits showed an increase in intrinsic water use efficiency—contrasted with similar results in non-glaciated populations in flat, sand plain New Jersey Pine Barrens (Mikita-Barbato *et al.* 2015; Schafer and Bohrer 2016). In general, though, there is a correlation between higher elevations and increases in photosynthesis, stomatal conductance, and leaf N ( Körner *et al*., 1986; Friend *et al*., 1989; Bresson *et al*. 2009). Likewise, in a Massachusetts study of low elevation, non-glaciated barrens, we saw increased iWUE in trees which were exposed to natural and proscribed fire (Licht and Smith 2020). What is noteworthy at Mt. Desert is evidence that higher elevation invariably favors a stress tolerance response (to higher wind turbulence, drying potential and lower soil water retention (SWR) consistent with earlier reports (Wang *et al.* 2017) and photosynthetic growth at lower heights in a recent paper (Butak 2014). On another track, we speculate a linear model demonstrates a significant influence of fire history on foliar N at Gorham cliffs and South Cadillac trails.

Our foliar element results derived from burned and unburned sites are similar to those reported by others in New Jersey (e.g., Renninger *et al.* 2013) corresponding with fire-reduced soil C as well. Foliar Zn availability was greater at lower elevations at Mt. Desert Island consistent with findings by others (Kolker *et al.* 2013), but higher concentrations of foliar Ca2+ and K+ at lower elevation is not confirmed elsewhere as far as we could tell.~~but how widespread that response is requires further investigation.but recovery capacity was more likely~~

~~connected to higher P.~~

*Plant-level Traits*

At higher elevations on Mt. Desert there is the possibility that an extended fire interval removes the competitive advantage pitch pine have in outlasting nutrient- and moisture-demanding, late-successional species, which thrive in the high moisture and dense canopy conditions in undisturbed locations (Nowacki and Abrams, 2008; Schwartz *et al*., 2016). Competition dynamics appear to be closely connected to topography as for example, where a combination of aspect, slope, open exposure are similar at several Mt. Desert sub-summits (north Cadillac mountain trail, Norumbega mountain trail and Champlain mountain trail, sites which were not included in this study) are situated at approximately the same altitude (+/- 290 m) as the mean waypoint of the South Cadillac trail. According to our data, living in an exposed situation may be just as important as other factors to this species as a means of evolving phenotypic variation among the *refugia* at Mt. Desert (a phenomenon referred to by Ledig, Smouse and Hom 2015). Specifically, to reinforce this observation, we refer to vigorous pitch pine clustering (stand density) in spaces conspicuously lacking shade, where this species outcompetes red spruce (*Picea rubens*), hemlock (*Tsuga canadensis*) and balsam fir (*Abies balsamea*). Wonderland trail recommends itself as the best cluster candidate for future expansion based solely on the solar exposure factor.

Furthermore, we anticipated that low elevation (<50 m) populations would feature a greater number of close conspecific neighbors as a function of no fire history, a relatively gentle slope (<10°), and tendency towards a southerly aspect (*µ*=180°). At high elevation ledge communities, we found little to suggest a stimulus for reproduction (fecundity) save for one particular location encompassing a pitch-and-jack pine (*Pinus banksiana*) sympatry (overlapping species) mostly east of the South Cadillac mountain trail (between 189 and 270 m elevation). ~~This assertion is partly confirmed by the disappearance of serotiny and epicormic sprouting, found formerly at higher sites on Cadillac mountain three decades ago.~~ A shift back to fire, accompanied by a re-introduction of serotinous characteristics, might enable this overlapping enclave to expand even further in every direction in the future. However, despite a significant fuel buildup in the forests on the island, its seems unlikely that current management policies will embrace significant proscriptive fire or allow forest fire; coupled with climate projections (Fernandez *et al.* 2015), we can predict the sympatry is left to its own devices rather than anthropogenic intervention.

*Disturbance, Climate Factors and Predictions for Species Status*

Until now disturbances such as mechanical thinning and bioturbation (Abney *et al.* 2019), disease such as *Ploioderma lethale* (needle cast, Little and Garrett 1990) and insect herbivory (Lesk *et al.* 2017) are not management factors at Mt. Desert as they are in barrens elsewhere. No doubt warming climate, is having the greatest impact on island vegetative prospects including the fortunes of pitch pine. According to several authors (Day *et al*. 2005; Lee *et al*. 2019) warming climate impacts habitat suitability and pitch pine tendencies to consolidate, regenerate or migrate. What has been clear for almost three decades is the effect of global climate change on physiological traits. Day, Greenwood and White (2001) found that an uptick in annual temperatures signaled increased leaf-air vapor pressure deficits that negatively impacted pitch pine stomatal conductance and limited gas exchange. In a related report, scientists found warming trends (Kunkel *et al* 2013) increased pitch pine reproductive difficulties (Ledig, Smouse and Hom 2015). These trends include weather-related effects such as episodic drought, harsh winds, and salt spray (Fernandez *et al.* 2015) as well as increased cold intolerance (Steiner and Berrang 1990). What is not clear istree will be shaped by a continuing rise in What appears to be more certain is the prediction (Day *et al.* 2005) that pitch pine colonies will suffer due to a combination of diminished open space capacity, loss of enriched substrates and elimination of suitable habitats ~~(). but these do not specifically address the adaptability of pitch pine~~ Thus, in acknowledgingscientists forecast ing

*Anticipation of Southern Pine Beetle Invasion*A prolonged fire interval coupled with increases in annual winter temperatures (Lesk *et al.* 2017) raises the spectre of still another, different disturbance—namely the potential invasion within the next decade of an herbivore, Southern pine beetle (*Dendroctonus frontalis* Zimmer or ‘SPB’). Although deer browsing and rodent damage historically impede tree survival in pine barrens (Ledig, Hom and Smouse 2013), SPB has already paid a deadly visit to New Jersey and Long Island NY (Dodds *et al.* 2018). Unless SPB’s progress is deterred by other insect predators like double checkered clerid (*Thanasimus dubius*; Coulson and Klepzig 2011), or some undetermined climate factor, it is possible that pitch pines along with understory plants, butterflies and moth members of the Acadia ecosystem will suffer the same fate in Maine experienced in more southerly locations (Lesk *et al.* 2017).

~~pine is considered an important guardian of underlying heath communities at Mt. Desert Island; it is foundational as a necessary ecosystem component in a stressed environment.~~ ~~The model we proposed is not built on a quantitative framework nor is it intended as a predictive model,~~ *~~per se~~*~~, yet results attached to this model are useful in several ways. First, these metrics provide a context for describing recovery or persistence in mathematical relationships along an adaptivity curve. Second, our method operationalizes recovery and persistence mechanisms fit to an ecological framework (Brand and Jax 2007). Finally, our model~~

*Colony management at Mt Desert and beyond*

Our pitch pine data are preliminary based on the need for future replication of trait studies; yet there is already sufficient information to inform National Park Service (Miller *et al.* 2014) management charged with protection of this species. The importance of this species cannot be overstated from an ecological (globally threatened) standpoint and a regional need to preserve a highly environmentally sensitive barrens and heathland ecosystem which anchors so many other plant, animal and insect species. Depending on similarities with other pitch pine ecosystems outside of the Northeast U.S. (Fuller and Quine 2016), our findings may provide further understanding to those studying fire history and topographic parameters which influence persistence in other *refugia*.

**CONCLUSION**

~~Here, we present an explanatory model of pitch pine post-fire recovery and persistence capacities to analyze population status as a function of fire and topography.~~ We found topography, even more than fire history, is tied to pitch pine persistence as demonstrated in various metrics which lend themselves to a better understanding of biological stoichiometry (Van de Waal *et al.* 2018) at Mt. Desert Island, Given the length of the current seventy-five year lapse in fire events it is unsurprising that cone serotiny and bark thickening are on the decline. Several factors are of interest including insights into flat, cliff and ledge colonization as well as adaptivity to stress tolerance or growth depending on topographic, soil, leaf and whole plant traits. Our data begin the task of unraveling at least a part of the enigma witnessing pitch pine persistence in a post-fire milieu during a critical phase of the Anthropocene age (Crutzen and Stoermer 2000). At a time when continued climate change appears to be tipping the scale away from pitch pine survival at Mt. Desert, our findings suggest trees are slowly adopting phenotypic responses to some of the stresses and disturbance in their refugia. We anticipate our data enables forest managers to gain a better purchase on the effects of fire history and topographic factors which affect persistence of this globally threatened species.

## Data Availability Statement

Data used in this article can be found at the following repository: <https://github.com/SmithEcophysLab/mtDesertIsland_Pinusrigida> (DOI:10.5281/zenodo.4663255). Additional soil inorganic data is available at this site.

## Author Contributions

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

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**REFERENCES**

Abney, R., Kuhn, T., Chow, A., Hockaday, W., Fogel, M., and Berhe, A. (2019). Pyrogenic carbon erosion after the rim fire, yosemite national park: the role of burn severity and slope. *JGR Biogeosciences* 124, 432–449. doi: 10.1029/2018JG004787

Agostinelli, C. and Lund, U. (2017). R package 'circular': Circular Statistics (version 0.4-93). URL

<https://r-forge.r-project.org/projects/circular/>

~~Brand, F. and Jax, K. (2007). Focusing the meaning (s) of resilience: resilience as a descriptive concept and a boundary object.~~ *~~Ecology and society~~*~~,~~ *~~12~~*~~(1). https://www.jstor.org/stable/26267855~~

Buma, B., Brown, C., Donato, D., Fontaine, J. and Johnstone, J. (2013). The impacts of changing disturbance regimes on serotinous plant populations and communities. *BioScience*, *63*(11), 866-876. doi.org/10.1525/bio.2013.63.11.5

Butak, A. (2014). Vegetation Composition, Structure, and Ecophysiology of Maritime Ledge Ecosystems, University of Maine, Orono (<http://digitalcommons.library.umaine.edu/etd/2212>).

Caldwell, M. and J. Richards. (1989). Hydraulic lift: water efflux from upper roots improves effectiveness of water uptake by deep roots. *Oecologia,* 79, 1-5. doi.org/10.1007/BF00378231

Carlo, N., Renninger, H., Clark, K., and Schäfer, K. (2016). Impacts of prescribed fire on Pinus rigida Mill. in upland forests of the Atlantic Coastal Plain. *Tree physiology*, *36*(8), 967-982. doi: 10.1093/treephys/tpw044

Certini, G. (2005) Effects of fire on properties of forest soils: a review. *Oecologia* 143:1–10. doi.org/10.1007/s00442-004-1788-8

~~Charpentier, J. (2020). Wildland Fire Disturbance - Recovery Dynamics in Upland Forests at Acadia National Park, Maine. Doctoral dissertation, Antioch University. <https://aura.antioch.edu/etds>~~

Chen, Z., Wang, G. and Jia, Y. (2017). Foliar d13C Showed No Altitudinal Trend in an Arid Region and Atmospheric Pressure Exerted a Negative Effect on Plant d13C, *Frontiers in Plant Science*, 8, 1-9. https://doi.org/10.3389/fpls.2017.01070

Churchill, D., Larson, A., Dahlgreen, M., Franklin, J., Hessburg, P. and Lutz, J. A. (2013). Restoring forest resilience: from reference spatial patterns to silvicultural prescriptions and monitoring. *Forest Ecology and Management*, *291*, 442-457. https://doi.org/10.1016/j.foreco.2012.11.007

Conkey, L. , Keifer, M., and Lloyd, A. (1995). Disjunct jack pine (Pinus banksiana Lamb.) structure and dynamics, Acadia National Park, Maine. *Ecoscience*, *2*(2), 168-176. doi.org/10.1080/11956860.1995.11682281

Connell, J. and Slatyer, R. (1977). Mechanisms of succession in natural communities and their role in community stability and organization. *The American Naturalist*, *111*(982), 1119-1144. doi.org/10.1086/283241

Copenheaver, C., White, A. and Patterson, W., III (2000). Vegetation development in a southern Maine pitch pine-scrub oak barren. *Journal of the Torrey Botanical Society*, 19-32. doi.org/10.2307/3088744

Coulson, R. and Klepzig, K. (2011). Southern Pine Beetle II. Gen. Tech. Rep. SRS-140. Asheville, NC: U.S. Department of Agriculture Forest Service, Southern Research Station. 153-160. doi.org/10.2737/SRS-GTR-140

Crutzen, P. and E. Stoermer 2000. The “Anthropocene.” *Global Change Newsletter* (41): 17–18. doi.org/10.12987/9780300188479-041

Day, M., Schedlbauer, J., Livingston, Greenwood, M., White, M. and Brissette, J. (2005). Influence of seedbed, light environment, and elevated night temperature on growth and carbon allocation in pitch pine (*Pinus rigida*) and jack pine (*Pinus banksiana*) seedlings. *For Ecol & Manag*, *205*(1), 59-71. doi.org/10.1016/j.foreco.2004.10.004

Day, M., Greenwood, M. and White, A. (2001). Age-related changes in foliar morphology and physiology in red spruce and their influence on declining photosynthetic rates and productivity with tree age. *Tree Physiology*, *21*(16), 1195-1204. doi.org/10.1093/treephys/21.16.1195

~~Day, M., and Greenwood, M. (2011). Regulation of ontogeny in temperate conifers. In~~*~~Size-and age-related changes in tree structure and function~~*~~(pp. 91-119). Springer, Dordrecht. doi.org/10.1007/978-94-007-1242-3\_4~~

Day, M., Zazzaro, S. and Perkins, L. (2014). Seedling ontogeny and environmental plasticity in two co‐occurring shade‐tolerant conifers and implications for environment–population interactions. *American journal of botany*, *101*(1), 45-55. doi.org/10.3732/ajb.1300253

Dodds, K., Aoki, C., Arango-Velez, A., Cancelliere, J., D’Amato, A., DiGirolomo, M., and Rabaglia, R. (2018). Expansion of southern pine beetle into northeastern forests: Management and impact of a primary bark beetle in a new region. *Journal of Forestry*, *116*(2), 178-191. doi.org/10.1093/jofore/fvx009

Doerr, S., Santin, C., Merino, A., Belcher, C., and Baxter, G. (2018). Fire as a removal mechanism of pyrogenic carbon from the environment: effects of fire and pyrogenic carbon characteristics. *Frontiers in Earth Science*, *6*, 127. doi: 10.3389/feart.2018.00127

Dunne, J., Saleska, S., Fischer, M. and Harte, J. (2004). Integrating experimental and gradient methods in ecological climate change research. *Ecology*, *85*(4), 904-916. doi.org/10.1890/03-8003

Evans, S., Dueker, M., Logan, J. and Weathers, K. (2019). The biology of fog: results from coastal Maine and Namib Desert reveal common drivers of fog microbial composition. *Science of the Total Environment*, *647*, 1547-1556. https://doi.org/10.1016/j.scitotenv.2018.08.045

Farquhar G., Ehleringer J. and Hubick K. (1989) Carbon Isotope Discrimination and Photosynthesis. *Annual Review of Plant Physiology and Plant Molecular Biology* 40, 503–537. doi: 10.1146/annurev.pp.40.060189.002443

Fernandez, I. (2008). *Carbon and nutrients in Maine forest soils* (Vol. 200). Department of Plant, Soil & Environmental Sciences, University of Maine.

Fernandez, I., Schmitt, C., Birkel, S., Stancioff, E., Pershing, A., Kelley, J., Runge, J., Jacobson, G. *et al* (2015). Maine’s climate future: 2015 update. University of Maine, Orono, ME. 24 pp. https://digitalcommons.library.umaine.edu/climate\_facpub/5?utm\_source=digitalcommons.library.umaine.edu%2Fclimate\_facpub%2F5&utm\_medium=PDF&utm\_campaign=PDFCoverPages

Foereid, B., Lehmann, J., Wurster, C., and Bird, M. (2015). Presence of black carbon in soil due to forest fire in the New Jersey pine barrens. *J. Earth Sci. Eng.* 5, 91–97. doi: 10.17265/2159-581X/2015.02.001

Fuller, L. and Quine, C. (2016). Resilience and tree health: a basis for implementation in sustainable forest management. *Forestry: An International Journal of Forest Research*, *89*(1), 7-19. doi.org/10.1093/forestry/cpv046

Harris, T., Rajakaruna, N., Nelson, S. and P. Vaux. (2012). Stressors and threats to the flora of Acadia National Park, Maine: Current knowledge, information gaps, and future directions. *Journal of the Torrey Botanical Society*, 139 (3), 323-344. doi.org/10.3159/TORREY-D-11-00086.1

Heuss, M. (2018). Evaluating The Impacts Of Southern Pine Beetle On Pitch Pine Forest Dynamics In A Newly Invaded Region. Masters thesis, University of Vermont, pp.67. ScholarWorks @ UVM ISSN: 2576-7550

Howard, L. (2010). Community composition and fire dynamics of high elevation pitch pine woodlands in northeastern West Virginia. *WV Division of Natural Resources, Elkins, WV*.

Howard, L. and Stelacio, M. (2011). Fire and the development of high-elevation pitch pine communities in northeastern West Virginia. *Bulletin of the New Jersey Academy of Science*, *56*(2), 19-23. GALE|A303351456

Ibáñez, I., Acharya, K., Juno, E., Karounos, C., Lee, B., McCollum, C., ... and Tourville, J. (2019). Forest resilience under global environmental change: Do we have the information we need? A systematic review. *PloS one*, *14*(9), e0222207. doi.org/10.1371/journal.pone.0222207

Inglett, P., Reddy, K., Newman, S., and Lorenzen, B. (2007). Increased soil stable nitrogen isotopic ratio following phosphorus enrichment: historical patterns and tests of two hypotheses in a phosphorus-limited wetland. *Oecologia*, *153*(1), 99-109. doi.org/10.1007/s00442-007-0711-5

Jagels, R., Jiang, M., Marden, S. and Carlisle, J. (2002). Red spruce canopy response to acid fog exposure. Atmos. Res 64: 169-178. doi.org/10.1016/S0169-8095(02)00089-3

Qi, Z., Jingfang, S. and Wenwei, L. (2018). A survey about characteristics of soil water retention curve. In *IOP Conference Series: Earth and Environmental Science* (Vol. 153, No. 6, p. 062076). IOP Publishing.

Jordan, M., Patterson III, W. and Windisch, A. (2003). Conceptual ecological models for the Long Island pitch pine barrens: implications for managing rare plant communities. *Forest Ecology and Management*, *185*(1-2), 151-168. doi:[10.1016/S0378-1127(03)00252-4](http://dx.doi.org/10.1016/S0378-1127(03)00252-4" \t "_blank)

Kunkel, K., Stevens, L., Stevens, Sun, Janssen, S., Wuebbles, D. and Dobson, J. (2013). Regional climate trends and scenarios for the US national climate assessment: Part 1. Climate of the Northeast United States. NOAA technical report NESDIS 142-1. Washington, DC. 87 pp. Digital Commons, University of Nebraska.

Lafon, C., Grissino-Mayer, H., Aldrich, S., DeWeese, G., Flatley, W., LaForest, L. and Hoss, J. (2014). Three centuries of Appalachian fire history from tree rings. *Three centuries of Appalachian fire history from tree rings.*, (SRS-199), 99-103. USDA, Southern Research Station.

Lambers, H., Chapin, F. and Pons, T. (2006). Photosynthesis, respiration and long distance transport. In *Plant Physiology Ecology*: 11-99, Springer, New York. DOI: 10.1007/978-3-030-29639-1\_2

Ledig, F., Hom, J. and Smouse, P. (2013). The evolution of the New Jersey pine plains. *American journal of botany*, *100*(4), 778-791. doi.org/10.3732/ajb.1200581

Ledig, F., Smouse, P. and Hom, J. (2015). Postglacial migration and adaptation for dispersal in pitch pine (Pinaceae). *American journal of botany*, *102*(12), 2074-2091. doi: 10.3732/ajb.1500009

Lee, C., Robinson, G., Robinson, I., and Lee, H. (2019). Regeneration of pitch pine (Pinus rigida) stands inhibited by fire suppression in Albany Pine Bush Preserve, New York. *Journal of forestry research*, *30*(1), 233-242. doi: 10.1007/s11676-018-0644-3

Lenth, R., and Lenth, M. (2018). Package ‘lsmeans’. *The American Statistician*, *34*(4), 216-221. http://glmmadmb.r-forge.r-project.org/repos

Lesk, C., Coffel, E., D'Amato, A., Dodds, K., and Horton, R. (2017). Threats to North American forests from southern pine beetle with warming winters. *Nat. Clim. Change* 7, 713–717. doi: 10.1038/nclimate3375

Licht, J. and Smith, N. (2018). The influence of lignocellulose and hemicellulose biochar on photosynthesis and water use efficiency in seedlings from a Northeastern US pine-oak ecosystem. *Journal of Sustainable Forestry*, *37*(1), 25-37. doi: 10.1080/10549811.2017.1386113

Licht, J. and Smith, N. (2020). Pyrogenic Carbon Increases Pitch Pine Seedling Growth, Soil Moisture Retention, and Photosynthetic Intrinsic Water Use Efficiency in the Field. *Frontiers in Forests and Global Change*, *3*, 31. doi: 10.3389/ffgc.2020.00031

Little, S. Jr. (1953). Prescribed burning as a tool of forest management in the northeastern states. *J. For*. 51, 496–500. doi: 10.1093/jof/51.7.496

Little, S. and Garrett, P. (1990). Pinus rigida Mill. pitch pine. *Silvics of North America*, *1*, 456-462.

Lubinski, S., Hop, K., and Gawler, S. (2003). US Geological Survey-National Park Service Vegetation Mapping Program, Acadia National Park, Maine. *Project Report*. U.S. Department of Interior.

Luo, J., Walsh, E., Miller, S., Blystone, D., Dighton, J., and Zhang, N. (2017). Root endophytic fungal communities associated with pitch pine, switchgrass, and rosette grass in the pine barrens ecosystem. Fung. Biol. 121, 478–487. doi: 10.1016/j.funbio.2017.01.005

Miller, K., Mitchell, B., Curtin, P. and Wheeler, J. (2014). Forest Health Monitoring, Northeast Temperate Report, 2006-2013 NPS/NETN. <https://www.amazon.com/stream>

Miller, D., Castañeda, I., Bradley, R. and MacDonald, D. (2017). Local and regional wildfire activity in central Maine (USA) during the past 900 years. *Journal of Paleolimnology*, *58*(4), 455-466. doi.org/10.1007/s10933-017-0002-z

Mosseler, A., Rajora, O. and Major, J. (2004). Reproductive and genetic characteristics of rare, disjunct pitch pine populations at the northern limits of its range in Canada. *Conservation Genetics*, *5*(5), 571-583. doi.org/10.1007/s10592-004-1850-4

Neill, C., Patterson, W., and Crary, D. (2007). Responses of soil carbon, nitrogen and cations to the frequency and seasonality of prescribed burning in a cape Cod oak-pine forest. *Forest Ecol. Manage.* 250, 234–243. doi: 10.1016/j.foreco.2007.05.023

Niinemets Ü., Keenan T. and Hallik L. (2015). A worldwide analysis of within-canopy variations in leaf structural, chemical and physiological traits across plant functional types. *New Phytologist* **205**, 973–993. doi.org/10.1111/nph.13096

Nowacki, G., and Abrams, M. (2008). The demise of fire and “mesophication” of forests in the eastern United States. *Bioscience* 58, 123–138. doi: 10.1641/B580207

Parker, J., Fernandez, I., Rustad, L., and Norton, S. (2001). Effects of nitrogen enrichment, wildfire, and harvesting on forest-soil carbon and nitrogen. *Soil Science Society of America Journal*, *65*(4), 1248-1255. doi: 10.2136/sssaj2001.6541248x

Parshall, T. and Foster, D. (2002). Fire on the New England landscape: regional and temporal variation, cultural and environmental controls. *Journal of Biogeography*, *29*(10‐11), 1305-1317.

Patel, K., Jakubowski, M., Fernandez, I., Nelson, S. and Gawley, W. (2019). Soil nitrogen and mercury dynamics seven decades after a fire disturbance: a case study at Acadia National Park. *Water, Air, & Soil Pollution*, *230*(2), 29. doi.org/10.1007/s11270-019-4085-1

~~Parshall, T., Foster, D., Faison, E., MacDonald, D., and Hansen, B. (2003). Long-term history of vegetation and fire in pitch pine–oak forests on Cape Cod, Massachusetts.~~ *~~Ecology~~* ~~84, 736–748. doi: 10.1890/0012-9658(2003)084~~

~~Patterson, T., Maxwell, R., Harley, G., Oliver, J., Speer, J., Collins, S., ... and Russell, C. (2016). Climate–Growth Relationships of Pinus rigida (Mill.) at the Species’ Northern Range Limit, Acadia National Park, ME.~~*~~Northeastern naturalist~~*~~,~~*~~23~~*~~(4), 490-500.~~

Patterson, III, W., Saunders, K. and Horton, L. (1983). Fire regimes of the coastal Maine forests of Acadia National Park. U.S. Department of the Interior, National Park Service, North Atlantic Region, Office of Scientific Studies, Boston, Mass. Publ. OSS 83-3.

Patterson, III, W., Edwards, K. and Maguire, D. (1987). Microscopic charcoal as a fossil indicator of fire. *Quaternary Science Reviews*, *6*(1), 3-23. doi.org/10.1016/0277-3791(87)90012-6

Plain, A., Kuser, J., and Ledig, F. (1987). Provenance and Progeny Variation in Pitch Pine from the Atlantic Coastal Plain. *Forest Science*, *33*(2), 558-564.

Renninger, H., Clark, K., Skowronski, N. and Schäfer, K. (2013). Effects of a prescribed fire on water use and photosynthetic capacity of pitch pines. *Trees*, *27*(4), 1115-1127. doi: 10.1007/s00468-013-0861-5

Shakesby, R. and Doerr, S. (2006). Wildfire as a hydrological and geomorphological agent. *Earth-Science Reviews*, *74*(3-4), 269-307. doi.org/10.1016/j.earscirev.2005.10.006

Schier, G. and McQuattie, C. (1996). Response of ectomycorrhizal and nonmycorrhizal pitch pine (Pinus rigida) seedlings to nutrient supply and aluminum: growth and mineral nutrition. *Canadian journal of forest research*, *26*(12), 2145-2152. doi.org/10.1139/x26-243

Stambaugh, M., Varner, J., Noss, R., Dey, D., Christensen, N., Baldwin, R., ... and Waldrop, T. (2015). Clarifying the role of fire in the deciduous forests of eastern North America: reply to Matlack. *Conservation Biology*, *29*(3), 942-946. https://www.jstor.org/stable/24483128

Steiner, K., and Berrang, P. (1990). Microgeographic adaptation to temperature in pitch pine progenies. *American Midland Naturalist*, 292-300. doi.org/10.2307/2426557

Swanston, C., Brandt, L., Janowiak, M., Handler, S., Butler-Leopold, P., Iverson, L., et al (2018). Vulnerability of forests of the Midwest and Northeast United States to climate change. *Clim. Change* 146, 103–116. doi: 10.1007/s10584-017-2065-2

Szpakowski, D. and Jensen, J. (2019). A review of the applications of remote sensing in fire ecology. *Remote Sensing*, *11*(22), 2638. doi.org/10.3390/rs11222638

Van de Waal, D., Elser, J., Martiny, A., Sterner, R. and Cotner, J. (2018). Editorial: progress in ecological stoichiometry. Front Microbiol 9: 1957.

Verma, S. and Jayakumar, S. (2012). Impact of forest fire on physical, chemical and biological properties of soil: A review. *Proceedings of the International Academy of Ecology and Environmental Sciences*, *2* (3), 168.

Wang, H., Prentice, I., Davis, T., Keenan, T., Wright, I. and Peng, C. (2017) Photosynthetic responses to altitude: an explanation based on optimality principles. *New Phytologist*, **213**, 976–982. doi.org/10.1111/nph.14332

Watson, G. Goodness of fit tests on a circle. (1962) II. *Biometrika*, 49, 57-63. doi.org/10.2307/2333135