**Title Page**

Pitch Pine (*Pinus rigida*) Response to Fire Absence and Topographic Factors at Mt. Desert Island

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

**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; since then there has been no recurrence of fire. Other populations have been unaffected by fire disturbance for over one hundred and twenty years. Despite the absence of fire, pitch pine persists at Mt. Desert Island, suggesting that other environmental drivers may be as or more important than fire in that system. We examined the influence of fire history and topography (i.e., elevation, aspect, and slope) on individual trees in four separate stands at Mt. Desert Island. Generally, topography was found to be a more important driver of leaf and plant level traits than fire history, with individuals possessing greater stress tolerance traits at high elevation. We attribute this to changes in topographical and soil characteristics along the gradient. These results challenge the suggestion that fire is the primary driver of pitch pine persistence at Mt. Desert Island and indicate that pitch pine has the capacity to thrive across a wider array of environments. These results can serve to better understand and manage this species in an ever-changing future world.

**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) in heathland, pine barren communities. Over millennia, their persistence (ability to remain in a particular setting) is defined by frequent fire disturbance that regulates competition, removes post-fire pyrogenic carbon (C) from the soil and drives the radiation of fire adaptations. Among the most significant fire adapatations are serotinous cones (which typically open only when fire engulfs the tree), thickened bark to withstand scorching and epicormic sprouting along branches and trunk (Little 1953). These features were present on Mt. Desert in 1947 (Fig. 1) when an intense October 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 has been used to avoid a repetition of the tragic consequences from that fire. Interestingly, in ensuing decades, tree pyrogenic adaptations have diminished, perhaps as the result of phenotypic plasticity, shifting away from cone serotiny (Conkey, Keifer and Lloyd 1994; Jordan, Patterson and Windisch 2003). As there is less pressure to produce seeds that survive in the midst of a fire (Givnish 1981), there may also be less need for thick bark or epicormic sprouting (Renninger *et al.* 2013). Past studies have speculated that tree defenses are shifting from fire resiliency to traits that may help deal with other abiotic conditions such as warmer temperatures and increasing summer drought (Day *et al.* 2005; .

Recent history of pitch pine population success in fire-suppressed locations such as Mt. Desert Island defies 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). While fire responses have been studied previously (Foereid *et al.* 2015; Carlo *et al.* 2016; Neill *et al.* 2007), there is a critical need to understand other factors that might be influencing pithc pine persistence in the absence of fire at Mt. Desert Island.

Here, we address one such factor that has not yet been thoroughly assessed at Mt. Desert in comparison with fire history, topography (Parshall and Foster 2002; Fig. 2). Specifially, we use four populations that lie along a topographical and fire history gradient (Fig. 3) as proxies for more than a dozen other colonies, to examine the effects of elevation, aspect and slope (Bolstad and Stowe 1994) on soil (ecosystem), leaf, and plant-level 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, 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 less soil carbon (DeBano 1981), greater alkali cations (Kolden *et al.* 2017), and increased solubilized minerals (Caldwell and Richards 1989) in soils which 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).

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 hypothesized 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 be smaller in heigh and DBH, have narrower canopy, and be more sparsely clustered (greater distance between conspecific neighbors) at high elevation, again as a result of the topography- and soil-induced stress. We expected to find 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.

**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 two trail transects St. Sauveur and South Cadillac trails. Soils at all four sites were overlain with rapidly drying needle duff, porous, and comprised of acidic hornblende granite or Ellsworth schist (Day *et al.* 2005). In addition they were uniformly shallow (varying between 0.7-2.5 cm), homogeneous, and low in fertility (Butak 2014). In some cases, sampling was limited by time, weather and site access yielding uneven sample accumulations. Our analytical methods were designed to deal with uneven sample sizes.

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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. 70 mL soil samples were extracted at fifteen tree locations at four sites, from <10.5 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). We also used a set of #10-#120 mesh sieves (Advantech, Wisconsin, USA) to determine presence of close-to-the-surface fine charcoal particulate matter symptomatic of recalcitrant pyrogenic material at all four sites.

**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**

calibration between two ,, Mean distances between sampled trees were calculated including up to five of the nearest, reproductively mature conspecific (within 5 m) neighbors (Churchill *et al.* 2012)—this clustering 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 as a continuous independent factor and presence of the 1947 fire (yes or no) as a categorical independent factor. The interaction between elevation and presence of the 1947 fire was also included as an independent factor 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), soil Ca2+, P, Al+, Zn, 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, while 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). Type II F-tests were used to determine the statistical significance of each factor in each model using the ‘Anova’ function in the ‘car’ package in R (Fox and Weisberg, 2019). Slopes and intercepts for plotting were determined 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 4.0.5 (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*

Soil C concentrations were greater at lower elevations (*P* < 0.05), but were unaffected by fire history or their interaction (*P* > 0.05 in all cases, Fig. TBD and Tab. 3). Soil N and C/N did not vary with elevation, fire history, or their interaction (*P* > 0.05 in all cases, Fig. TBD and Tab. 3).

Soil Ca2+ decreased with elevation (*P* < 0.05, Fig. TBD and Tab. 4), regardless of fire history. Soil P, Mg2+, and Zn did not vary with elevation, fire history, or their interaction (Tab. 4). Fire accounted for a 48% reduction in K+ at fire-experienced sites (*P* < 0.05, Fig. TBD and Tab. TBD), regardless of elevation. There was an interaction between fire history and elevation (*P* < 0.01, Tab. 4) that indicated that soil Al+ increased with elevation in sites that did not experience the 1947 fire and decreased with elevation at sites that did experience the 1947 fire (Fig. TBD).

There was an interaction between elevation and fire history on soil water retention (SWR; *P* < 0.01, Fig. TBD and Tab. 3), driven by higher SWR at sites that experienced the 1947 fire at low elevation, an effect that was diminished at higher elevations (Fig. TBD).

*Leaf Isotopes and Elements*

Trees at higher elevations experienced less negative δ13C (*P* < 0.01, Fig. TBD and Tab. 5), reflecting greater water use efficiency, regardless of fire history. There were no significant effect of fire history, elevation, or their interaction on δ15N (*P* > 0.05 in all cases, Fig. TBD and Tab. 5)*.*

Foliar C was greater in trees at sites that experienced the 1947 fire (*P* < 0.05, Fig. TBD and Tab. 5), regardless of elevation; however there was no effect of fire history, elevation, or their interaction on foliar N or C/N (P > 0.05 in all cases, Fig. TBD and Tab. 5).

Foliar Ca2+ was negatively impacted by increasing elevation (*P* < 0.001, Fig. TBD and Tab. 6), regardless of fire history. Our model indicated that foliar P was significantly higher at fire-involved sites (*P* < 0.01, Fig. TBD and Tab. 6), regardless of fire history. Foliar K+ was reduced by fire involvement at high elevations, but not low elevations (elevation x fire: *P* < 0.05, Fig. 8C and Tab. 6). Neither foliar Al+ nor Mg2+ differed by fire history, elevation, or their interaction (*P* > 0.05 in all cases; Fig. TBD and Tab. 6). Foliar Zn concentrations decreased with increasing elevation (*P* < 0.01, Fig. TBD and Tab. 6), regardless of fire history.

*Plant-level Traits*

There was a significant interaction between fire and elevation on tree height (*P* < 0.01, Tab. 7), which indicated that historical fire presence had a negative impact on tree height at high, but not low, elevation (Fig. TBD). Increasing elevation reduced DBH (P < 0.001; Fig. TBD and Tab. 7), regardless of fire history. Canopy spread was reduced at high elevation (*P* < 0.01, Fig. 9B and Tab. 7), regardless of fire history. Distance between neighbors was greater at high elevation sites (*P* < 0.001, Fig. 9D and Tab. 7), regardless of fire history.

**DISCUSSION**

*Topographic Traits*

Topography, specifically elevation, is found to be a dominant driver of plant and ecosystem processes ~~we measured~~ and may play a role in ecosystem resilience during an extended fire absence interval (Buma *et al.* 2013). Topography (slope) was found to shape populations where elevation, exclusive of fire disturbance, was influential. ~~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.~~  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. 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. At higher elevations on Mt. Desert there is the possibility that an extended fire interval (Buma *et al*. 2013) 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).

*Soil Characteristics*

Soil fertility and water retention vary, understandably, across the four colonies and their elevation gradients. It is apparent fire history, on its own or interacting with topography, plays a role in determining tree-level response to wind and other disturbances such as competition from other evergreen trees which are sparse over terrain at the two upper summits. We were curious about the influence of subsurface charcoal as a soil component in fire-exposed areas. At nearby, burned-over Cadillac Brook (below the heights of South Cadillac trail) earlier paleo (Lafon *et al.* 2014) and fossil indicator reports (Patterson, Edwards and Maguire 1987; Verma and Jayakumar 2012) underscore the presence of charcoal. ~~To support this contention, there are previous findings which report post-fire pyrogenic C remnants endure in the soil layer (DeBano 1981)~~ ~~often accompanied by increased alkali cations (Kolden~~ *~~et al.~~* ~~2017) and solubilized minerals (Caldwell and Richards 1989).~~ However, our shallow excavation and subsequent screening did not reveal noticeable charcoal particulate in sifted fines from samples at South Cadillac or Gorham cliffs, places where it was most expected, or at Wonderland and St. Sauveur where it was not. The fact that we did not find noteworthy charcoal remnants in our sampling may be contraindicative of selective soil C availability in certain study precincts. 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 shaped by a previous pine barren study which features experiments with non-glaciated soils and very juvenile trees exposed to forest fire, anthropogenic fire and no fire treatments (Licht and Smith 2020). We reported pyrolysis (either natural or anthropogenic) is shown to increase SWR (Licht and Smith 2020); however at Mt Desert this was not experienced, At Wonderland and even more at Gorham cliffs, absence of erosion mechanics, negligible consumption of Ca2+, K+, and Mg2+ (Licht and Smith 2020) and greater soil C availability likely account for higher SWR. If anything, this reinforced our reckoning that trees at upper ledges ~~and cliffs~~ would be more likely to suffer from moisture shortages from steeper pitches, less ~~appealing~~ advantageous aspects and greater drainage in formerly burned areas. In particular, when we dissected these results we concluded greater carbonate availability (e.g., Ca2+ and K+), from fire events, coupled with greater slope and drainage yields better opportunities for stand density especially at low elevations like Gorham cliffs (Churchill *et al.* 2012).

*Leaf Traits*

Intrinsic water use capacity served as a crucial metric of plant response across terrain and in relation to fire history. iWUE findings underscore phenotypic pathways for trees favoring C depletion or abundance consistent with findings by others (Wang *et al.* 2017; Chen, Wang and Jia 2017). We found elevational gradients below St. Sauveur and South Cadillac summits highlighted more positive iWUE. These results provide at least a partial confirmation of previous research showing 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). At Mt. Desert, where elevation gradients are a significant feature of the landscape, attributions of abundance or depletion of C, leading to positive or negative iWUE underscore plant stress tolerance response (to higher wind turbulence and more quickly drying soils) as a feature of upper elevation life (Wang *et al.* 2017). On another tack, though we found no significant results after studying leaf N, with regard to topography, we speculate a linear model demonstrates a fit between N, fire history and tree response at Gorham cliffs and South Cadillac trails. ~~Foliar~~ carbonate concentrations (Ca2+ and K+) were slightly higher in non-fire situations which confounded us based on the supposition we would see greater availability in formerly burned sites (Licht and Smith 2020),~~observed at lower elevation but not confirmed elsewhere as far as we could tell, thus obviating an ability to draw any conclusions about their effects.but how widespread that response is requires further investigation.but recovery capacity was more likely~~

~~connected to higher P.~~

*Plant-level Traits*

Yet based on metrics like conspecific neighbor clustering, this is not the case. Instead, we observed a trend whereby a combination of aspect, slope, open exposure are similar at the two Mt. Desert sub-summits. According to our findings, exposure to an exposed situation is as or more important to evolving phenotypic variation among the *refugia* at Mt. Desert (a phenomenon referred to by Ledig, Smouse and Hom 2015).We anticipated 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°). However, we note examples of vigorous pitch pine clustering (stand density) in spaces both lacking in shade, such as Wonderland, and those where shade is present at Gorham cliffs. The difference between the two is stark when it comes to competition with red spruce (*Picea rubens*), hemlock (*Tsuga canadensis*) and balsam fir (*Abies balsamea*); the competitive response was greater at Wonderland trail. This factor, alone, represents an opportunity, if this trend persists, for trees, there, to continue to expand their ownership of that precinct in comparison with trees at the other three locations. ~~recommends itself as the best cluster candidate for future expansion based solely on the solar exposure factorAt 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 further spur dispersal, beyond an existing toehold, but, 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 which would accelerate advance. Coupled with climate projections (Fernandez *et al.* 2015), we can predict potential ledge population enlargement is unlikely to occur as a function of 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), deer browsing and rodent damage (Ledig, Hom and Smouse 2013), and insect herbivory (Lesk *et al.* 2017) are not management factors at Mt. Desert as they are in barrens elsewhere. Yet, a possibly catastrophic problem may occur due to a combination of a prolonged fire interval and increases in annual winter temperatures (Lesk *et al.* 2017)—namely the potential invasion within the next decade of an herbivore, Southern pine beetle (*Dendroctonus frontalis* Zimmer or ‘SPB’). This herbivore has already paid a deadly visit to New Jersey and Long Island NY (Dodds *et al.* 2018). Unless its progress is deterred by predators like double checkered clerid (*Thanasimus dubius*; Coulson and Klepzig 2011), or some undetermined climate factor, pitch pines along with understory plants, butterflies and moth members of the Acadia ecosystem are vulnerable to predation (Lesk *et al.* 2017).

No doubt warming climate, is having the greatest impact on island vegetative prospects including the fortunes of pitch pine. Specific, r,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 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 resources.

*~~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 condition which could lead to 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), herbivores such as SPB are equipped to produce a more dire result. 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~~ factored into colony persistence depending on a combination of slope, aspect and grade ~~(e.g., flat versus cliff or ledge orientation~~ ~~individual colony slope, a~~ ~~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.~~ In addition, several leaf and soil traits, notably iWUE and soil inorganics combined with topographic traits ~~flat, cliff and ledge colonization as well as adaptivity to stress tolerance or growth depending on topographic, soil, leaf and whole plant trait~~ to provide a synergistic impression ~~of synergies~~. Our data undertake the task of unraveling at least a part of the enigma of 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 scales 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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