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On The Edge: Pitch Pine Persistence in the Absence of Fire Under the Influence of Elevation and 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

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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 stand-replacing conflagration enveloped a portion of the island in 1947; 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 such as elevation and topography, known to impact traits of this species. We studied pitch pine resistance in the absence of fire under the influence of elevation and topography (including slope and aspect). This was achieved based on examining traits of individual trees in four separate stands. Significant differences were found in growth, stand density, photosynthetic water use efficiency, foliar nutrients and soil water retention. Elevation was found to have a greater influence on measured traits; trees at higher elevation displayed greater water use efficiency, indicating a preference for stress resistance over growth. At lower elevation, trees exhibited greater capacity for growth and stand density due to more favorable conditions, including greater soil moisture retention. 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, which dot the northeastern and mid-Atlantic U.S. coast.

**INTRODUCTION**

On Mt. Desert Island in Maine USA, pitch pine (*Pinus rigida* Miller) dwell at the edge of their northeastern range (Fig. 1). Over millenia, fire is a constant disturbance in pine barrens enabling persistence through reduced competition, added pyrogenic C by way of post-fire charcoal and long evolved adaptations. These modifications feature serotonous cones which typically open only when fire engulfs the tree, thickened bark to withstand scorching and epicormic sprouting following fire to provide additional photosynthetic stimulation. ~~Even though fire is considered an obligatory pitch pine bellwether, long-standing indicators point to the evolution away from fire-inspired characteristics in its suppression.~~ ~~Thus, trees bear witness to physiological and morphological changes at Mt. Desert (first described by Little 1953 elsewhere), first described almost three decades ago when only a modest amount of remaining serotiny was~~ reported. ~~Over time,~~ On Mt. Desert, in 1947, an incredibly 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 (Fig. 2A). Since that time, fire suppression is used to avoid a repetition of the tragic consequences seen long ago. Yet, according to our survey of seventeen populations on the island, including trees still in the throes of recovery from the 1947 fire on Cadillac mountain) and those which were uninvolved, persistence is a hallmark. This despite insistence by researchers that fire intervals ideally are between six and twenty-five years (Jordan *et al* 2003). Certainly the National Park Service (Miller *et al* 2014) is aware of this as it is charged with protection of this threatened species which anchors an environmentally sensitive barrens ecosystem, similar in many respects to those located in nearly twenty other states to the south. Crucially, if fire is truly a necessity to prolong longevity, investigators are compelled to seek an explanation for persistence in its absence.

Absence of fire bears witness to the disappearance of formerly adaptive traits such as cone serotony which began its withdrawal decades ago (Conkey *et al* 1994), confirmed in more recent reports (Jordan *et al* 2003). Cone serotony is a unique adaptation in fire-prone systems where seeds are spurred to survival by being expelled forcefully away from the tree in the midst of a fire (Givnish 1981). Other features such as thick bark and epicormic re-sprouting (Renninger *et al* 2013) are no longer as common--sprouting is noticeable as it frequently trails up the trunk. One further reason for adaptive trait dissipation (Heuss 2018) stems from an urgent requirement to adapt to warmer temperatures and increasingly volatile changes in summer precipitation (Day *et al* 2005). Given the lack of a fire threat, pitch pine are compelled to find alternative means to compete with other evergreens (Buma *et al* 2013). A key question which arises is whether individual tree plasticity is sufficient to adapt to the increasing frequency of stressful stimuli unrelated to fire disturbance.

**Hypothesis testing**

A variety of fire, elevation and topographic gradients provide a remarkable testbedto untangle connections and differences between disturbance and environmental factors and tree traits on the island (Fig. 2B). with a backdrop of island ecology continuing through a post-pyrogenic era, we hypothesize low elevation coupled with cliff and ledge topography plays a significant role in the form of increased plasticity in physical traits such as increased foliar C, increased intrinsic water use efficiency and increased soil water holding capacity. These were studied in a low elevation pine barren in north central Massachusetts (Licht and Smith 2020).

Three categories of conditions and traits were examined. The first comprises elevation, aspect and slope. Competition for expansion and colonization was observed in all seventeen of the populations identified on the island. We found the most intense struggles between evergreens occurred at lower elevation where pitch pine are destined to fail if they are unable to master evergreen competitors. Investigators also observed a combination of fire absence at low elevation results in a de-emphasis on colony retreat and encouragement of expansion (Swanston *et al* 2018) ultimately encouraging greater stand density (Churchill *et al* 2012) although the same propensity to density occurred at Gorham cliffs (a casualty of the 1947 fire). In general though, at higher elevations such as the north side of Cadillac mountain, on Norumbega mountain, or Champlain mountain, there is a significant lack of shade and shade-intolerant pitch pine outlast red spruce (*Picea rubens*), hemlock (*Tsuga canadensis*) and balsam fir (*Abies balsamea*) in those situations nearly as much as at lower elevation locations.

Very little is written about the influence of elevation on physical traits of pitch pine species at Mt. Dessert (Butak 2014). However, there are indications, elsewhere, that high elevation trees exhibit high intrinsic water use efficiency signaling a depletion of foliar C in an effort to withstand stress (e.g., Wang *et al* 2017). When investigators examine the effect of elevation on pitch pines in Pennsylvania and West Virginia (Howard and Stelacio 2011), they found trees at higher elevation took advantage of this condition to outcompete other trees. In the absence of fire disturbance (Brand and Jax 2007) other scientists find elevation and topography are likely to increase in importance where persistence is the focus. To this point, though, natural fire (Foereid *et al* 2015), anthropogenic controlled burns (Carlo *et al* 2016) and opening of canopies (Neill *et al* 2007) remain at the center of interest. Second, where pitch pine are in a constant struggle to outgrow or outlast competitors, the use of their photosynthetic apparatus is required to adjust to very frequent stresses and dealing with drought as a result of decreased seasonal precipitation. Evidence exists of positive iWUE (Butak 2014) in low lying, minimal slope, fully exposed sites, like Wonderland on the western side of the island, conferring a high growth functional trait. We consider if the same results obtain at higher elevations (Stambaugh *et al* 2015) and, specifically, within the 1947 fire zone. In particular, at upper ledge elevations where fire events occur with some frequency (Howard and Stelacio 2011) researchers find limits on clustering (stand density), colonization (Lafon *et al* 2014) and expansion. Again, the study attempts to determine if these outcomes may be replicated in forests with much greater height and elevation deviation. In a third group lie traits, namely height, canopy and DBH (diameter at base height), which can be used to better understand the extent to which allometrics coupled with intra tree relations within individual populations. In generating and analyzing data of these types, we aim to provide greater understanding of how to promote pitch pine persistence in communities of the northeastern and mid-Atlantic U.S. coast where elevation and topographical gradients present themselves.

**METHODS**

**Study Extraction Sites**

We investigated fifteen pitch pine specimens at each of four sites at Mt. Desert Island (Tab. 1), factorially crossed in a fire history (Miller *et al* 2017) by elevation design: (1) Wonderland trail at an average of 16.27 m elevation (low elevation, outside the footprint of the 1947 fire), (2) Gorham cliffs at an average of30.74 m (low elevation, within the footprint), (3) St. Sauveur trail at an average of182 m (high elevation, outside the footprint) and (4) South Cadillac trailat an average of 284.43 m (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.

**Allometric relations**

We measured individual tree height, canopy spread and stem diameter of the bole at breast height (DBH). Tree height was estimated using a plastic clinometer (Kager, Lunenberg, MA USA) and 30 m tape. DBH was measured at 1.06 m using an expandable cloth measuring tape. Canopy spread across the first nodal branch expanse below the crown was measured using two calibrated, nested aluminum flags as a ground truth reference. This method was selected to sort out upper canopy spread x height differences where trees across all four stands with very similar height and DBH characteristics dominated.

**Clustering**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 all 2012)—this method served as a surrogate, but inverse, measure for stand density (Mosseler Rajora and Major 2004).  
**Topographic features**

A Kodak Trimble Juno 3B was used to obtain horizontal resolution of data plotted using between five and seven satellite telecommunication vehicles to maintain a maximum Position Dilution of Precision. These data were differentially corrected and have estimated accuracies in the horizontal and vertical direction of 2 meters, while selective availability was set to zero. Multiple satellite-configured GPS data (USGS 2m LIDAR 2010) determined coordinates for individual trees (Lubinski Hop and Gawler 2003) as well as slope and aspect attributes using ArcGIS (version 10). Mapping of this type of data has been used in the past to compare physiography and recalcitrant chemical biogeography, particularly in fire prone contexts (Szpakowski and Jensen 2019).

**Isotopic analysis**

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).

**Foliar tissue analysis**

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.

**Soil Elemental, CEC and pH Analyses**

Soil C, N and C/N were calculated from elemental analysis in a similar fashion to method above (foliar samples). Soil cation exchange capacity (CEC) was derived using Formic acid (HCO2H) and pH was measured using proton activity of a 1:1 slurry.

**Soil Water Retention (SWR)**

Soils were excavated by hand trowel and soil probe (Accuproducts, Saline, MI, USA); 70 mL 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 (Jingfang and Wenwei 2018).

**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 2018).

Because aspect data is circular in nature, we analyzed aspect data using a Watson’s Two-Sample Test of Homogeneity as implemented in the R package ‘circular’ (Agostinelli and Lund 2017). Specifically, one-to-one comparisons were done between each site in all six possible combinations.

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

**RESULTS**

*Aspect*

Watson’s two sample t-tests indicated that the aspects of all sites differed with respect to one another except for the two sites that experienced the 1947 fire (Gorham cliffs and South Cadillac Trail), which had similar aspects (Fig. 3 and Tab. 2).

*Allometry and Stand Density*

There was a significant interaction between fire and elevation on tree height (*P* < 0.01, Fig. 4A, Tab. 3) and DBH (P < 0.05; Fig. 4C and Tab. 3), with trees at higher elevation that experienced the 1947 fire being shorter than those at low elevation that did not experience the fire and having a smaller DBH than all other sites. Canopy spread tended to be reduced at high elevation (*P* < 0.01, Fig. 4B and Tab. 3), 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. 4D and Tab. 3).

*Foliar Isotopes*

Trees at higher elevations experienced less negative δ13C (*P* < 0.01, Fig. 5A 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. 5B and Tab. 4)

*Foliar Organics*

On average, foliar C was greater at upper elevations, however the results were not statistically significant (*P* > 0.05, Fig. 5C and Tab. 4); nor was there a difference in C/N between sites (*P* > 0.05, Fig. 5E and Tab. 4). Our linear model suggested that fire accounted for a significant influence on foliar N (*P* < 0.05, Tab. 4), however post-hoc Tukey’s tests found no difference between sites at α = 0.05 (Fig. 5D).

*Foliar Inorganics*

Foliar Ca2+ was negatively impacted by increasing elevation (*P* < 0.001, Fig. 6A and Tab. 5). Our linear model suggested that foliar P was significantly higher at fire-involved sites (*P* < 0.01, Fig. 6B and Tab. 5), although this was not confirmed by post-hoc Tukey’s tests (Fig. 6B). 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. 6C and Tab. 5). Neither foliar Al+ nor Mg2+ differed by site (*P* > 0.05 in both cases; Fig. 6D, Fig. 6E, and Tab. 5). Foliar Zn concentrations were 9% lower in the high elevation sites than on the low elevation sites (*P* < 0.01, Fig. 6F and Tab. 5), due to a particularly strong reduction at the high elevation site that experienced fire.

*Soil Organics*

Soil C concentrations were greater at lower elevations (*P* < 0.05) and sites that did not experience the 1947 fire (*P* < 0.05, Fig. 7A and Tab. 6). Soil N did not vary between sites (*P* > 0.05, Fig. 7B and Tab. 6). Soil C/N was 15% lower at high elevation sites (*P* < 0.05, Fig. 7C and Tab. 6), 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).

*Soil Water Retention*

There was an interaction between elevation and fire history on soil water retention (SWR; *P* < 0.01, Fig. 7D and Tab. 6), with markedly higher values at Gorham cliffs, the low elevation site that experienced fire, as compared to other sites.

**DISCUSSION**

Elevation, as opposed to fire history, was the dominant driver of plant and ecosystem processes ~~we measured~~ according to our measurements. ~~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. Elevation~~ This factor played a role in several meaningful ways. First, we confirmed increased elevation favored ~~efficiency (e.g.,~~ foliar water use efficiency (Wang *et al* 2017; Chen, Wang and Jia 2017) over growth. Further, we found trees at higher elevation, particularly those in the former 1947 fire district, persevered despite noteworthy challenges including less density, greater distance between conspecific neighbors and evidence of less reproduction. 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 was found to be instrumental in shaping population expansion especially in combination with elevation exclusive of disturbance effects at lower elevation. 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°). Of greater interest was the finding that, despite an absence of recent fire history at Wonderland (none since at least 1900 or so) contrasted with a much more recent fire event at Gorham cliffs, population density, mean distance between population members and overall growth dimensions were more robust at Wonderland.

At high elevation ledge communities, where one might expect it, we found little compelling empirical evidence that recovery after the 1947 fire is as strong a stimulus save for pitch pines found within a sympatry off the South Cadillac mountain trail. ~~This assertion is partly confirmed by the disappearance of serotiny and epicormic sprouting, found formerly at higher sites on Cadillac mountain three decades ago.~~ Fire return intervals have lengthened at Mt. Desert Island to the point where they tend to be too intermittent to perpetuate previous fire resistance traits. A shift back to fire, accompanied by a re-introduction of serotinous characteristics, is not impossible in the future; however, current climate projections suggest the reoccurrence of fire is unlikely (Fernandez *et al* 2015). Despite the absence of fire, fire remnants endure long after the 1947 event. Previously, scientists found subsurface charcoal deposits on the north side of Cadillac Mountain on Mt. Desert (Patterson Edwards and Maguire 1987; Verma and Jayakumar 2012). One could argue that charcoal remnants very probably play a role in recovery capacity at burned-over Cadillac Brook (below the heights of South Cadillac trail), but it is not known to what extent these benefit the larger ecosystem located higher up in that mountain community. Now that recovery from fire is no longer an acute environmental response, we consider to what extent pyrogenic carbon will continue to be available to several generations removed from the 1947 inferno.

Previous studies reported that anthropogenic fire charcoal (PyC) was associated with greater foliar water use efficiency, negligible consumption of Ca2+, K+, and Mg2+ and enhanced soil moisture holding capacity (Licht and Smith 2020). On Mt. Desert Island, we found higher foliar water use efficiencyat high elevations at both burned and unburned sites, consistent with reported outcomes for non-glaciated populations in flat, sand plain New Jersey Pine Barrens (Mikita-Barbato *et al* 2015; Schafer and Bohrer 2016). There is evidence from previous investigations that post-fire PyC remnants endure in the soil layer (DeBano 1981) and that this increases alkali cations (Kolden *et al* 2017), solubilize minerals (Caldwell and Richards 1989) and ~~are likely linked to~~ thermal exfoliation (Shakesby and Doerr 2006). From the standpoint of reproduction, the absence of fire, at locations such as ~~persistence capacity-oriented~~ Wonderland trail (Butak 2014), does not appear to be slowing down expansion in that flat-sloped region nor ~~or~~ on ledge locations (e.g., St. Sauveur) that we studied on the island or which were studied by others in West Virginia ~~and others~~ (Howard 2010) ~~have studied~~. Developing further insights into the ecological stoichiometry of pitch pine at Mt. Desert Island marks a step in achieving a firmer understanding of the relationship between biogeochemistry, fire history and topography.

Our foliar nutrient results derived from burned and unburned sites are similar to those reported by others in New Jersey (e.g., Renninger *et al* 2013) and indicate that historical fire reduced soil C. However we also found a reduction in soil C at upper locations not in the fire path. Alternately, foliar C was similar across sites, inconsistent with findings by others in New Jersey (Renninger *et al* 2013; Alkañiz *et al* 2018), complicating the soil-plant connection. The interaction between elevation and foliar nutrient is still not resolved; foliar Zn availability was higher at lower elevations at Mt. Desert Island. This result was consistent with findings by others in another New Jersey investigation (Kolker *et al* 2013). Our findings led us to speculate that persistence capacity may be tied to higher concentrations of foliar Ca2+ and K+ but how widespread that response is requires unsupported speculation.~~but recovery capacity was more likely connected to higher P~~.

Climate is already considered as a ~~the final a~~ more significant arbiter of population decline rather than stand-replacing fire disturbance due to its absence ~~in the case of long-term pitch pine livelihood~~. Recent climate change models anticipate a negative impact on future vegetative status at Mt. Desert Island (Fernandez *et al* 2015; Swanston *et al* 2018), but these do not specifically address the adaptability of pitch pine nor the extent to which plasticity (Day *et al* 2014) will continue to shape persistence if warming temperatures continue to rise. 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). This included weather-related effects such as episodic drought, harsh winds, and salt spray (Schmitt 2015; Fernandez *et al* 2015) as well as conditions that increased cold intolerance (Berang and Steiner 1985).

Increases in annual winter temperatures (Lesk *et al* 2017) coupled with an absence of fire cause concern about a quite different disturbance—potential invasion within the next decade of an herbivore, Southern pine beetle (*Dendroctonus frontalis* Zimmer or ‘SPB’). Although deer browsing and rodent damage historically impeded tree survival in pine barrens (Ledig *et al* 2013), SPB has already paid a deadly visit to 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), it is possible that pitch pines along with understory plants, butterflies and moth members of the Acadia ecosystem will suffer the same fate experienced in more southerly locations (Lesk *et al* 2017). 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 may be in jeopardy ~~These effects are likely to eventually limit aspects of persistence capacity such as niche expansion, if they have not already,~~ through a combination of diminished open space capacity, loss of enriched substrates and elimination of suitable habitats (Day *et al* 2005).

Pitch 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. Despite increasing climate pressures, tree retreat into ever more sparse conditions reinforces their facilitator status (Connell and Slatyer 1977) for this species explicitly maintains the livelihood of underlying flora through a sharing and distribution of ecoservices. ~~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~~ Our findings may be used by other scientists (Fuller and Quine 2016) to better understand how pitch pine in other ecosystems, outside of the Northeast U.S., take advantage of elevation and topographic parameters to gain advantage over competitors. The present data yields a firmer purchase on current regeneration and expansion concepts—essential to an appreciation of influences on persistence in the absence of forest or prescribed fire.

**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 elevation and topography signaled adaptivity effects (growth, expansion into greater stand density) which account for greater growth and stand density on more hospitable terrain, with little impact from fire history. This is undoubtedly due to the fact that fire return intervals are so infrequent as to reduce recovery features found elsewhere (e.g., where cone serotony and epicormic sprouting still prevail). Flat and ledge pitch pine populations exhibited greater buoyancy than trees in more strenuous cliff situations. We also identified a selective preference for either growth at low elevations or stress tolerance at high elevations using multiple plant and ecosystem metrics. Our findings unravel part of the enigma about persistence in a post-fire milieu during a critical phase of the Anthropocene age (Crutzen and Stoermer 2000). At lower elevations, which represent the vast majority of pitch pine populations in the Northeast US, we predict newly pioneered locations reflect a continuation of persistence signaled by significant differences in density, slope and aspect. At a time when continued climate change may tip the scale away from survival, our findings encourage the use of ~~a model~~ our data by forest managers to better understand the imposition of fire absence on flat and ledge communities.

## 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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**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>

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