**Title Page**

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

Authors and affiliations:

Jeff Licht1, Risa McNellis2 and Nicholas G. Smith3

1School for the Environment, University of Massachusetts, Dorchester, MA, USA 02110

2, 3 Department of Biological Sciences, Texas Tech University, Lubbock, TX, USA 79409

Key words

*Pinus rigida*, Pitch pine, Mount Desert Island, fire history, elevation, resilience, topography, iWUE, soil water retention

**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 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**

Over millennia, fire has been a constant disturbance in pitch pine (*Pinus rigida*) barrens, enabling persistence through reduced competition, added pyrogenic carbon (C) by way of post-fire charcoal, and long evolved adaptations. These adaptations include serotinous cones, which rely on the brief extreme heat of fire to release seeds (Givnish 1981), thickened bark to withstand scorching (xxx), and epicormic sprouting following fire to provide additional photosynthetic stimulation (xxx). However, historic fire prevention and suppression has resulted in a significant loss of pitch pine barrens throughout the Northeast United States (Noss *et al.* 2006; Nowacki and Abrams 2008; Hanberry *et al.* 2012), despite the occurrence of other forms of disturbance, such as land clearing and insect herbivory. Nevertheless, pitch pine communities do persist.

Interestingly, there has been a disappearance of fire-adaptive traits in pitch pines that no longer experience regular fire. For example, cone serotiny is low in jack pine populations in Maine that haven’t experienced fire in over 100 years (Conkey *et al.* 1995). Other traits, such as thick bark and epicormic re-sprouting (sprouting of needles from the trunk), have disappeared as well (xxx). One reason for the dissipation of adaptive traits are warmer temperatures and increasingly volatile changes in summer precipitation (xxx), in which fire-adaptive traits are not beneficial. Given the lack of a fire threat, pitch pine are also more directly competing with other evergreens (Nowacki and Abrams 2008; Schwartz *et al.* 2016). A key question which arises is, in the absence of fire, what conditions favor the persistence of pitch pine communities?

Elevation and topography have been shown to be important factors in the dominance of pitch pine barrens due to their influence on the severity and extent of wildfires. Pitch pines favor dry, infertile soils with open forest canopies (Nowacki and Abrams 2008; Hanson 2017). Although pines vary in the aspect (or a position facing a particular direction) they occupy, areas with medium to high slopes often support pine communities due to good soil drainage (Howard and Stelacio 2011; Hanson 2017). Because of the strong positive relationship between elevation and precipitation, low elevation sites tend to have better established and more resilient pitch pine communities (Nowacki and Abrams 2008), and persist even in the absence of fire. At higher elevations where moisture is higher, lack of fire removes the competitive advantage pitch pines have in outlasting nutrient- and moisture-demanding, late-successional species, which thrive in the high moisture and dense canopy conditions created when left undisturbed (Nowacki and Abrams 2008; Schwartz *et al.* 2016). Elevational gradients have also been shown to have a strong impact on photosynthesis, with photosynthesis, stomatal conductance, and leaf N increasing with elevation (Körner *et al.* 1986; Körner and Diemer 1987; Friend *et al.* 1989; Bresson *et al.* 2009). In addition, C13 isotope discrimination decreases with altitude and is associated with greater carboxylation efficiency at high altitudes (Körner *et al.* 1991; Zhu *et al.* 2010; Chen *et al.* 2017).

On Mt. Desert Island in Acadia National Park (ME, USA), pitch pine dwell at the edge of their northeastern range (Fig. 1). In October 1947, an intense fire started just west of Bar Harbor, on the east side of the island (Miller *et al.* 2017), burning 17,188 acres in two weeks (Fig. 2A). Since then, fire suppression has been used at Mt. Desert Island to avoid the tragic consequences of such intense fires. According to our survey of seventeen populations on the island, trees are still recovering from the 1947 fire (xxx) and trees which were not burned persist despite expected dependence on fire intervals of 6-25 years (Jordan *et al.* 2003).

The fire, elevational, and topographic gradients at Mt. Desert Island provide a unique testbedto untangle connections and differences between disturbance and environmental factors and tree traits in pitch pines on the island (Fig. 2B). 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 characterized 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 explored 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 expected that 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). We also expected soil water retention to be greater at low elevations due to flat terrain (alleviating erosion mechanics).

We 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. We also expected a reduction in leaf nutrients at high elevation, mimicking expected reductions in the soil. However, we expected that fire history might alleviate these stress indicators, as a result of increased soil nutrients and water retention. At the plant level, we expected to see plants with 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. We also expected smaller trees in areas that had experienced the 1947 fire due to age, but that the difference would be less at high elevation due to stress-reducing effects of fire on the soil environment.

**METHODS**

**Study Extraction Sites**

We investigated 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 were 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.

*et al.* (Szpakowski and Jensen 2019).

**Soil Analysis**

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 *et al.* 2018).

**Foliar Analysis**

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.

**Tree & Canopy Characteristics**

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.* 2013)—this method served as a surrogate, but inverse, measure for stand density (Mosseler *et al.* 2004).

**Statistical Analysis**

All data were analyzed using a similar mixed effects model structure with elevation as a continuous fixed factor and presence of the 1947 fire (yes or no) as a categorical fixed factor. The interaction between elevation and presence of the 1947 fire was also included in each model and site was included as a random factor. In total, 26 models were fit with the following dependent variables: slope (°), 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), soil calcium (Ca2+ %), soil phosphorus (P, %), soil potassium (K+, %), soil magnesium (Mg2+, %), soil aluminum (Al+, ppm), soil zinc (Zn, ppm), and soil water retention (%). Tree height, canopy spread, DBH, foliar P, foliar K+, foliar Zn, soil P, soil Al+, soil 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 2020). Significance tests for each fixed factor was performed using the ‘Anova’ function in R (R Core Team 2020). Post-hoc comparisons of means and slopes were done using Tukey’s HSD tests at 95% confidence using the ‘emmeans’ package in R (Lenth 2020). 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 3.6.3 (R Core Team 2020).

**RESULTS**

**Topographical Features**

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). Slope was not significantly different between high and low elevation sites or between sites with different fire history (Tab. 7).

**Soil Nutrients and Water Retention**

Soil C concentrations were greater at lower elevations (*P* < 0.05), with no difference due to fire history (*P* < 0.05, Fig. 5A and Tab. 3). Soil N did not vary between sites (*P* > 0.05, Tab. 3). Soil C/N was 15% lower at high elevation sites (*P* < 0.05, Fig. 5B and Tab. 3), but we found no significant difference in C/N due to fire history (*P* > 0.05 in both cases). There was no impact of either elevation or fire history on soil water retention (SWR; *P* < 0.01, Tab. 3). Soil Ca (Fig. 6A), soil K+ (Fig. 6B), and soil P (Fig 6C) were all higher at low elevations (Tab. 4). Soil Al+ (Fig. 6D) and soil Zn (Fig. 6E) both had significant relationship with the interaction between elevation and fire history (Tab. 4). Both soil Al+ and Zn had a positive relationship with elevation in sites with no fire history and a negative relationship in sites with a history of fire (Fig. 6D and Fig 6E).

**Foliar Traits**

Trees at higher elevations experienced less negative δ13C (*P* < 0.01, Fig. 7A and Tab. 5), reflecting greater water use efficiency, regardless of fire history. There were no significant differences between tree populations for δ15N (*P* > 0.05, Tab. 5)*.* Foliar C was slightly higher at sites with a history of fire than sites with no fire history (*P* > 0.05, Fig. 7B and Tab. 5); however there was no difference in foliar N or foliar C/N between sites (*P* > 0.05, Tab. 5). Foliar Ca2+ was higher at low elevations (*P* < 0.001, Fig. 7C and Tab. 6). Foliar K+ showed an interaction between elevation and fire history, with a positive relationship between foliar K+ in sites with no history of fire and a negative relationship in sites with a history of fire (elevation x fire: *P* < 0.05, Fig. 7D and Tab. 6). Foliar P, foliar Mg2+, foliar Al+, and foliar Zn showed no relationship with either elevation or fire history (Tab. 6).

**Tree & Canopy Characteristics**

Both canopy spread (P < 0.05; Fig. 8A and Tab. 7) and DBH (*P* < 0.01, Fig. 8B and Tab. 7), were higher in trees at low elevations. Distance between neighbors was greater at high elevation sites, particularly in trees that have no history of fire (*P* < 0.01, Fig. 8C and Tab. 7).There was a significant interaction between fire and elevation on tree height (*P* < 0.01, Fig. 8E, Tab. 7), with a positive relationship between tree height and elevation at sites with no fire history and a negative relationship at sites with a history of fire.

**DISCUSSION**

**Topographical Features**

Topography, specifically elevation, is found to be a dominant driver of plant and ecosystem processes during an extended fire absence interval. We confirmed trees at lower elevations favored growth over stress tolerance consistent with findings by others with regard to intrinsic water use efficiency (Körner *et al.* 1991; Zhu *et al.* 2010; Chen *et al.* 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 varies across elevation. 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 (xxx). 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 *et al.* 1987; Verma *et al.* 2005). To support this, there are previous findings which report that 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 low elevations (Wonderland and St. Sauveur), 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* (2019) 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 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 conjure 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.* 2013; Lafon *et al.* 2014; Swanston *et al.* 2018).

**Leaf Traits**

High elevations (Gorham Cliffs and South Cadillac) 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.

**Tree & Canopy 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, 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 refugiaat Mt. Desert (a phenomenon referred to by Ledig et al., 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 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). 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* (needlecast, Little and Garrett 1990) and insect herbivory (Lesk *et al.* 2017) are not management factors at Mt. Desert as they are in pine barrens elsewhere. (Fernandez *et al.* 2015; Swanston *et al.* 2018).No doubt warming climate, is having the greatest impact on island vegetative prospects including the fortunes of pitch pine. According to several authors warming climate impacts habitat suitability and pitch pine tendencies to consolidate, regenerate or migrate (Day *et al.* 2005; Lee *et al.* 2019). What has been clear for almost three decades is the effect of global climate change on physiological traits. Day et al. (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 increased pitch pine reproductive difficulties (Ledig *et al.* 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. What is not clear istree (Day *et al.* 2014)will be shaped by a continuing rise in What appears to be more certain is the prediction that pitch pine colonies will suffer due to a combination of diminished open space capacity, loss of enriched substrates, and elimination of suitable habitats (Day *et al.* 2005). Thus, in acknowledgingscientists forecast ing(Connell and Slatyer 1977)

**Anticipation of Southern Pine Beetle Invasion**

A prolonged fire interval coupled with increases in annual winter temperatures raises the spectre of still another, different disturbance—namely the potential invasion within the next decade of an herbivore, Southern pine beetle (*Dendroctonus frontalis* or ‘SPB’). Although deer browsing and rodent damage historically impede tree survival in pine barrens (Ledig *et al.* 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).

**Pitch pine 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 the National Park Service management charged with protection of this species. The importance of this species cannot be overstated from an ecological and 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**

We found that 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 at Mt. Desert Island. Given the length of the current 75 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. 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.

**ACKNOWLEDGEMENTS**

Research at Mt. Desert Island was conducted under permit ACAD-2020-SCI-0014 from the U.S. Department of Interior granted to Jeff Licht. Mike Day, PhD, suggested topics for study and located some of the sites for the study. Cartographer Jill Phelps Kern created geospatial figures. Remote sensing devices were supplied by Tora Johnson, PhD. Field sampling was assisted by Mimi Licht and Laura Brumleve. Site measurements were greatly facilitated by staff at National Park Service, Mt. Desert Island, Bar Harbor, ME. Our thanks to several anonymous reviewers prior to submission.

**ORCID**

Jeff Licht: <https://orcid.org/0000-0002-2248-2050>

Risa McNellis: https://orcid.org/0000-0002-3538-9269

Nicholas Smith: <https://orcid.org/0000-0001-7048-4387>

**FUNDING INFORMATION**

NGS and JL acknowledge support from the United States Department of Interior (grant P20AP00312). NGS acknowledges support from Texas Tech University. RM was supported by the Texas Tech Climate Center, with funding from the United States Department of Interior.

**REFERENCES**

Abney RB, Kuhn TJ, Chow A, *et al.* 2019. Pyrogenic carbon erosion after the Rim Fire, Yosemite National Park: The Role of Burn Severity and Slope. *J Geophys Res Biogeosciences* **124**: 432–49.

Agostinelli C and Lund U. 2017. R package “circular”: Circular Statistics (version 0.4-93).

Bresson CC, Kowalski AS, Kremer A, and Delzon S. 2009. Evidence of altitudinal increase in photosynthetic capacity: gas exchange measurements at ambient and constant CO2 partial pressures. *Ann For Sci* **66**: 505–505.

Caldwell MM and Richards JH. 1989. Hydraulic lift: water efflux from upper roots improves effectiveness of water uptake by deep roots. *Oecologia* **79**: 1–5.

Chen Z, Wang G, and Jia Y. 2017. Foliar δ13C Showed No Altitudinal Trend in an Arid Region and Atmospheric Pressure Exerted a Negative Effect on Plant δ13C. *Front Plant Sci* **8**: 1–9.

Churchill DJ, Larson AJ, Dahlgreen MC, *et al.* 2013. Restoring forest resilience: From reference spatial patterns to silvicultural prescriptions and monitoring. *For Ecol Manage* **291**: 442–57.

Conkey LE, Keifer M, and Lloyd AH. 1995. Disjunct jack pine (Pinus banksiana Lamb.) structure and dynamics, Acadia National Park, Maine. *Ecoscience* **2**: 168–76.

Connell JH and Slatyer RO. 1977. Mechanisms of Succession in Natural Communities and Their Role in Community Stability and Organization. *Am Nat* **111**: 1119–44.

Coulson RN and Klepzig KD. 2011. Southern pine beetle II General Technical Report SRS-140. Asheville, NC.

Day ME, Greenwood MS, and White AS. 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 Physiol* **21**: 1195–204.

Day ME, Schedlbauer JL, Livingston WH, *et al.* 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 Manage* **205**: 59–71.

Day ME, Zazzaro S, and Perkins LB. 2014. Seedling ontogeny and environmental plasticity in two co-occurring shade-tolerant conifers and implications for environment-population interactions. *Am J Bot* **101**: 45–55.

Dodds KJ, Aoki CF, Arango-Velez A, *et al.* 2018. Expansion of Southern Pine Beetle into Northeastern Forests: Management and Impact of a Primary Bark Beetle in a New Region. *J For* **116**: 178–91.

Doerr SH, Santín C, Merino A, *et al.* 2018. Fire as a Removal Mechanism of Pyrogenic Carbon From the Environment: Effects of Fire and Pyrogenic Carbon Characteristics. *Front Earth Sci* **6**: 1–13.

Farquhar GD, Ehleringer JR, and Hubick KT. 1989. CARBON ISOTOPE DISCRIMINATION AND PHOTOSYNTHESIS. *Annu Rev Plant Physiol Plant Mol Biol* **40**: 503–37.

Fernandez IJ, Schmitt C, Stancioff E, *et al.* 2015. Maine’ s Climate Future: 2015 Update Repository Citation.

Friend AD, Woodward FI, and Switsur VR. 1989. Field Measurements of Photosynthesis, Stomatal Conductance, Leaf Nitrogen and δ 13 C Along Altitudinal Gradients in Scotland. *Funct Ecol* **3**: 117.

Fuller L and Quine CP. 2016. Resilience and tree health: a basis for implementation in sustainable forest management. *Forestry* **89**: 7–19.

Givnish TJ. 1981. Serotiny, Geography, and Fire in the Pine Barrens of New Jersey. *Evolution (N Y)* **35**: 101–23.

Hanberry BB, Dey DC, and He HS. 2012. Regime Shifts and Weakened Environmental Gradients in Open Oak and Pine Ecosystems (KP Van Niel, Ed). *PLoS One* **7**: e41337.

Hanson AA. 2017. Distribution Patterns in Appalachian Table Mountain Pine and Pitch Pine Stands. *J Chem Inf Model*.

Howard LF and Stelacio MA. 2011. Fire and the Development of High-Elevation Pitch Pine Communities in Northeastern West Virginia. *Bull New Jersey Acad Sci* **56**: 19–22.

Jordan MJ, Patterson WA, and Windisch AG. 2003. Conceptual ecological models for the Long Island pitch pine barrens: implications for managing rare plant communities. *For Ecol Manage* **185**: 151–68.

Kolden C, Bleeker T, Smith A, *et al.* 2017. Fire Effects on Historical Wildfire Refugia in Contemporary Wildfires. *Forests* **8**: 400.

Körner C, Bannister P, and Mark AF. 1986. Altitudinal variation in stomatal conductance, nitrogen content and leaf anatomy in different plant life forms in New Zealand. *Oecologia* **69**: 577–88.

Körner C and Diemer M. 1987. In situ Photosynthetic Responses to Light, Temperature and Carbon Dioxide in Herbaceous Plants from Low and High Altitude. *Funct Ecol* **1**: 179.

Körner C, Farquhar GD, and Wong SC. 1991. Carbon isotope discrimination by plants follows latitudinal and altitudinal trends. *Oecologia* **88**: 30–40.

Lafon CW, Grissino-mayer HD, Aldrich SR, *et al.* 2014. Three centuries of appalachian fire history from tree rings. : 99–103.

Ledig FT, Hom JL, and Smouse PE. 2013. The evolution of the New Jersey Pine Plains. *Am J Bot* **100**: 778–91.

Ledig FT, Smouse PE, and Hom JL. 2015. Postglacial migration and adaptation for dispersal in pitch pine (Pinaceae). *Am J Bot* **102**: 2074–91.

Lee C-S, Robinson GR, Robinson IP, and Lee H. 2019. Regeneration of pitch pine (Pinus rigida) stands inhibited by fire suppression in Albany Pine Bush Preserve, New York. *J For Res* **30**: 233–42.

Lenth R. 2020. emmeans: Estimated Marginal Means, aka Least-Squares Means.

Lesk C, Coffel E, D’Amato AW, *et al.* 2017. Threats to North American forests from southern pine beetle with warming winters. *Nat Clim Chang* **7**: 713–7.

Licht J and Smith NG. 2020. Pyrogenic Carbon Increases Pitch Pine Seedling Growth, Soil Moisture Retention, and Photosynthetic Intrinsic Water Use Efficiency in the Field. *Front For Glob Chang* **3**: 1–10.

Mikita-Barbato RA, Kelly JJ, and Tate RL. 2015. Wildfire effects on the properties and microbial community structure of organic horizon soils in the New Jersey Pinelands. *Soil Biol Biochem* **86**: 67–76.

Miller DR, Castañeda IS, Bradley RS, and MacDonald D. 2017. Local and regional wildfire activity in central Maine (USA) during the past 900 years. *J Paleolimnol* **58**: 455–66.

Mosseler A, Rajora OP, Major JE, and Kim KH. 2004. Reproductive and genetic characteristics of rare, disjunct pitch pine populations at the northern limits of its range in Canada. *Conserv Genet* **5**: 571–83.

Noss RF, Franklin JF, Baker WL, *et al.* 2006. Ecology and Management of Fire-prone Forests of the Western United States. *Soc Conserv Biol Sci Panel Fire West US For* **1**: 1–72.

Nowacki GJ and Abrams MD. 2008. The Demise of Fire and “Mesophication” of Forests in the Eastern United States. *Bioscience* **58**: 123–38.

Patel KF, Jakubowski MD, Fernandez IJ, *et al.* 2019. Soil Nitrogen and Mercury Dynamics Seven Decades After a Fire Disturbance: a Case Study at Acadia National Park. *Water, Air, Soil Pollut* **230**: 29.

Patterson WA, Edwards KJ, and Maguire DJ. 1987. Microscopic charcoal as a fossil indicator of fire. *Quat Sci Rev* **6**: 3–23.

Qi Z, Jingfang S, and Wenwei L. 2018. A survey about characteristics of soil water retention curve. *IOP Conf Ser Earth Environ Sci* **153**: 062076.

R Core Team. 2020. R: A language and environment for statistical computing.

Renninger HJ, Clark KL, Skowronski N, and Schäfer KVR. 2013. Effects of a prescribed fire on water use and photosynthetic capacity of pitch pines. *Trees* **27**: 1115–27.

Schafer K and Bohrer G. 2016. Effects of Disturbance on Carbon Sequestration in the New Jersey Pine Barrens. Argonne, IL (United States).

Schwartz NB, Urban DL, White PS, *et al.* 2016. Vegetation dynamics vary across topographic and fire severity gradients following prescribed burning in Great Smoky Mountains National Park. *For Ecol Manage* **365**: 1–11.

Shakesby R and Doerr S. 2006. Wildfire as a hydrological and geomorphological agent. *Earth-Science Rev* **74**: 269–307.

Swanston C, Brandt LA, Janowiak MK, *et al.* 2018. Vulnerability of forests of the Midwest and Northeast United States to climate change. *Clim Change* **146**: 103–16.

Szpakowski DM and Jensen JLR. 2019. A Review of the Applications of Remote Sensing in Fire Ecology. *Remote Sens* **11**.

Verma SB, Dobermann A, Cassman KG, *et al.* 2005. Annual carbon dioxide exchange in irrigated and rainfed maize-based agroecosystems. *Agric For Meteorol* **131**: 77–96.

Wang H, Prentice IC, Davis TW, *et al.* 2017. Photosynthetic responses to altitude: an explanation based on optimality principles. *New Phytol* **213**: 976–82.

Zhu Y, Siegwolf RTW, Durka W, and Körner C. 2010. Phylogenetically balanced evidence for structural and carbon isotope responses in plants along elevational gradients. *Oecologia* **162**: 853–63.