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

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**ABSTRACT**

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

**INTRODUCTION**

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

At MDI, trees in low-lying undisturbed (non-1947 fire) areas (Figure 2) appear to engage in more seedling recruitment than trees in the upper elevation fire zone. Indeed, reaction to fire absence manifests as physiological and morphological adjustments over many years (Little 1953). On the island, cone serotiny (Givnish 1981), thick bark, and epicormic re-sprouting (Renninger *et al* 2013) have disappeared in formerly fire-prone pitch pine ecosystems (Jordan *et al* 2003). Suppression makes it likely that such former fire adaptive mechanisms are no longer required for stand sustenance and are unnecessary investments which reduce competition with other evergreens (Buma *et al* 2013). Critically, it is not clear if, in combination with a long period without fire, recovery accelerates the disappearance of adaptive traits (Heuss 2018) or if this is a result of extrinsic responses to other, low intensity disturbances. Previous studies (e.g., Ibáñez *et al* 2019) have framed resilience as an artifact of recovery (Charpentier 2020) specifically in the absence of further fire disturbance and adaptation to climate change (Swanston *et al* 2018). We attempt to distinguish between recovery and persistence capacity through a new qualitative model which explains pitch pine responses to fire history and non-fire environmental constraints as a function of elevation and topography (Dunne *et al* 2004) (Figure 3). The model is informed by earlier resilience theories (Jordan Patterson and Windisch 2003; Howard and Stelacio 2011; Ibáñez *et al* 2019). Here, we hypothesize that pitch pine populations exhibit non-mutually exclusive responses: (1) **recovery capacity** (*RECC*) as a measure of plant performance (Ibáñez *et al* 2019) long after fire disturbance (Patterson Saunders and Horton 1983) and (2) **persistence capacity** (*PERC*) that reflects responses in the absence of disturbance (Brand and Jax 2007).

Each capacity metric reflects physical responses, such as the tradeoffs between growth and stress avoidance and colony retreat and expansion (Swanston *et al* 2018), as a function of stand density (Churchill *et al* 2012) and as an ‘ecologically stable strategy’ (Day and Greenwood 2011). *RECC* is the better understood of the two pathways given the extensive literature covering resilience (Ibáñez *et al* 2019) and tree health (Fuller and Quine 2016). *PERC,* on the other hand, explains a trend where shade-intolerant pitch pine out-compete other evergreens, such as red spruce (*Picea rubens*), hemlock (*Tsuga canadensis*) and balsam fir (*Abies balsamea*), thus expanding into new, mostly uninhabited territory. There is a scarcity of the biogeochemical, elevation, and topographical data at MDI needed to inform the functionalities within this model. To remedy this, we consider soil and plant nutrition including carbon (C), nitrogen (N), and stable isotope analysis to determine how intrinsic water use efficiency (iWUEδ13C), soil moisture retention, growth and stand density are affected by fire history and topography.

Fire history is revealed by subsurface charcoal remnants found in previous fire zones. Charcoal pyrogenic carbon (PyC) is abundant in selected areas of the north side of Cadillac Mountain (Patterson Edwards and Maguire 1987) and downslope pockets along the Park Loop Road at Gorham cliffs. These deposits suggest the possibility of recalcitrant soil C and high mineral holding capacity long after a fire event (Pingree and DeLuca 2017). Both fire history artifacts like charcoal (Licht *et al* 2017) and increasing elevation have been shown to increase water use efficiency (Wang *et al* 2017). Given the difference in fire histories between populations, this provides a nearly ideal testbed to better clarify aspects of chemical geography (Verma and Jayakumar 2012) and address a number of key questions with regard to leaf traits, tree growth, and stand dynamics.

Our foremost aim is to examine a proposed model through an analysis of four key pitch pine populations according to the interactive influence of fire and elevation. Given previous studies of fire involvement and post-fire photosynthetic response (Chen Wang and Jia 2017), we hypothesize that pitch pine growth and population expansion is greater at non-fire sites with low elevation due to higher soil C, higher foliar C (Butak 2014), more negative iWUEδ13C (Licht and Smith 2020), and greater soil water retention (positive indicators of *PERC*). We further theorize that trees at low elevations display a greater propensity for growth in height, canopy, and DBH through more competitive resource conservation (Stambaugh *et al* 2015). Additionally, we hypothesize that ubiquitous contours (Howard and Stelacio 2011) at upper ledge elevations, which limit clustering (stand density) elsewhere, will be less stressful for colonization (Lafon *et al* 2014) and expansion on lower elevation flat and cliff surfaces. We predict this will increase pioneering efforts at gentler slopes and more southerly aspect.

**METHODS**

**Study Extraction Sites**

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

**Allometry** We measure individual tree height (m), canopy spread (m), and stem diameter at breast height (DBH; cm). Tree height was estimated using nested, 2 m calibrated, aluminum rods (Garelick, St. Paul, MN, USA). DBH was measured at 1.06 m using a ProSkit electronic digital caliper (Amelia, VA, USA).

**Clustering** Mean distances were calculated between sampled trees (*N* = 167) and up to five of their nearest, reproductively mature, conspecific neighbors (within 5 m) in the same clump (Churchill et all 2012). Mean neighbor distance is a surrogate, but inverse, measure for stand density (Mosseler Rajora and Major 2004).

**Topographic Features**

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

**Isotopic Analysis**

We obtained C isotopic data (δ13C) and N isotopic data (δ15N) of fully expanded leaves (needle cluster) for 15 individual pitch pines at each site. Sample fascicles were separated and dried for two days at 60 ◦C, ground in a SPEX ball mill (Metuchen, NJ, USA), weighed to 2 mg for leaf tissue and 5 mg for soil using a micro analytic balance (Cole-Palmer, Vernon Hills, IL, USA), and rolled in 5 x 9 mm tin capsules (Costech, Valencia, CA, USA). Combustion gasses were separated on a gas chromatograph column, passed through a diluter and reference gas box, and introduced into the spectrometer (Thermo Delta V+ IR-MS, Waltham, MA, USA). 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 height. 50 mL samples of needles were separated, cut and dried for two days at 60 ◦C. Then they were ground in a SPEX ball mill (Metuchen, NJ, USA), sieved to <10 mm, and <2 mL were fed to a Leco C/N-2000 Carbon-Nitrogen Analyzer (Leco Corp., St. Joseph, MI) coupled with the spectrometer to determine C and N concentrations. 35 mL aliquots were submitted for standard plant tissue nutrient analysis using a TJA Model 975 AtomComp ICP-AES (Thermo Jarrell-Ash Corp., Franklin, MA). The method comprised submersion in a 5 mL trace-metal-grade HNO3 treatment, then refluxed on hot block at 80 ◦C for two hours and diluted to 25 mL with 0.4 micron PTFE syringe filters to access extractable macro and micro inorganics.

**Soil Analysis**

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

**Soil Water Retention (SWR)**

70 mL soil samples were extracted at 15 tree locations at each of 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, %), nitrogen (N, %), carbon/nitrogen (C/N, unitless), δ13C (‰), δ15N (‰), calcium (Ca2+, g g-1), phosphorus (P, g g-1), potassium (K+, g g-1), magnesium (Mg2+, g g-1), aluminum (Al+, g g-1), zinc (Zn, g g-1), soil: C (g g-1), N (g g-1), C/N (unitless), Ca2+ (g g-1), P (g g-1), K+ (g g-1), Mg2+ (g g-1), Al+ (g g-1), Zn (g g-1), water retention (%), pH (unitless), and CEC (cmolc kg-1). 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 2019). Significance tests for each fixed factor was performed using the ‘anova’ function in R (R Core Team 2019). Post-hoc Tukey’s tests were done to examine significant interactions between elevation and the presence of the 1947 fire using the ‘emmeans’ package in R (Lenth 2018).

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

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

**RESULTS**

**Aspect**

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

**Allometry and Stand Density**

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

**iWUEδ13C**

Trees at higher elevations experienced less negative δ13C (*P* < 0.01, Figure 6A and Table 4), reflecting greater water use efficiency, regardless of fire history. There were no significant differences between tree populations for δ15N (*P* > 0.05, Figure 6B and Table 4)

**Foliar Organics**

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

**Foliar Macronutrients**

Foliar Ca+2 was negatively impacted by increasing elevation (*P* < 0.001, Figure 8A and Table 6). Our linear model suggested that foliar P was significantly higher at fire-involved sites (*P* < 0.01, Table 6), although this was not confirmed by post-hoc Tukey’s tests (Figure 8B). Foliar K+ was reduced in the high elevation site that experienced fire as compared to the other sites (elevation x fire: *P* < 0.05, Figure 8C and Table 6). Neither foliar Al+ nor Mg2+ differed by site (*P* > 0.05 in both cases; Figure 8C and Table 6). Foliar Zn concentrations were 9% lower in the high elevation sites than on the low elevation sites (*P* < 0.01, Figure 8F and Table 6), due to a particularly strong reduction at the high elevation site that experienced fire.

**Soil Organics**

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

**Soil Macronutrients**

Soil Ca+2 decreased with elevation (*P* < 0.05, Figure 10A and Table 8). P, Mg2+ and Zn were not significantly different across sites (Table 8). However, fire accounted for a 48% reduction in K+ at sites with fire history (*P* < 0.01, Figure 10C and Table 8). There was an interaction between elevation and fire history for Al+ (*P* < 0.01, Figure 10E and Table 8), which indicated….

**Soil Water Retention, CEC, and pH**

There was an interaction between elevation and fire history on SWR (*P* < 0.01, Figure 11A and Table 9), with markedly higher values at Gorham cliffs, the low elevation site that experienced fire, as compared to other sites. Soil pH was not different between sites (*P* > 0.05, Table 9). Our linear model indicated that CEC was higher at the high elevation sites (*P* < 0.05, Table 9), but this was not confirmed by our post-hoc Tukey’s tests, which indicated no difference between sites (Figure 11C).

**DISCUSSION**

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

Elevation played a role in several meaningful ways. We confirmed that increased elevation tends to improve efficiency (increased iWUEδ13C over growth (Wang *et al* 2017; Chen, Wang and Jia 2017). Further, we found distance between neighbors at higher elevation was greater compared to lower elevation sites, thus generating sparser tree numbers aggregated within *RECC* compared to *PERC.* At the highest elevation, South Cadillac trail, we expected to find the steepest slopes, but they were far less steep than those at Gorham cliffs, a low elevation site. We anticipated that low elevation (<50 m) populations would feature a greater number of conspecific neighbors as a function of no fire history, flat or cliff orientation, evidenced by a gentle slope (<10°), and tendency towards a southerly aspect (*µ* = 180°). In fact, this theory was found correct, as Wonderland, which was by far the flattest terrain, trees achieved the widest distribution with the greatest distance between trees over the widest contiguous area as a function of *RECC.* There was sufficient variability in some of the data, like stand density, to produce valuable information about differences between flat, cliff and ledge communities, even if at a small spatial scale.

Fire history was less important than elevation in the response variables we measured, even at high elevation ledge communities. We found little compelling empirical evidence that fire is a necessary ingredient in perpetuation at MDI. Fire return intervals have lengthened at MDI to the point where they are quite likely to be too intermittent to perpetuate previous fire resistance traits. A shift back to fire, accompanied by a re-introduction of serotinous characteristics, is not impossible in the future; however, current climate projections advise against this occurrence. Despite the absence of fire, there is the presence of fire remnants. The current study builds on previous work (Licht and Smith 2020) to determine how an obvious post-fire effect—anthropogenic fire charcoal (PyC)— changes according to elevation and topography in association with greater (more negative) iWUEδ13C, negligible consumption of Ca2+, K+ and Mg2+,and increased soil moisture holding capacity. In this study we hypothesized that iWUEδ13C , stored plant C, and soil water retention would change significantly as a result of fire history. However, besides an increase in soil water retention with fire at the low elevation site, this hypothesis was not supported. Instead, we found lower iWUEδ13C at high elevations regardless of fire history, 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). We also found congruence between low elevation outcomes in the present study and those reported (*µ* = 33m above sea level) in the New Jersey pine barrens (Carlo *et al* 2016). However, we could not draw any other useful comparisons between the studies due to a lack of data concerning clustering (stand density), slope, or aspect factors. There is evidence from previous investigations that post-fire PyC remnants, which endure in the soil layer (DeBano 1981), increase alkali cations (Kolden *et al* 2017) and solubilized 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 *PERC*-oriented Wonderland trail (Butak 2014) does not appear to be slowing down expansion in that flat-sloped region nor in other cliff locations that we and others studied (Howard 2010).

Developing further insights into the ecological stoichiometry of pitch pine at MDI is a worthwhile goal given earlier discoveries by Fernandez (2008). Our nutrient analysis derived from burned and unburned trees was similar to a methodology in a New Jersey study (Renninger *et al* 2013) and produced some similar results. Since elevation is a key factor, we noted foliar Zn was higher at lower elevations at MDI; this was consistent with findings by others in another New Jersey investigation (Kolker *et al* 2013). In both Maine and New Jersey, it is possible *PERC* may be enhanced by higher concentrations of foliar Ca2+, K+, Mg2+, P, Al+ and Zn (Mg2+ foliar availability was not significant in this study). We were particularly interested in P, a limiting factor (Verma and Jayakumar 2012); it is sometimes found to co-occur with pools of greater C (Preston and Schmidt 2006). Scientists elsewhere assert that fire-induced sedimentary charcoal produces soil C enrichment (Patel *et al* 2016) as measured in soil columns (Hart Horn and Grissino-Mayer 2008). One could argue that charcoal remnants likely play a role in *RECC* 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. We conjecture that soil C persistence since the 1947 fire at burned-over areas such as South Cadillac trail reflects a lack of pyrogenic carbon removal (Doerr *et al* 2018), though elsewhere lower C availability is attributable to greater consumption by fungi (Luo *et al* 2017). P concentration at upper elevations at MDI contrasted with more modest availability at other, low-lying pinelands at MDI and in New Jersey (Renninger *et al* 2013; Alkañiz *et al* 2018). One explanation for substantial soil P availability is that it derives from charcoal remnants; however, lacking mycorrhizal studies we were unable to confirm the extent of P liberated from the charcoal in the two 1947 fire precincts.

Climate is likely the final arbiter of decline rather than stand-replacing fire disturbance in the case of long-term pitch pine livelihood. Recent climate change models anticipate negative impact on future vegetative status at MDI (Fernandez *et al* 2015), but these do not specifically address the adaptability of pitch pine nor the extent to which plasticity (Day *et al* 2014) is shaping tendency towards *PERC* or *RECC*. What has been clear for at least two decades is the effect of global climate change on ecophysiology traits. Day, Greenwood and White (2001) found that an uptick in annual temperatures signaled increased leaf-air vapor pressure deficits which negatively impacted pitch pine stomata response and limited gas exchange. In a related report, scientists found that warming trends (Kunkel *et al* 2013) increased pitch pine difficulties in reproduction (Ledig Smouse and Hom 2015). This includes 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* or ‘SPB’). Although deer and rodent damage (Ledig *et al* 2013) historically impeded tree survival in pine barrens, SPB has already paid a deadly visit to Long Island, NY (Dodds *et al* 2018). Unless its progress is deterred by other insect predators like Dubious Checkered Beetle (*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 the suitability of habitat and pitch pine tendencies to consolidate, regenerate or migrate may be in jeopardy. These effects are likely to eventually limit aspects of *PERC* such as niche expansion, if they have not already, through a combination of diminished open space capacity, loss of enriched substrates, and elimination of ‘safe sites.’

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

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 may be used to better understand how pitch pine in other ecosystems outside of the Northeast U.S. discriminate between *RECC* and *PERC* at a given elevation and within certain topographic parameters. The data presented here provides a fuller understanding of current regeneration and expansion concepts which are 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 adaptivity effects (growth, expansion into greater stand density) account for greater growth and stand density on more hospitable terrain, with little impact from fire history. This is likely due to the fact that fire return intervals are so infrequent as to reduce recovery features found elsewhere (e.g., cone serotiny). 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 an 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 *PERC* 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 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).

## Author Contributions

JL and NS conceived the work, 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, conducting statistical analyses and formulating figures and tables.

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