

1 **Title Page**

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

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6 Authors and affiliations:

7 Jeff Licht¹, Risa McNellis², and Nicholas G. Smith²

8

9 ¹School for the Environment, University of Massachusetts, Dorchester, MA, USA 02110

10 ²Department of Biological Sciences, Texas Tech University, Lubbock, TX, USA 79409

11

12 Key words

13 *Pinus rigida*, Pitch pine, Mount Desert Island, fire, elevation, resilience, adaptivity, chemical,
14 geography

15

16 **ABSTRACT**

17 Globally rare pitch pine (*Pinus rigida*) is thought to depend on intermittent fire, which
18 encourages reproduction and niche preservation. At Mt. Desert island in Acadia National Park
19 (ME, USA) a stand-replacing conflagration enveloped a portion of the island in 1947. However,
20 there has been no recurrence of fire. Other populations on the island have been unaffected by fire
21 disturbance for over one hundred years. Fire history is shown to influence plant form and
22 functioning, yet these impacts are not well quantified for pitch pine in relation to factors such as
23 elevation and topography, which are also known to impact traits of this species. We studied the
24 impact of fire history on traits of pitch pine individuals across elevation (9.5 to 404 m) and
25 topographic (flat, ledge and cliff) gradients at Mt. Desert Island. Traits included growth, stand
26 density, photosynthetic water use efficiency, and foliar nutrients. We also measured site data
27 such as soil nutrients, soil water retention, elevation, slope, and aspect. Elevation was found to be
28 a greater driver of persistence than fire history and there was little interaction between elevation
29 and fire history. Our data indicates that fire return intervals were likely too infrequent to support
30 selection for recovery capacity traits; instead, persistence capacity traits increased in response to
31 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.

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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).

Commented [RM2]: I don't think abbreviating Mt Desert Island is necessary unless you're working with a page or word limit. More abbreviations tends to just be more confusing for readers!

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

63 qualitative model which explains pitch pine responses to fire history and non-fire environmental
 64 constraints as a function of elevation and topography (Dunne *et al* 2004) (Figure 3). The model
 65 is informed by earlier resilience theories (Jordan Patterson and Windisch 2003; Howard and
 66 Stelacio 2011; Ibáñez *et al* 2019). Here, we hypothesize that pitch pine populations exhibit non-
 67 mutually exclusive responses: (1) **recovery capacity** (*REC_C*) as a measure of plant performance
 68 (Ibáñez *et al* 2019) long after fire disturbance (Patterson Saunders and Horton 1983) and (2)
 69 **persistence capacity** (*PER_C*) that reflects responses in the absence of disturbance (Brand and Jax
 70 2007).

71 Each capacity metric reflects physical responses, such as the tradeoffs between growth
 72 and stress avoidance and colony retreat and expansion (Swanston *et al* 2018), as a function of
 73 stand density (Churchill *et al* 2012) and as an ‘ecologically stable strategy’ (Day and Greenwood
 74 2011). *REC_C* is the better understood of the two pathways given the extensive literature covering
 75 resilience (Ibáñez *et al* 2019) and tree health (Fuller and Quine 2016). *PER_C*, on the other hand,
 76 explains a trend where shade-intolerant pitch pine out-compete other evergreens, such as red
 77 spruce (*Picea rubens*), hemlock (*Tsuga canadensis*) and balsam fir (*Abies balsamea*), thus
 78 expanding into new, mostly uninhabited territory. There is a scarcity of the biogeochemical,
 79 elevation, and topographical data at MDI needed to inform the functionalities within this model.
 80 To remedy this, we consider soil and plant nutrition including carbon (C), nitrogen (N), and
 81 stable isotope analysis to determine how intrinsic water use efficiency (*iWUE_{δ13C}*), soil moisture
 82 retention, growth and stand density are affected by fire history and topography.

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

Commented [RM3]: Again, more abbreviations are more confusing. I recommend just referring to recovery capacity and persistence capacity to reduce the number of acronyms

Commented [RM4]: Do you mean that each capacity metric reflects an ecologically stable strategy?

Commented [RM5]: Recovery capacity needs a better explanation here. This paragraph would be a great spot to clearly link recovery capacity to fire history and persistence capacity to elevation so that it's very obvious why you chose those as independent variables for the analysis

Commented [SN6]: Elevation is an aspect of topography, right?

Commented [SN7]: Citation for this?

Commented [RM8]: Between which populations?

Commented [RM9]: Which aspects?

93 Our foremost aim is to examine a proposed model through an analysis of four key pitch
 94 pine populations according to the interactive influence of fire and elevation. Given previous
 95 studies of fire involvement and post-fire photosynthetic response (Chen Wang and Jia 2017), we
 96 hypothesize that pitch pine growth and population expansion is greater at non-fire sites with low
 97 elevation due to higher soil C, higher foliar C (Butak 2014), more negative $\delta^{13}\text{C}$ (Licht and
 98 Smith 2020), and greater soil water retention (positive indicators of $PERC$). We further theorize
 99 that trees at low elevations display a greater propensity for growth in height, canopy, and DBH
 100 through more competitive resource conservation (Stambaugh *et al* 2015). Additionally, we
 101 hypothesize that ubiquitous contours (Howard and Stelacio 2011) at upper ledge elevations,
 102 which limit clustering (stand density) elsewhere, will be less stressful for colonization (Lafon *et*
 103 *al* 2014) and expansion on lower elevation flat and cliff surfaces. We predict this will increase
 104 pioneering efforts at gentler slopes and more southerly aspect.

Commented [SN10]: Higher than what?

Commented [SN11]: What about the low elevation site with the more recent fire history?

Commented [RM12]: Not sure what "contours" refers to. I checked the referenced paper, but I'm still unclear on how it connects

Commented [SN13]: Is this the expectation regardless of fire history?

106 METHODS

107 Study Extraction Sites

108 We investigated fifteen pitch pine specimens at each of four sites at MDI (Table 1),
 109 factorially crossed in a fire history (Miller *et al* 2014) by elevation design: (1) Wonderland trail
 110 between 9 and 25 m elevation (low elevation, outside the footprint of the 1947 fire), (2) Gorham
 111 cliffs between 24 and 36 m (low elevation, within the footprint), (3) St. Sauveur trail between
 112 134 and 198 m (high elevation, outside the footprint) and (4) South Cadillac trail between 188
 113 and 417 m (high elevation within the footprint).

114 Allometry

115 We measure individual tree height (m), canopy spread (m), and stem diameter at breast
 116 height (DBH; cm). Tree height was estimated using nested, 2 m calibrated, aluminum rods
 117 (Garelick, St. Paul, MN, USA). Canopy spread was measured using the span between the same
 118 calibrated aluminum rods fixed with two landscape flags as a ground truth reference. DBH was
 119 measured at 1.06 m using a ProSkit electronic digital caliper (Amelia, VA, USA).

120 Clustering

121 Mean distances were calculated between sampled trees ($N = 167$) and up to five of their
 122 nearest, reproductively mature, conspecific neighbors (within 5 m) in the same clump (Churchill

et al. 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 ($\delta^{13}\text{C}$) and N isotopic data ($\delta^{15}\text{N}$) 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). $\delta^{13}\text{C}$ was used to indicate water use efficiency (iWUE $\delta^{13}\text{C}$) (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 HNO_3 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.

154 **Soil Analysis**

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

166 **Soil Water Retention (SWR)**

167 70 mL soil samples were extracted at 15 tree locations at each of four sites, from <7.5 cm
168 (O_a-A_b) horizon above bedrock. In a laboratory, 50 g H₂O were added to each aliquot to assess
169 net water retention as a subset of soil moisture evaporation (ψ_g) to determine net evaporative loss
170 or adsorption to surfaces. Soil water retention analysis was conducted according to the Fields
171 method (Licht and Smith 2018). Retention effects of gravitational and evaporation forces was
172 made on a wet basis where $W_m = g \text{ H}_2\text{O} \bullet (\text{g moist soil})^{-1}$ (Jingfang and Wenwei 2018).

173 **Statistical Analysis**

174 All data were analyzed using a similar linear model structure with elevation (high or low)
175 and presence of the 1947 fire (yes or no) as categorical fixed factors. The interaction between
176 elevation and presence of the 1947 fire was also included in each model. In total, 27 models were
177 fit with the following dependent variables: tree height (m), canopy spread (m), DBH (cm), mean
178 distance between neighbors (m), foliar: carbon (C, %), nitrogen (N, %), carbon/nitrogen (C/N,
179 unitless), $\delta^{13}\text{C}$ (‰), $\delta^{15}\text{N}$ (‰), calcium (Ca^{2+} , g g⁻¹), phosphorus (P, g g⁻¹), potassium (K^+ , g g⁻¹),
180 magnesium (Mg^{2+} , g g⁻¹), aluminum (Al^+ , g g⁻¹), zinc (Zn, g g⁻¹), soil: C (g g⁻¹), N (g g⁻¹), C/N
181 (unitless), Ca^{2+} (g g⁻¹), P (g g⁻¹), K^+ (g g⁻¹), Mg^{2+} (g g⁻¹), Al^+ (g g⁻¹), Zn (g g⁻¹), water retention
182 (%), pH (unitless), and CEC (cmol_c kg⁻¹). Tree height, canopy spread, DBH, foliar P, foliar K,
183 foliar Zn, soil P, soil Al, soil Zn, and soil C/N were log transformed to meet model assumptions

Commented [SN14]: This is the first time a date is mentioned I think, so it is not clear how this relates to the other sampling dates. If sampling was all done at similar times, then this probably isn't needed. If there was substantial differences, then maybe include everywhere.

Commented [J15]: NGS to take a further look at this explanation

184 of normality and heterogeneity of variances. Soil water retention was arcsin square root
185 transformed to meet model assumptions.

186 All linear models were fit using the 'lm' function in R (R Core Team 2019). Significance
187 tests for each fixed factor was performed using the 'anova' function in R (R Core Team 2019).
188 Post-hoc Tukey's tests were done to examine significant interactions between elevation and the
189 presence of the 1947 fire using the 'emmeans' package in R (Lenth 2018).
190 Because aspect data is circular in nature, we analyzed aspect data using a Watson's Two-Sample
191 Test of Homogeneity as implemented in the R package 'circular' (Agostinelli and Lund 2017).
192 Specifically, one-to-one comparisons were done between each site in all six possible
193 combinations.

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

195

196 RESULTS

197 Aspect

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

201 Allometry and Stand Density

202 There was a significant interaction between fire and elevation on tree height ($P < 0.01$;
203 Figure 5A and Table 3) and DBH ($P < 0.05$; Figure 5C and Table 3), with trees at higher
204 elevation that experienced the 1947 fire being shorter than those at low elevation that did not
205 experience the fire and having a smaller DBH than all other sites. Canopy spread tended to be
206 reduced at high elevation ($P < 0.01$, Figure 5B and Table 3), although Tukey's HSD tests
207 revealed no difference between sites at $\alpha = 0.05$. Distance between neighbors was greater at high
208 elevation sites, particularly the one that experienced the 1947 fire ($P < 0.01$, Figure 5D and Table
209 3).

210 $iWUE_{\delta^{13}C}$

211 Trees at higher elevations experienced less negative $\delta^{13}C$ ($P < 0.01$, Figure 6A and Table
212 4), reflecting greater water use efficiency, regardless of fire history. There were no significant
213 differences between tree populations for $\delta^{15}N$ ($P > 0.05$, Figure 6B and Table 4)

214 Foliar Organics

Commented [SN16]: C. Agostinelli and U. Lund (2017). R
package 'circular': Circular Statistics (version 0.4-93). URL
<https://r-forge.r-project.org/projects/circular/>

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

220 **Foliar Macronutrients**

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

229 **Soil Organics**

230 Soil C concentrations were greater at lower elevations ($P < 0.05$) and sites that did not
231 experience the 1947 fire ($P < 0.05$, Figure 9A and Table 7). Soil N did not vary between sites (P
232 > 0.05 , Figure 9B and Table 7). Soil C/N was 15% lower at high elevation sites ($P < 0.05$, Figure
233 9C and Table 7), but we found no significant disparity in C/N when either fire history or fire
234 history by elevation interactions were examined ($P > 0.05$ in both cases).

235 **Soil Macronutrients**

236 Soil Ca^{+2} decreased with elevation ($P < 0.05$, Figure 10A and Table 8). P, Mg^{2+} and Zn
237 were not significantly different across sites (Table 8). However, fire accounted for a 48%
238 reduction in K^+ at sites with fire history ($P < 0.01$, Figure 10C and Table 8). There was an
239 interaction between elevation and fire history for Al^+ ($P < 0.01$, Figure 10E and Table 8), which
240 indicated....

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

242 There was an interaction between elevation and fire history on SWR ($P < 0.01$, Figure
243 11A and Table 9), with markedly higher values at Gorham cliffs, the low elevation site that
244 experienced fire, as compared to other sites. Soil pH was not different between sites ($P > 0.05$,
245 Table 9). Our linear model indicated that CEC was higher at the high elevation sites ($P < 0.05$,

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246 Table 9), but this was not confirmed by our post-hoc Tukey's tests, which indicated no
247 difference between sites (Figure 11C).

248

249 DISCUSSION

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

256 Elevation played a role in several meaningful ways. We confirmed that increased
257 elevation tends to improve efficiency (increased $iWUE_{\delta^{13}C}$ over growth (Wang *et al* 2017; Chen,
258 Wang and Jia 2017). Further, we found distance between neighbors at higher elevation was
259 greater compared to lower elevation sites, thus generating sparser tree numbers aggregated
260 within REC_C compared to PER_C . At the highest elevation, South Cadillac trail, we expected to
261 find the steepest slopes, but they were far less steep than those at Gorham cliffs, a low elevation
262 site. We anticipated that low elevation (<50 m) populations would feature a greater number of
263 conspecific neighbors as a function of no fire history, flat or cliff orientation, evidenced by a
264 gentle slope (<10°), and tendency towards a southerly aspect ($\mu = 180^\circ$). In fact, this theory was
265 found correct, as Wonderland, which was by far the flattest terrain, trees achieved the widest
266 distribution with the greatest distance between trees over the widest contiguous area as a function
267 of REC_C . There was sufficient variability in some of the data, like stand density, to produce
268 valuable information about differences between flat, cliff and ledge communities, even if at a
269 small spatial scale.

270 Fire history was less important than elevation in the response variables we measured,
271 even at high elevation ledge communities. We found little compelling empirical evidence that
272 fire is a necessary ingredient in perpetuation at MDI. Fire return intervals have lengthened at
273 MDI to the point where they are quite likely to be too intermittent to perpetuate previous fire
274 resistance traits. A shift back to fire, accompanied by a re-introduction of serotinous
275 characteristics, is not impossible in the future; however, current climate projections advise
276 against this occurrence. Despite the absence of fire, there is the presence of fire remnants. The

Commented [RM18]: Are they all significant? I count only 20 response variables with significant relationships

Commented [NGS19]: Not clear what this means

Commented [RM20]: You measured distance between neighbors, not number of neighbors. So, would you expect a lower mean distance between neighbors at low elevations?

Commented [NGS21]: Is this correct?

Commented [RM22R21]: Wonderland has the lowest mean distance between neighbors, which I think means the trees are denser. Not sure how this relates to cliff orientation or aspect. Also- not sure if you can claim that this is a function of recovery capacity?

Commented [RM23]: Since we used mean distance between neighbors in the analysis, not stand density, it's worth it to be careful about how you reference stand density in the results/discussion. Also, you state that there is valuable information about differences between flat, cliff, and ledge communities but then you don't elaborate.

Commented [RM24]: Climate projections advise against resuming prescribed fire or they don't believe natural fires will return? Is there a citation for this?

277 current study builds on previous work (Licht and Smith 2020) to determine how an obvious post-
 278 fire effect—anthropogenic fire charcoal (PyC)— changes according to elevation and topography
 279 in association with greater (more negative) $iWUE_{\delta^{13}C}$, negligible consumption of Ca^{2+} , K^{+} and
 280 Mg^{2+} , and increased soil moisture holding capacity. In this study we hypothesized that $iWUE_{\delta^{13}C}$
 281 , stored plant C, and soil water retention would change significantly as a result of fire history.
 282 However, besides an increase in soil water retention with fire at the low elevation site, this
 283 hypothesis was not supported. Instead, we found lower $iWUE_{\delta^{13}C}$ at high elevations regardless of
 284 fire history, consistent with reported outcomes for non-glaciated populations in flat, sand plain
 285 New Jersey Pine Barrens (Mikita-Barbato *et al* 2015; Schafer and Bohrer 2016). We also found
 286 congruence between low elevation outcomes in the present study and those reported ($\mu = 33m$
 287 above sea level) in the New Jersey pine barrens (Carlo *et al* 2016). However, we could not draw
 288 any other useful comparisons between the studies due to a lack of data concerning clustering
 289 (stand density), slope, or aspect factors. There is evidence from previous investigations that post-
 290 fire PyC remnants, which endure in the soil layer (DeBano 1981), increase alkali cations (Kolden
 291 *et al* 2017) and solubilized minerals (Caldwell and Richards 1989) and are likely linked to
 292 thermal exfoliation (Shakesby and Doerr 2006). From the standpoint of reproduction, the
 293 absence of fire at locations such as *PERC*-oriented Wonderland trail (Butak 2014) does not
 294 appear to be slowing down expansion in that flat-sloped region nor in other cliff locations that
 295 we and others studied (Howard 2010).

296 Developing further insights into the ecological stoichiometry of pitch pine at MDI is a
 297 worthwhile goal given earlier discoveries by Fernandez (2008). Our nutrient analysis derived
 298 from burned and unburned trees was similar to a methodology in a New Jersey study (Renninger
 299 *et al* 2013) and produced some similar results. Since elevation is a key factor, we noted foliar Zn
 300 was higher at lower elevations at MDI; this was consistent with findings by others in another
 301 New Jersey investigation (Kolker *et al* 2013). In both Maine and New Jersey, it is possible *PERC*
 302 may be enhanced by higher concentrations of foliar Ca^{2+} , K^{+} , Mg^{2+} , P, Al^{+} and Zn (Mg^{2+} foliar
 303 availability was not significant in this study). We were particularly interested in P, a limiting
 304 factor (Verma and Jayakumar 2012); it is sometimes found to co-occur with pools of greater C
 305 (Preston and Schmidt 2006). Scientists elsewhere assert that fire-induced sedimentary charcoal
 306 produces soil C enrichment (Patel *et al* 2016) as measured in soil columns (Hart Horn and
 307 Grissino-Mayer 2008). One could argue that charcoal remnants likely play a role in *REC* at

Commented [NGS25]: This is already said above (without the citations)

Commented [NGS26]: μ is never defined

Commented [RM27R26]: μ is used previously for aspect in degrees

Commented [RM28]: mean distance between neighbors?

Commented [RM29]: Is this correct? You associate Wonderland with recovery capacity in the previous paragraph. If each site typically uses a different pathway, it would be worth explaining that at the beginning of the discussion as well as the evidence supporting why.

Commented [RM30]: What earlier discoveries?

Commented [RM31]: Which are?

Commented [RM32]: Citation?

Commented [RM33]: Foliar or soil? A limiting factor to what?

308 burned-over Cadillac Brook (below the heights of South Cadillac trail), but it is not known to
 309 what extent these benefit the larger ecosystem. We conjecture that soil C persistence since the
 310 1947 fire at burned-over areas such as South Cadillac trail reflects a lack of pyrogenic carbon
 311 removal (Doerr *et al* 2018), though elsewhere lower C availability is attributable to greater
 312 consumption by fungi (Luo *et al* 2017). P concentration at upper elevations at MDI contrasted
 313 with more modest availability at other, low-lying pinelands at MDI and in New Jersey
 314 (Renninger *et al* 2013; Alkañiz *et al* 2018). One explanation for substantial soil P availability is
 315 that it derives from charcoal remnants; however, lacking mycorrhizal studies we were unable to
 316 confirm the extent of P liberated from the charcoal in the two 1947 fire precincts.

317 Climate is likely the final arbiter of decline rather than stand-replacing fire disturbance in
 318 the case of long-term pitch pine livelihood. Recent climate change models anticipate negative
 319 impact on future vegetative status at MDI (Fernandez *et al* 2015), but these do not specifically
 320 address the adaptability of pitch pine nor the extent to which plasticity (Day *et al* 2014) is
 321 shaping tendency towards *PERC* or *REC_C*. What has been clear for at least two decades is the
 322 effect of global climate change on ecophysiology traits. Day, Greenwood and White (2001)
 323 found that an uptick in annual temperatures signaled increased leaf-air vapor pressure deficits
 324 which negatively impacted pitch pine stomata response and limited gas exchange. In a related
 325 report, scientists found that warming trends (Kunkel *et al* 2013) increased pitch pine difficulties
 326 in reproduction (Ledig Smouse and Hom 2015). This includes weather-related effects such as
 327 episodic drought, harsh winds, and salt spray (Schmitt 2015; Fernandez *et al* 2015), as well as
 328 conditions that increased cold intolerance (Berang and Steiner 1985). Increases in annual winter
 329 temperatures (Lesk *et al* 2017) coupled with an absence of fire cause concern about a quite
 330 different disturbance—potential invasion within the next decade of an herbivore, Southern Pine
 331 Beetle (*Dendroctonus frontalis* or ‘SPB’). Although deer and rodent damage (Ledig *et al* 2013)
 332 historically impeded tree survival in pine barrens, SPB has already paid a deadly visit to Long
 333 Island, NY (Dodds *et al* 2018). Unless its progress is deterred by other insect predators like
 334 Dubious Checkered Beetle (*Thanasimus dubius*; Coulson and Klepzig 2011), it is possible that
 335 pitch pines along with understory plants, butterflies and moth members of the Acadia ecosystem
 336 will suffer the same fate experienced in more southerly locations (Lesk *et al* 2017). According to
 337 several authors (Day *et al* 2005; Lee *et al* 2019) warming climate impacts the suitability of
 338 habitat and pitch pine tendencies to consolidate, regenerate or migrate may be in jeopardy. These

339 effects are likely to eventually limit aspects of PER_C such as niche expansion, if they have not
340 already, through a combination of diminished open space capacity, loss of enriched substrates,
341 and elimination of 'safe sites.'

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

350 The model we proposed is not built on a quantitative framework nor is it intended as a
351 predictive model, *per se*, yet results attached to this model are useful in several ways. First, these
352 metrics provide a context for describing recovery or persistence in mathematical relationships
353 along an adaptivity curve. Second, our method operationalizes recovery and persistence
354 mechanisms fit to an ecological framework (Brand and Jax 2007). Finally, our model may be
355 used to better understand how pitch pine in other ecosystems outside of the Northeast U.S.
356 discriminate between REC_C and PER_C at a given elevation and within certain topographic
357 parameters. The data presented here provides a fuller understanding of current regeneration and
358 expansion concepts which are essential to an appreciation of influences on persistence in the
359 absence of forest or prescribed fire.

360

361 CONCLUSION

362 Here, we present an explanatory model of pitch pine post-fire recovery and persistence
363 capacities to analyze population status as a function of fire and topography. We found adaptivity
364 effects (growth, expansion into greater stand density) account for greater growth and stand
365 density on more hospitable terrain, with little impact from fire history. This is likely due to the
366 fact that fire return intervals are so infrequent as to reduce recovery features found elsewhere
367 (e.g., cone serotiny). Flat and ledge pitch pine populations exhibited greater buoyancy than trees
368 in more strenuous cliff situations. We also identified a selective preference for either growth at
369 low elevations or stress tolerance at high elevations using multiple plant and ecosystem metrics.

Commented [RM34]: Do you mean suitable habitat?

370 Our findings unravel an enigma about persistence in a post-fire milieu during a critical phase of
371 the Anthropocene age (Crutzen and Stoermer 2000). At lower elevations, which represent the
372 vast majority of pitch pine populations in the Northeast US, we predict newly pioneered
373 locations reflect a continuation of *PERC* signaled by significant differences in density, slope, and
374 aspect. At a time when continued climate change may tip the scale away from survival, our
375 findings encourage the use of a model by forest managers to better understand the imposition of
376 fire absence on flat and ledge communities.

378 **Data Availability Statement**

379 Data used in this article can be found at the following repository:
380 https://github.com/SmithEcophysLab/mtDesertIsland_Pinusrigida
381 (DOI:10.5281/zenodo.4663255).

383 **Author Contributions**

384 JL and NS conceived the work, contributed substantially to the interpretation of the data
385 and to drafting the manuscript, gave final approval of the version submitted, and agreed to be
386 accountable for all aspects of the work. Questions related to the accuracy or integrity of any part
387 of the work are appropriately investigated and resolved. JL carried out sample collection and
388 field measurements, conducted soil water retention tests and prepared samples for EA-IRMS
389 analysis. NS performed C/N foliar analysis, conducting statistical analyses and formulating
390 figures and tables.

392 **ACKNOWLEDGEMENTS**

393 Research at MDI was conducted under permit ACAD-2020-SCI-0014 from the U.S.
394 Department of Interior granted to Jeff Licht. Mike Day, PhD, suggested topics for study and
395 located some of the sites for the study. Cartographer Jill Phelps Kern created geospatial figures.
396 Remote sensing devices were supplied by Tora Johnson, PhD. Field sampling was assisted by
397 Mimi Licht and Laura Brumleve. Site measurements were greatly facilitated by staff at National
398 Park Service, Mt. Desert Island, Bar Harbor, ME. Our thanks to several anonymous reviewers
399 prior to submission.

400

ORCID

Jeff Licht: <https://orcid.org/0000-0002-2248-2050>

Nicholas Smith: <https://orcid.org/0000-0001-7048-4387>

Risa McNellis: <https://orcid.org/0000-0002-3538-9269>

FUNDING INFORMATION

Professor Nick Smith was supported by funding at Texas Tech and partial funding for Jeff Licht to complete this paper was supported by a grant (P20AP00312) from the U.S. Department of Interior.

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