

1 **Title Page**

2
3 Pitch Pine Stands Recover, Adapt And Persist In The Absence Of Fire Under The Influence Of Elevation
4 And Topographic Factors

5
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11
12 Key words
13 *Pinus rigida*, Pitch pine, Mount Desert Island, fire, elevation, resilience, adaptivity, chemical geography

14 **ABSTRACT**

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

32
33
34 **INTRODUCTION**

35 On Mt. Desert Island in Maine USA, globally threatened pitch pine (*Pinus rigida* Miller) dwell at the edge
36 of their northeastern range. Some fire ecologists in Northeast USA suggest ~~that~~ wildfire is required every
37 six to twenty-five years to perpetuate and rejuvenate pitch pine (Jordan *et al* 2003). ~~In New England,~~
38 ~~scientists stipulate that disturbance, especially fire, is critical to pitch pine management (Dodds et al 2018).~~
39 Yet, on Mt. Desert Island, pitch pine survive despite fire suppression (Miller *et al* 2017), which has persisted
40 in the aftermath of the infamous 1947 conflagration (Fig. 1). ~~Recovery from fire and persistence in the~~
41 ~~absence of fire are key to understanding population self-management; however, it~~ is not entirely clear what
42 factors contribute to ~~pitch pine responses to~~ the absence of fire (Patterson Saunders and Horton 1983;
43 Parshall *et al* 2003). In coastal Atlantic states further south, ~~recovery and persistence are further complicated~~
44 by a combination of natural fire (Foereid *et al* 2015) and anthropogenic controlled burns (Carlo *et al* 2016),
45 which comprise a system where there is reduced fuel, removal of evergreen competition, and opening of
46 canopies (Neill *et al* 2007).

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At Mt. Desert Island, trees in low-lying, undisturbed (non-1947 fire) areas (Fig. 2) appear engaged in seedling recruitment superior to 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 former fire adaptive mechanisms like these (no longer required for stand sustenance) are wasted investments which likely encourage under-competition with other evergreens (Buma *et al* 2013). Critically, it is not clear if, in reaction to the former pyrogenic forest effect, 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 through the lens of topography (Dunne *et al* 2004) (Fig. 3). The model is informed by earlier resilience theories (Jordan Patterson and Windisch 2003; Howard and Stelacio 2011; Ibáñez *et al* 2019). Here, we posit that pitch pine populations exhibit non-mutually exclusive responses to environmental drivers: (1) recovery capacity as a measure of plant performance (Ibáñez *et al* 2019) after fire disturbance (Patterson Saunders and Horton 1983) and (2) persistence capacity that reflects responses to temporally consistent environmental gradients (e.g., topography) in the absence of disturbance (Brand and Jax 2007).

Each capacity metric reflects an ecologically stable strategy (e.g., tradeoffs between growth and stress avoidance; Day and Greenwood 2011) including colony retreat and expansion (Swanston *et al* 2018), as a function of stand density (Churchill *et al* 2012). Recovery capacity, linked to fire history, 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). Persistence capacity, on the other hand, is not well described to this point, and we stipulate that it is linked to topography on Mt. Desert Island. For example, on Mt. Desert Island, shade-intolerant pitch pine out-compete other evergreens such as red spruce (*Picea rubens*), hemlock (*Tsuga canadensis*) and balsam fir (*Abies balsamea*) when expanding into harsh, previously uninhabited high elevation locations. There is currently a scarcity of biogeochemical and topographical data at Mt. Desert Island to inform this model.

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 at Mt. Desert Island (Patterson Edwards and Maguire 1987). These deposits suggest the possibility of recalcitrant soil C and high mineral holding capacity long after a fire event (Pingree and DeLuca 2017). These fire history artifacts are known to influence plant functioning (e.g., Licht *et al* 2017). However, similar traits may also be driven by mountain topography (e.g., Wang *et al* 2017). Given the difference in fire histories between Mt. Desert Island populations that lie along a topographic gradient, Mt. Desert Island provides a testbed to disentangle fire history and topographic effects on site chemical geography status (Verma and Jayakumar 2012) that influence key plant functional traits that drive growth and stand dynamics.

Here, our aim was to examine the proposed model through an analysis of four key pitch pine populations that lie along a factorial fire history by elevation gradient. We hypothesized greater pitch pine growth and population expansion at low elevation sites as compared to high elevation sites, as a result of greater soil

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moisture retention and soil C (Butak 2014) that confer high growth functional traits such as more negative water use efficiencies. This expected increase in growth was hypothesized also to be the result of greater competition for resources at low versus high elevation (Stambaugh *et al* 2015). Concomitantly, we expected that upper ledge elevations (Howard and Stelacio 2011) would limit clustering (stand density), colonization (Lafon *et al* 2014), and expansion. We expected that the occurrence of the 1947 stand replacing fire would limit topographical differences because it would cause plants to adopt recovery persistence traits that confer low growth.

METHODS

Study Extraction Sites

We investigated fifteen pitch pine specimens at each of four sites at Mt. Desert Island, 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, canopy spread and stem diameter of the bole at breast height (DBH). Tree height was estimated using nested, 2 m calibrated, aluminum rods (Garellick, 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.

Clustering

We calculated mean distances 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 al* 2012) as mean neighbor distance—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 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 (Szapkowski and Jensen 2019).

Isotopic analysis

We obtained C isotopic data ($\delta^{13}\text{C}$) and N isotopic data ($\delta^{15}\text{N}$) of fully expanded leaves (needle cluster) of 15 individual 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. $\delta^{13}\text{C}$ was used to indicate water use efficiency (iWUE $_{\delta^{13}\text{C}}$) (Farquhar *et al.* 1989).

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223 Foliar tissue analysis

224 Leaf tissue was obtained from excision of basal fascicle bundles at 1.06 m. 50 mL samples of needles were
225 separated, cut and dried for two days at 60 °C. Then they were ground in a SPEX ball mill (Metuchen, NJ,
226 USA), sieved to <10 mm, and <2 mL were fed to a Leco CN-2000 Carbon-Nitrogen Analyzer (Leco Corp.,
227 St. Joseph, MI) coupled with the spectrometer to determine C and N concentrations. 35 mL aliquots were
228 submitted for standard plant tissue nutrient analysis using a TJA Model 975 AtomComp ICP-AES (Thermo
229 Jarrell-Ash Corp., Franklin, MA). The method comprised submersion in a 5 mL trace-metal-grade HNO₃
230 treatment, then refluxed on hot block at 80 °C for two hours and diluted to 25 mL with 0.4 micron PTFE
231 syringe filters to access extractable macro and micro inorganics.

232 Soil analysis

233 Soils (porous and acidic hornblende granite or Ellsworth schist) were uniformly shallow, homogeneous,
234 low fertility (varying between .7-2.5 cm) and overlain with rapidly drying needle duff (Day *et al* 2005). All
235 sites were excavated similarly by hand trowel and soil probe (Accuproducts, Saline, MI, USA). Aliquots
236 were extracted from O_a-A_b horizon soil pockets of organic and mineral deposits within 50 cm of the tree
237 base. 250 mL soil samples were sieved (#10) and measured. Drying was performed in an oven at 100°C for
238 two days. Analysis was performed using a modified Mehlich method using inductively coupled plasma
239 spectroscopy, pH measurement via proton activity of a 1:1 slurry and effective soil cation exchange capacity
240 (CEC) via formic acid extraction. These methods are described more fully elsewhere (Licht and Smith
241 2018). Soil C and N were calculated using elemental analysis in a similar fashion to method above for foliar
242 samples.

243 Soil Water Retention (SWR)

244 70 mL soil samples were extracted at fifteen tree locations at four sites, from <7.5 cm (O_a-A_b) horizon
245 above bedrock. In a laboratory 50 g H₂O were added to each aliquot to assess net water retention as a subset
246 of soil moisture evaporation (ψ_g) to determine net evaporative loss or adsorption to surfaces. Soil water
247 retention analysis was conducted according to the Fields method (Licht and Smith 2018). Retention effects
248 of gravitational and evaporation forces was made on a wet basis where $W_m = g \text{ H}_2\text{O} \bullet (\text{g moist soil})^{-1}$
249 (Jingfang and Wenwei 2018).

250 Statistical Analysis

251 All data were analyzed using a similar linear model structure with elevation (high or low) and presence of
252 the 1947 fire (yes or no) as categorical fixed factors. The interaction between elevation and presence of the
253 1947 fire was also included in each model. In total, 27 models were fit with the following dependent
254 variables: tree height (m), canopy spread (m), DBH (cm), mean distance between neighbors (m), foliar
255 carbon (C, %), foliar nitrogen (N, %), foliar C/N (unitless), foliar $\delta^{13}\text{C}$ (‰), foliar $\delta^{15}\text{N}$ (‰), foliar calcium
256 (Ca²⁺, g g⁻¹), foliar phosphorus (P, g g⁻¹), foliar potassium (K⁺, g g⁻¹), foliar magnesium (Mg²⁺, g g⁻¹), foliar
257 aluminum (Al³⁺, g g⁻¹), foliar zinc (Zn, g g⁻¹), soil C (g g⁻¹), soil N (g g⁻¹), soil C/N (unitless), soil Ca²⁺ (g g⁻¹),
258 soil P (g g⁻¹), soil K⁺ (g g⁻¹), soil Mg²⁺ (g g⁻¹), soil Al³⁺ (g g⁻¹), soil Zn (g g⁻¹), soil water retention (%),
259 soil pH (unitless), and soil CEC (cmol_e kg⁻¹). Tree height, canopy spread, DBH, foliar P, foliar K⁺, foliar
260 Zn, soil P, soil Al³⁺, soil Zn, and soil C/N were log transformed to meet model assumptions of normality
261 and heterogeneity of variances. Soil water retention was arcsin square root transformed to meet model
262 assumptions.

263 All linear models were fit using the 'lm' function in R (R Core Team 2019). Significance tests for each
264 fixed factor was performed using the 'anova' function in R (R Core Team 2019). Post-hoc Tukey's tests

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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).

278

279 RESULTS

280

281 *Aspect*

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

285

286 *Allometry and Stand Density*

287 There was a significant interaction between fire and elevation on tree height ($P < 0.01$) and DBH ($P < 0.05$;
288 Fig. 6A and Tab. 3), with trees at higher elevation that experienced the 1947 fire being shorter than those
289 at low elevation that did not experience the fire and having a smaller DBH than all other sites. Canopy
290 spread tended to be reduced at high elevation ($P < 0.01$, Fig. 6B and Tab. 3), although Tukey’s tests revealed
291 no difference between sites at $\alpha = 0.05$. Distance between neighbors was greater at high elevation sites,
292 particularly the one that experienced the 1947 fire ($P < 0.01$, Fig. 6D and Tab. 3).

293

294 *Foliar $\delta^{13}\text{C}$*

295 Trees at higher elevations experienced less negative $\delta^{13}\text{C}$ ($P < 0.01$, Fig. 7A and Tab. 6), reflecting greater
296 water use efficiency, regardless of fire history. There were no significant differences between tree
297 populations for $\delta^{15}\text{N}$ ($P > 0.05$, Fig. 7B and Tab. 6)

298

299 *Foliar organics*

300 On average, foliar C was greater at upper elevations, however the results were not statistically significant
301 ($P > 0.05$, Fig. 8A and Tab. 4); nor was there a difference in C/N between sites ($P > 0.05$, Fig. 8C and Tab.
302 4). Our linear model suggested that fire accounted for a significant influence on foliar N ($P < 0.05$, Fig. 8B
303 and Tab. 4), however post-hoc Tukey’s tests found no difference between sites at $\alpha = 0.05$ (Fig. 8B).

304

305 *Foliar macronutrient*

306 Foliar Ca^{2+} was negatively impacted by increasing elevation ($P < 0.001$, Fig. 9A and Tab. 5). Our linear
307 model suggested that foliar P was significantly higher at fire-involved sites ($P < 0.01$, Fig. 9B and Tab. 5),
308 although this was not confirmed by post-hoc Tukey’s tests (Fig. 9B). Foliar K^+ was reduced in the high
309 elevation site that experienced fire as compared to the other sites (elevation x fire: $P < 0.05$, Fig. 9C and
310 Tab. 5). Neither foliar Al^+ nor Mg^{2+} differed by site ($P > 0.05$ in both cases; Fig. 9C and Tab. 5). Foliar Zn
311 concentrations were 9% lower in the high elevation sites than on the low elevation sites ($P < 0.01$, Fig. 9F
312 and Tab. 5), due to a particularly strong reduction at the high elevation site that experienced fire.

313

314 *Soil organics*

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Soil C concentrations were greater at lower elevations ($P < 0.05$) and sites that did not experience the 1947 fire ($P < 0.05$, Fig. 10A and Tab. 7). Soil N did not vary between sites ($P > 0.05$, Fig. 10B and Tab. 7). Soil C/N was 15% lower at high elevation sites ($P < 0.05$, Fig. 10C and Tab. 7), 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 macronutrient

Soil Ca^{2+} decreased with elevation ($P < 0.05$, Fig. 11A and Tab. 8). P, Mg and Zn were not significantly different across sites (Tab. 8). However, fire accounted for a 48% reduction in K at fire-experienced sites ($P < 0.01$, Fig. 11C and Tab. 8). While there was no significant interaction between elevation and fire history according to foliar Al^+ availability, we found that interaction was significant for soil Al^+ ($P < 0.01$, Fig. 11E and Tab. 8), suggesting soil Al^+ was reduced by elevation in the sites experiencing the 1947 fire.

Soil Water Retention, CEC and pH

There was an interaction between elevation and fire history on soil water retention (SWR) ($P < 0.01$, Fig. 12A and Tab. 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 ($P > 0.05$, Tab. 9). Our linear model indicated that cation exchange capacity (CEC) was higher at the high elevation sites ($P < 0.05$, Fig. 12C and Tab. 9), but this was not confirmed by our post-hoc Tukey's tests, which indicated no difference between sites (Fig. 12C).

DISCUSSION

Elevation, as opposed to fire history, was the dominant driver of plant and ecosystem processes we measured. This result indicates 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 absence.

Elevation played a role in several meaningful ways. We confirmed that increased elevation tended to favor efficiency (e.g., foliar water use efficiency; Wang *et al* 2017; Chen, Wang and Jia 2017), over growth. Further, we found distance between neighbors at higher elevation was greater compared to lower elevation sites, suggesting that sparser tree aggregation was more a reflection of persistence than recovery capacity. At the highest elevation, South Cadillac trail, we expected to find the steepest slopes but they were far less inclined than those at Gorham cliffs. 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 ($\mu=180^\circ$). This was borne out most forcefully at Wonderland, where trees, living on by far the flattest terrain, achieved the widest distribution over the widest contiguous area with the lowest mean distance between population members. This result suggests that individuals in the Wonderland population were able to take advantage of the hospitable conditions and compete well with co-occurring species in the absence of disturbance.

Fire was less meaningful than elevation, even at high elevation ledge communities. We found little compelling empirical evidence that fire is a necessary ingredient in population perpetuation at Mt. Desert Island. Fire return intervals have lengthened at Mt. Desert Island to the point where they are quite likely to

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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. ~~Discounting~~ topography and elevation, ~~previous studies reported that~~ anthropogenic fire charcoal (PyC) was associated with ~~greater foliar water use efficiency~~, negligible consumption of Ca, K and Mg and enhanced soil moisture holding capacity (Licht and Smith 2020). Here ~~on Mt. Desert Island~~, we found ~~higher foliar water use efficiency~~ 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). 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) ~~and~~ 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 ledge locations (e.g., St. Sauveur) that we and others (Howard 2010) ~~have~~ studied.

One could argue that charcoal remnants likely 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. ~~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 nutrient ~~results~~ derived from burned and unburned ~~sites are~~ similar to others such as those in the pine barrens of New Jersey (e.g., Renninger *et al* 2013) ~~and indicate that historical fire reduced soil C. However, there was also a strong reduction in soil C with elevation.~~ We expected this ~~would be the result of variations soil P~~ (Preston and Schmidt 2006, Patel *et al* 2016, Hart Horn and Grissino-Mayer 2008), ~~but soil P was similar across sites. Instead, our results indicated that this may have been due to variations in other growth-limiting nutrients such as K, which was reduced due to fire history, and Al⁺, which was reduced with elevation in the sites experiencing fire. Nonetheless, foliar C was similar across sites, inconsistent with findings by others in New Jersey (Renninger *et al* 2013; Alkaniz *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 recovery capacity was more likely connected to higher P.

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 ~~a~~ negative impact on future vegetative status at Mt. Desert Island (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 persistence capacity or recovery capacity. What has been clear for at least two 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)

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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. Nevertheless, competitive advantages enjoyed currently may even give way to ‘mesophication’: a 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 recovery capacity and persistence capacity at a given elevation and within certain topographic parameters. The present data provides 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 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 persistence capacity signaled by significant differences in density, slope and aspect. At a time when

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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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