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Pitch Pine Make A Stand On Mt. Desert Island: An Explanatory Model of Resilience and Cushioning Strategies

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Key words

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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, however, there has been no recurrence. Other populations on the island have been unaffected by fire disturbance for over one hundred years. While it has been shown that fire history can have a strong influence on plant form and functioning, this has not been well quantified for pitch pine there, particularly in relation to other factors such as elevation and topography that are known to impact traits of this species. Here, we quantified the impact of fire history, elevation and their interaction on growth and functional traits of pitch pine individuals across a topographic gradient (9.5 to 404 m). Specifically, we measured allometric growth metrics, photosynthetic water use efficiency, soil and foliar nutrients, soil water retention and stand density. Unsurprisingly, we found 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 over growth driven by greater atmospheric pressure. Trees at modest elevation were also found to exhibit greater soil moisture retention than those in high elevation, fire-exposed situations. Compared to environmental constraints, fire history was not as an important driver of population establishment and stand density. In fact fire return intervals are so infrequent as to reduce resilience capacity features and increase cushioning capacity effects in longer fire absent locales in anticipation of other disturbances. These findings provide key data to inform management efforts to reinforce pitch pine survival especially where cushioning capacity is greatest.

**INTRODUCTION**

On Mt. Desert Island in Maine in the Northeast USA, globally threatened pitch pine (*Pinus rigida* Miller; Fig. 1) dwell at the edge of their range. In coastal Atlantic states further south, pitch pine is impacted by natural fire, or in its absence, by anthropogenic controlled burns (Foereid *et al* 2015; Carlo *et al* 2016) wherein the results (Lee *et al* 2019) reflect reduced fuel, removal of evergreen competition and opened canopies (Neill *et al* 2007). Fire ecologists in Northeast USA (Jordan *et al* 2003) suggest wildfire is required every six to twenty-five years to perpetuate and rejuvenate pitch pine. Yet, on the Maine island, hereafter MDI, species survival continues unabated despite fire suppression since the infamous 1947 conflagration and outside of the fire zone (Miller *et al* 2017), faring better than experts predicted in the past (Patterson Saunders and Horton 1983; Parshall *et al* 2003).

**Fig. 1 Fig. 2**

******Fig. 1 Contorted but striking *Pinus rigida* specimen hiked out on an outcrop across from Gorham Mountain cliffs on the Park Loop Road at Mt. Desert Island.

**Fig. 3**

Fig. 2. Pitch pine populations on Mount Desert island examined in the context of fire presence (1947) or absence, as much as one hundred twenty-five years or more on the west side of the island. Estimates of the extent of fire exposure shown in the right pane are recent (Miller et al 2014; Livingston, personal communication 2019).

Fig. 3. Contour features shown at four sites reveal differences between nearly subalpine (St. Sauveur and South Cadillac trails) and coastal plain (Wonderland and Gorham cliffs) sites, each with *N*=15 trees (blue dots).

Trees in low-lying undisturbed (non-fire) neighborhoods appear to engage in seedling recruitment superior to trees in the upper portion of the former 1947 fire zone (Fig. 2); yet there is a lack of data until now to support this theory. With stand density in mind our aim is to compare the proclivities of pitch pine resilience long after a fire event with cushioning effects elsewhere in response to anticipation of wind and other non-fire disturbance. During a sustained period of fire absence, physiological and morphological adaptations arise over many years (Little 1953). These include elimination of cone serotiny (Givnish 1981), thick bark and basal re-sprouting (Renninger *et al* 2013) in formerly fire-prone pitch pine ecosystems. A change in fire regimes (Jordan *et al* 2003) and suppression make it likely that any ongoing fire adaptive mechanisms (no longer required for stand sustenance) are wasted investments that could encourage under-competition with other evergreens (Buma *et al* 2013). 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. Nevertheless, in the case of former pyrogenic forests, it is not clear if recovery or cushioning caused adaptive traits to disappear or if these are a result of intrinsic, as opposed to extrinsic, post-fire re-generation.

Differences in elevation gradients and topography (Fig. 3) are crucial environmental constraints

(Dunne *et al* 2004) which we speculate are as, or more, important to either resilience or cushioning capacity than fire history encompassing flat, cliff and ledge orientations. We fit an empirical model for explanatory purposes to pitch pine niche capacity according to fire history and non-fire environmental constraints informed by previous models by Jordan Patterson and Windisch (2003) and Howard and Stelacio (2011). To describe and characterize pitch pine niche capacity, our maritime population prototype comprises either tree resilience capacity (*Rcapacity*) as a measure of plant performance (Ibáñez *et al* 2019) long after fire disturbance (Patterson Saunders and Horton 1983) or cushioning capacity (*Ccapacity*) to reduce the shock of disturbance absence (Brand and Jax 2007). Each mode exhibits properties inclusive of opportunistic individuals, population consolidation, or expanded colonization. The arc of pitch pine niche survival bends or expands according to a number of influences including growth or stress inoculation, colony retreat or expansion (Swanston *et al* 2018). *Rcapacity* 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). *Ccapacity*, on the other hand, manifests especially where shade-intolerant pitch pine out-compete other evergreens such as red spruce (*Picea rubens*), hemlock (*Tsuga canadensis*) and balsam fir (*Abies balsamea*). In this investigation we study competition as a means of protective stand density in bare, moisture-scarce soils, on flat, ledge or cliff surfaces. Where ledge features dominate, even at an upper elevation, we observe a contoured barren ecosystem (Howard and Stelacio 2011) dominated by pitch pine which utilize gaps in multi-evergreen colonies (Lafon *et al* 2014) such as those at MDI.

To date there is a paucity of data at MDI to inform our model. To remedy this, we consider the following measurable traits, set against fire history, elevation and topography: soil and plant nutrition including C and N, stable isotope analysis to produce a measure of intrinsic water use efficiency, soil moisture retention, multiple aspects of growth and stand density. Several previous studies lend support to this approach. For example, Wang *et al* (2017) found that increasing elevation increased negative iWUEδ13C (Lambers Chapin and Pons 2006). Charcoal is considered to be recalcitrant, even long after a fire event (Pingree and DeLuca 2017). In the form of soil pyrogenic carbon (PyC) it is quite likely to enhance *Rcapacity*. One example is PyC which festoons Cadillac Mountain (Patterson Edwards and Maguire 1987) and downslope pockets along the Park Loop Road at MDI. Below an otherwise infertile, glaciated bedrock (e.g., Ellsworth schist), charcoal remnants result in elevated soil C and mineral capacity. At higher elevations (between 190 and 404 m) where charcoal is found, sorption properties are similar to those revealed in an earlier investigation of hydrophobic repulsion transformed to uptake in soils embued with lignocellulosic charcoal (Licht and Smith 2018).

In a later controlled study of PyC effect, Licht and Smith (2020) demonstrated the potency of forest and anthropogenic fire charcoal blended with an Entisol, was associated with negative iWUEδ13C, negligible consumption of Ca, K and Mg(Kahl *et al* 2007) and enhanced soil moisture holding capacity. At lower elevations, we theorize PyC, undiminished by oxidation, acts as a magnet for moisture retention to enable larger clusters and denser tree colonies at Gorham cliffs even in thin, infertile soils. Particularly, PyC in a glaciated ‘O’ soil layer (DeBano 1981) similar to one at MDI, increased alkali cations (Kolden *et al* 2017) and solubilized minerals (Caldwell and Richards 1989) often resulting from thermal exfoliation (Shakesby and Doerr 2006). At non-fire Wonderland trail, devoid of as much PyC as one would find at South Cadillac trail, large clusters contributing to stand density signal cushioning to future disturbance. There, where ledge ecology exists and charcoal does not, we suspect stand density isserved by resource conservation traits (Stambaugh *et al* 2015) such as high stored plant C concentration (Butak 2014), greater tree longevity (Reich 2014), and high photosynthetic intrinsic water use efficiency (iWUEδ13C). Notwithstanding, we speculate previous fire involvement (Chen Wang and Jia 2017) does not create an overall impact compared to growth pulses at low elevation, low fire regions consistent with buffering inherent in *Ccapacity*.

We hypothesize trees assigned to *Rcapacity* or*Ccapacity* conditions will experience significant effects resulting from responses to fire or non-fire environmental constraints limited by elevation and topographical differences. In particular we theorize soil C, foliar C and iWUE would be more significant at ledge elevations related to *Rcapacity* and soil and foliar macronutrient, soil water retention, growth and density significantly higher at low elevations according to *Ccapacity*. In addition, we infer trees tend to more klinokinetic response due to an increase in one or the other of these capacities; in the case of extended fire absence, we anticipate a weak directional response as regards an increase in *Rcapacity*. Fortuitously, at MDI, there exists a nearly ideal testbed to accumulate data to better clarify aspects of chemical geography (Star *et al* 2015) in precincts defined by fire history or the lack thereof.

**METHODS**

**Study Extraction Sites**

Pitch pine at four sites at MDI, factorially crossed in a fire history (Miller *et al* 2014) by elevation design, were investigated: (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). Fifteen trees at each site were sampled.

**Laboratory measurementsCarbon and Nitrogen Stable Isotopes**C isotopic data (δ13C) and N isotopic data (δ15N) of fully expanded leaf (needle cluster) of each species and accompanying soil samples was obtained. 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. C abundance or depletion according to δ13C was used to indicate water use efficiency (iWUEδ13C) (Farquhar et al. 1989).

**Foliar Elemental Analysis**Leaf tissue was obtained from excision of basal fascicle bundles at 1.06 m; we acknowledge that leaf nutrients differ according to light environments impacted by the size (height and canopy) of tree subjects (Niinemets Keenan and Hallik 2015). 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 Perkins Elmer Elemental Analyzer ECS 4100 (Waltham, MA, USA) coupled with a Thermo Delta (Waltham, MA, USA) V+ IR-MS continuous flow isotope ratio mass spectrometer with a universal triple collector. Combustion gasses were separated on a gas chromatograph column, passed through a diluter and reference gas box, and introduced into the spectrometer. submitted for elemental analysis using Leco CN-2000 Carbon-Nitrogen Analyzer (Leco Corp., St. Joseph, MI) to determine C and N concentrations.   
**Foliar Inorganic Nutrients**The remainder of the same samples composed of 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 hotblock at 80 ◦C for two hours and diluted to 25 mL with 0.4 micron PTFE syringe filters to access macro and micro inorganic extractable fractions (Ca, P, K, Mg, Al and Zn). **Soil Nutrients**Soils comprised uniformly similar shallow, homogeneous, low fertility characteristics (varying between .7-2.5 cm) and are usually overlain with rapidly drying needle duff (Day *et al* 2005) overlaying porous and acidic hornblende granite or Ellsworth schist. 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 previously (Lichtand Smith 2018). Bedrock C and N were calculated using elemental analysis.

**Soil Water Retention (SWR)**

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

**Field Measurements**

**Allometry**Individuals were further characterized according to tree height, canopy spread and stem diameter of the bole at breast height (DBH). 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). Canopy spread was measured using the span between the same calibrated aluminum rods fixed with two landscape flags as a ground truth reference.

**Stand density**  
Distances between sampled trees (*N*=167) and up to five of their nearest, reproductively mature conspecific neighbors (within 5 m) were measured to calculate mean neighbor distance as a surrogate, but inverse, measure for stand density (Mosseler Rajora and Major 2004).

**Topographic features**

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| Stand | X | Y | Type | Elevation | Slope | Aspect | Compass |
| CAD | -68.221 | 44.328 | Ledge | 239.3 | 239.3 | 127.1 | SE |
| GCLIFFS | -68.185 | 44.327 | Cliff | 33 | 33 | 142 | SE |
| STSAUV | -68.326 | 44.310 | Ledge | 172 | 172 | 252 | W |
| WOND | -68.314 | 44.231 | Flat | 16 | 16 | 188 | S |

Tab. 1. An assortment of topographic features combined with GIS coordinates stated as mean values for tree population (*N*=60).

**Remote sensing to locate colonies**  
A Kodak Trimble Juno 3B unit was used to obtain horizontal resolution of combined elevation, slope and aspect data plotted using between five and seven satellite telecommunication vehicles to maintain a maximum PDOP (Position Dilution of Precision). These data were differentially corrected and have estimated accuracies in the horizontal and vertical direction of 2 meters, while SA (selective availability) is set to zero. Data points are used to establish not only elevation but to compute fire event sink-source metrics. For analysis purposes we constructed two categories, assigning soil and tree aliquots to either a proximate fire-path or no fire-path exposure. Mapping was achieved through geospatial, remote sensing technology (Tierney *et al* 2012) used in the past to compare physiography and recalcitrant chemical biogeography, particularly in fire prone contexts (Szpakowski and Jensen 2019). Individual trees were randomly selected but a distance-between-subjects was observed, requiring 5m as a setback between specimens. Multiple satellite-configured GPS data (USGS 2m LIDAR 2010) determined coordinates for individual trees (Lubinski Hop and Gawler 2003; Kim 2010). ArcGIS (version 10) as well as slope, aspect and rose compass direction attributes. The aggregated data were reduced to mean values for each measurement category.

**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, twenty four models were fit with the following dependent variables: tree height (m), canopy spread (m), DBH (cm), foliar C (%), foliar N (%), foliar C/N (unitless), foliar δ13C (‰), foliar δ15N (‰), foliar Ca (g g-1), foliar P (g g-1), foliar K (g g-1), foliar Mg (g g-1), foliar Al (g g-1), foliar Zn (g g-1), soil C (g g-1), soil N (g g-1), soil C/N (unitless), soil Ca (g g-1), soil P (g g-1), soil K (g g-1), soil Mg (g g-1), soil Al (g g-1), soil Zn (g g-1), and soil water retention (%). Tree height, canopy spread, DBH, foliar P, foliar K, foliar Zn, soil P, soil Al, soil Zn, and soil CN 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 models were fit using the ‘lm’ function in R. Significance tests for each fixed factor was performed using the ‘anova’ function in R. Post-hoc Tukey’s tests were done to examine significant interactions between elevation and the presence of the 1947 fire using the ‘emmeans’ package (Lenth 2018) in R. All analyses were performed with R version 3.5.1 (R Core Team 2019).

**RESULTS**

Fire, elevation and interaction between fire and elevation outcomes were significantly linked to tree population adaptivity due mostly to *Ccapacity* rather than *Rcapacity*. Statistically significant results are reported in Tab. 2.

|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  | Height | Canopy | DBH | Stand Den | iWUEδ13C | SWR | Soil C | Soil C/N | Soil Ca | Soil K | Soil Al | Soil Zn | Foliar K | Foliar P |
| Fire |  |  |  |  |  |  | *\** |  |  | *\*\** |  |  |  | *\** |
| Elevation |  | *\** |  | *\*\** | *\*\** | \*\*\* | \* | \* | \*\*\* |  | *\** | \* |  |  |
| Fire x Elevation | *\** |  | *\** |  |  |  |  |  |  |  |  |  | *\** |  |
| Residuals *(N*=59) |  |  |  |  |  |  |  |  |  |  |  |  |  |  |

Tab. 2. Displayed are statistically significant results for: tree height, canopy, stand density, DBH, iWUEδ13C, SWR (soil water retention), Soil C, Soil C/N, Soil Ca, Soil K, Soil Al, Soil Zn, Foliar K and Foliar P. Linear effects models \*\*\**P* < 0.001, \*\**P* < 0.01 and

\**P* < 0.05.

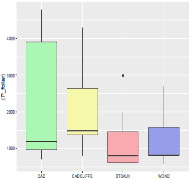
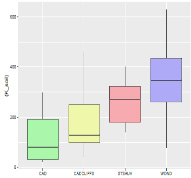
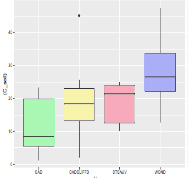


Fig. 4 Fig. 5 Fig. 6

Fig. 4, 5 and 6 are respectively dot and box plots of soil C, soil K and foliar P in relation to inclusion in 1947 fire path. Significant statistical results are reported in **Tab. 2**.

*Fire*

Contrary to our hypothesis soil C recalcitrance at one of two sites which experienced fire in 1947 (Fig. 4) was significantly lower (*P* < 0.05) than at other locations. While we found foliar C was more readily

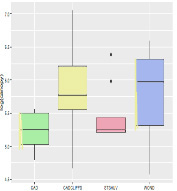
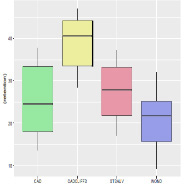
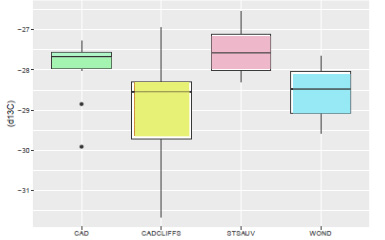


Fig. 7 Fig. 8 Fig. 9

Fig. 7, 8 and 9 are respectively dot and box plots of iWUEδ13C, soil water retention and tree canopy associated with fire exposure. Significant statistical results are reported in **Tab. 2**.

available at upper elevations, the results were not statistically significant. The only significant influence

of fire on soil minerals (*P* < 0.01) was a 48% reduction in Kat fire-experienced sites (Fig. 5). Foliar P was significantly higher (*P* < 0.05) at fire-involved sites (Fig. 6).

*Elevation*

As we hypothesized, elevation played a decisive role compared to fire or fire-elevation interactions. For example, trees at higher elevations did in fact experience more negative iWUEδ13C (Fig. 7, *P* < 0.01) but this was not fire-dependent. Also as predicted, soil water retention (Fig. 8,*P* < 0.001) was greatest at a low elevation site which experienced fire. Tree canopy growth (*P* < 0.05) was 8% lower at high elevation sites (Fig. 9).

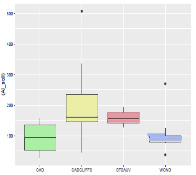
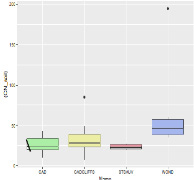
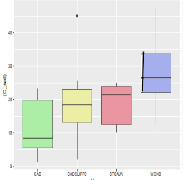


Fig. 10 Fig. 11 Fig. 12

Fig. 10, 11 and 12 comprise dot and box plots of soil C, soil C/N and soil Al+ availability based on elevation differences Significant statistical results are reported in **Tab. 2**.

Soil C was 37% lower (*P* < 0.05) at lower elevation sites (Fig. 10). Soil C/N (*P* < 0.05) was 15% lower at high elevation sites (Fig. 11) although there was no significant disparity in C/N when either fire history or fire history and elevation interactions were taken into account. Soil Al was significantly higher (*P* < 0.05) at lower elevations which did not experience fire (Fig. 12) as was soil Zn (Fig. 13).

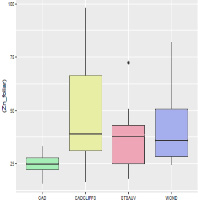
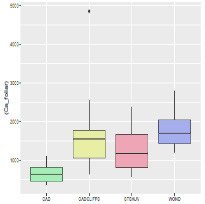
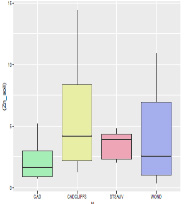
 Fig. 13 Fig. 14 Fig. 15

Fig. 13, 14 and 15 include dot and box plots of soil Zn, foliar Caand foliar Zn based on elevation differences. Significant statistical results are reported in **Tab. 2**.

Foliar mineral availability was impacted negatively as elevation increased as witnessed by a 48% decline in Ca+2 (*P* < 0.001) shown in Fig. 14 and 9% decrease (*P* < 0.01) in Zn (Fig. 15).

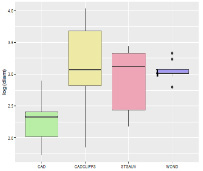
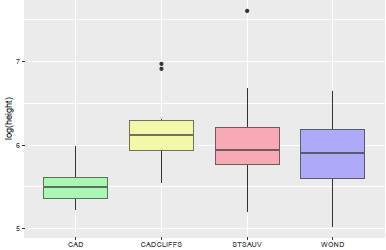
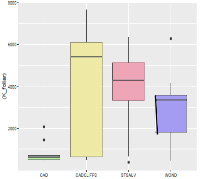
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Fig. 16 Fig. 17 Fig. 18

Fig. 16, 17 and 18 comprise dot and box plots of interactive effects of fire and elevation on tree height, DBH and tree foliar K+. Significant statistical results are reported in **Tab. 2**.

*Fire and Elevation interaction*

Notably, fire and elevation interactions affected several outcomes. An interaction between fire history and elevation was significant (*P* < 0.05) for tree height (Fig. 16) and for DBH (*P* < 0.001) shown in Fig. 17. Within trees that experienced the 1947 fire, the low elevation trees were taller (m) than the high elevation trees (Tukey’s HSD: *P* < 0.05). Trees that had experienced the 1947 fire at high elevation had smaller DBH (cm) values than trees at any of the other sites (Tukey’s HSD: *P* < 0.05). A significant interaction between fire history and elevation (*P* < 0.05) resulted in soil water retention (Fig. 11) achieving its apex at the low elevation site that experienced fire (Gorham cliffs) as compared to all other sites (Tukey’s HSD: *P* <0.05 in all cases). We found there was no interaction between fire history and elevation when it came to available soil C. However, there was a significant interaction between fire history and elevation on soil Al+ (*P* < 0.05, Fig. 12) which indicated that soil Al+ was higher at low elevation sites that did not experience fire (Tukey’s HSD: *P* < 0.05). An interaction between fire history and elevation (*P* < 0.05), yielded data which pointed to a reduction (Fig. 18) for tree foliar K+ (Tukey’s HSD: *P* < 0.001) as well.

**DISCUSSION**

Our study revealed response variable data which we interpreted to explain pitch pine *Rcapacity* and *Ccapacity* through a model which accounts for the influence of scaled fire and non-fire environmental constraints (e.g., elevation and topographical differences) on trees within a maritime cluster. We found elevation was a far stronger determinant of *Ccapacity* than fire history or an interaction between the two was for *Rcapacity*. In addition, our results suggest long fire return intervals since the 1947 fire and even longer in other non-fire communities, are insufficient to continue previous fire resistance traits. In this way pitch pine have adapted by adopting non-fire constraints to increase stand density where non-fire environmental constraints appear to be most robust. Previous research catalogued some of this change at Wonderland trail (Butak 2014); research elsewhere supports the premise that however important fire was previously to high elevation pitch pine communities, such as cliffs and ledges, growing fire absence (Howard 2010) does not appear to be slowing down reproduction and expansion, as previously thought. In regard to fire effects at low elevation,

a study at a low (*m*=33m above sea level) elevation (Carlo *et al* 2016) affirmed fire absence did not dictate a significant difference in physiological functioning compared to post-fire outcomes but no distinction was drawn between trees as to stand density or topographical factors considered here.

Our central findings include a result that foliar nutrient and growth limitations varied together at higher elevation gradients at cliff communities (as described by Wang *et al* 2017; Chen, Wang and Jia 2017). N, P and K foliar nutrients were higher in burned as opposed to unburned trees, similar to findings in a study in New Jersey (Renninger *et al* 2013). Second, greater stand density at flat and cliff sites was associated with more positive iWUEδ13C and photosynthetic growth, 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). Nevertheless, competitive advantages enjoyed currently may even give way to ‘mesophication’—negative feedback for shade intolerant trees like pitch pine (Nowacki and Abrams 2008). Third, pitch pine stand density was significantly greater at flat and lower cliff barrens despite warmer winter temperatures and heightened moisture. 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. Thus, these effects are likely to eventually limit niche expansion, if they have not already, according to these authors, through a combination of diminished open space capacity, loss of enriched substrates and elimination of ‘safe sites’.

Besides the main three factors assessed above, we sought to determine the effect of other biological phenomena. We theorized a significant relation existed between distances of sampled trees and their five nearest, reproductively mature conspecific neighbors (*N*=167) based on differences between environmental constraints such as topography and elevation set against the presence or absence of fire history. Intra-distance measures between the sample trees in the four stands and up to five of their nearest cohorts were used to construct a mean neighbor distance as a surrogate, but inverse, measure of stand density (Mosseler Rajora and Major 2004). Elevation, of the three variables, was the only statistically significant metric (*P* < 0.01, Table 2). Essentially, there existed 34.7% greater neighbor distance between trees at higher compared to lower elevation sites, representing greater *Ccapacity* than sparser tree numbers associated with *Rcapacity.*

An analysis of variance between elevation, compass regimentation, slope and aspect could not be performed due to an absence of replication of within-site opportunities. However, mean and standard deviation calculations revealed a low elevation, gentler slope and S-SE compass orientation favored Gorham cliffs pitch pine verticality (*µ*=6.2 m) and DBH (*µ*=40.1 cm) with Wonderland trees achieving the widest canopy *(µ*=4.2 m). High elevation and the steepest slope caused South Cadillac trail trees to deport a combination of the smallest height, canopy and DBH.

Recent climate change models anticipate negative impact on future vegetative status at MDI (Fernandez *et al* 2015) but the model does not specifically address the vicissitudes of pitch pine. There is nothing startling about this revelation since nearly two decades ago Day Greenwood and White (2001) found an uptick in annual temperatures signaled increased leaf-air vapor pressure deficits, which negatively impact pitch pine stomata response and limit gas exchange. In a related report, scientists see warming trends (Kunkel *et al* 2013) increase pitch pine difficulties in reproduction (Ledig Smouse and Hom 2015). In short, climate is most probably the final arbiter of decline rather than stand-replacing fire disturbance (Day *et al* 2005) in the case of long-term pitch pine livelihood. This includes weather-related effects such as episodic drought, harsh winds and salt spray (Schmitt 2015; Fernandez *et al* 2015) and cold intolerance (Berang and Steiner 1985).

Photosynthesized C dedicated to growth rather than to stress resistance in flat, Wonderland trail and semi-flat Gorham cliffs is consistent with a previous report (Butak 2014). Extrapolating from leaf level growth measurements, we theorized *Ccapacity* may be greater in these populations where growth (rather than stress resistance) is dominant. While foliar Zn was substantial at lower elevations strength grew fainter away from the coastline, up towards mountain summits, consistent with findings by others (Kolker *et al* 2013). However, in both Maine and New Jersey, *Rcapacity* may be illuminated by higher concentrations of foliar Ca, K, Mg, P, Al and Zn. Limiting factor P provided clues as to niche capacity and chemical geography as discussed elsewhere (Verma and Jayakumar 2012); P concentration at upper elevations at MDI contrasted with more modest availability at other, low-lying pinelands in New Jersey (Renninger *et al* 2013; Alkañiz *et al* 2018).

Scientists elsewhere assert fire-induced sedimentary charcoal produces soil C and N enrichment (Patel *et al* 2016) as measured in soil columns (Hart Horn and Grissino-Mayer 2008). One could argue that although charcoal remnants likely play role in *Rcapacity* at burned-over communities at Cadillac Brook (well below the heights of South Cadillac trail) compared to nearby, lower, unburned Hadlock Brook, it does not appear to be a necessary benefactor to forest well-being. Charcoal was found at burned sites near Cadillac mountain (Patterson Edwards and Maguire 1987; Laing 1993). We conjecture soil C persistence since the 1947 perturbance at burned-over areas such as South Cadillac trail reflects a failure of pyrogenic carbon removal (Doerr *et al* 2018), though elsewhere lower C availability is attributable to greater consumption by fungi (Luo *et al* 2017).

Allowing for differences between disjunct communities, other authors (Copenheaver White and Patterson 2000) found soil C and K+ alkali extractions were significantly higher in the nearby Waterboro Barren cohort. There existed a decidedly greater disparity in available P, between the two sites along with .39 % N, 50% higher than mean N at Cadillac South trail. Not surprisingly we were anxious to clarify why P sorption was so prominent in fire zone soils at South Cadillac trail, for example, in light of diminished growth there. One explanation for substantial P availability derives from an effect generated by charcoal remnants; however, lacking mycorrhizal studies we were unable to confirm the extent of P liberated from the charcoal working in tandem with ectomycorrhizal symbionts in 1947 fire precincts. Further, we note Mg+ and trace metal Zn (responsible for growth, enzyme and carbohydrate formation) micronutrient pulses at MDI thought to be associated with bedrock weathering occurred at a rate similar to earlier reports (Butak 2014).

In New Jersey Pine Barrens investigators report N is taken up by ectomycorrhizal pitch pine roots (Luo *et al* 2017) but there is some debate as to whether N in the form of NO3- is taken up by pitch pines at a meaningful level (Certini 2005). We lacked access to quantify those indicators at MDI, but suggest mineralization rates constitute a proxy for root N uptake, as others have asserted in δ15N measurement in pitch pine ecosystems (Inglett *et al* 2007). We were unable to account for comparatively greater soil 15N at unburned sites (St. Sauveur, Wonderland) similar to those on Norumbega Mountain, portions of North Cadillac Mountain trail and lower South Cadillac trail (separate unreported data).

Day (personal communication) proposes marine (occult) deposition on foliage and fall-through to bedrock modify *Rcapacity*. These appear to derive mainly from southeast and southerly mist and fog (Weathers *et al* 1986; Jagels *et al* 2002) during the summer and fall months. It is reasonable to theorize nutrient aerosols trapped in foliage, or accumulating after fall-through onto weathered bedrock below affect low altitude maritime pitch pine ecosystems such as Wonderland (Butak 2014) proximate to marine sources. Aside from the obvious presence of NaCl, we consider nitrate (NO3-) deposition from atmospheric sources (Weathers *et al* 2006)—nitrate is measured by a spectrophotometer limit (acceptable at +/1 mg/L), in excessive quantities, above 10mg/L, at which point it is deemed toxic. Experiments are conducted in a pine barren to pinpoint contamination effects with titrated nitrate injections into ectomycorrhizae. However, these failed to boost aluminum toxicity (Schier and McQuattie 2008). At MDI, it would be useful to determine the extent of NO3- presence as a function of microbial composition (Evans et al 2018) and quantify inhibition of pitch pine productivity.

Increases in annual winter temperatures (Lesk *et al* 2017) coupled with an absence of fire (though not occult deposition) cause concern about a quite different disturbance—potential invasion within the next decade of a bark beetle, Southern pine beetle (*Dendroctonus frontalis* Zimmer). This pest (SPB) is already making its presence known in southern Massachusetts, Rhode Island and Connecticut to the south (Dodds *et al* 2018). Unless its progress is deterred by other insect predators like double checkered clerid (*Thanasimus dubius*) (Coulson and Klepzig 2011), it is possible pitch pines along with understory plants, butterflies and moth members of the Acadia ecosystem will suffer the same fate as others experience in more southerly locations (Lesk *et al* 2017). Trapping efforts at MDI, by the authors, in 2020, revealed no SPB presence.

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, 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. There was sufficient variability in some of the data, like stand density, to produce valued information about differences between flat, cliff and ledge communities, even if at a small spatial scale.

The model we proposed is not a machine learning framework and is not designed as a predictive model, *per se*, yet results which attach to this model are useful to understand how pitch pine in other ecosystems, even those removed from the Northeast U.S., discriminate between *Rcapacity* and *Ccapacity* at both low and upper elevations. Further while investigators did not determine the precise impact of *Ccapacity* on seedling recruitment (Patterson *et al* 2014), it is safe to say that the present data offers an informed view of current trends towards regeneration and expansion—a view which is essential to appreciate where pitch pine conservation occurs in the absence of forest or prescribed fire.

**CONCLUSION**

We developed an explanatory model of pitch pine niche performance which comprised resilience and cushioning capacity. We determined fire return intervals are so infrequent as to reduce resilience features (e.g., former cone serotiny) and found evidence cushioning effects (growth, expansion into greater stand density) account for greater growth and stand density in longer fire absent locales in anticipation of other disturbances. The authors also identified a selective preference for either growth to expand or stress tolerance to conserve, water use efficiency, use of soil and foliar C and macronutrients and soil moisture retention. In general, pitch pine populations in flat and ledge communities exhibited greater buoyancy than trees in difficult cliff situations. Our findings unravel a survival enigma revealing resource conservation traits which take place during a critical phase of the Anthropocene age, in a post-fire milieu. At a time when continued climate change may tip the scale away from survival, our current findings encourage the use of available data to, at the very least, encourage management of pitch pine in niches where existing cushioning effects are likely to dominate.

## Data Availability Statement

All data used in this article can be found at the following repository: <https://github.com/SmithEcophysLab/pitchpine/releases/tag/v1.0> (doi: [10.5281/zenodo.3600547](https://doi.org/10.5281/zenodo.3600547)).

## 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 in ensuring that questions related to the accuracy or integrity of any part of the work are appropriately investigated and resolved. JL carried out field collection, and conducted preparation for sample analysis at the EA-IRMS laboratory at Boston University under the direction of Robert Michener. At Texas Tech University, NS was responsible for performing C/N foliar evaluation, conducting statistical analyses and formulating figures and tables.

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