1   **Title Page**

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3   Pitch Pine (*Pinus rigida*) Response to Fire Absence and Topographic Factors at Mt. Desert Island

4

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10

11   Key words

12   *Pinus rigida*, Pitch pine, Mt. Desert Island, fire history, elevation, resilience, topography, water use

13   efficiency, soil water retention

14

15

16   **Abstract**

17   Globally rare pitch pine (*Pinus rigida*) is thought to depend on intermittent fire, which encourages

18   reproduction and niche preservation. At Mt. Desert Island in Acadia National Park (ME, USA) a major,

19   stand-replacing conflagration enveloped a portion of the island in 1947; since then there has been no

20   recurrence of fire. Other populations have been unaffected by fire disturbance for over one hundred and

21   twenty years. Despite the absence of fire, pitch pine persists at Mt. Desert Island, suggesting that other

22   factors such as topography may be as or more important than fire in that system. We examined the

23   influence of fire history and topography on individual trees in four separate stands at Mt. Desert Island.

24   Generally, topography was found to be a more important driver of leaf and plant level traits than fire

25   history, with individuals possessing greater stress tolerance traits at high elevation. We attribute this to

26   changes in topographical and soil characteristics along the gradient. These results challenge the

27   suggestion that fire is the primary driver of pitch pine persistence at Mt. Desert Island and indicate that

28   pitch pine has the capacity to thrive across a wider array of environments. These results can serve to

29   better understand and manage this species in an ever-changing future world.

30

31   **Introduction**

32   On Mt. Desert Island at Acadia National Park in Maine USA, pitch pine (*Pinus rigida*), the most

33   northerly member of the southern yellow pines (Plain *et al*. 1987), dwell at the edge of their northeastern

34   range (Fig. 1) in heathland-pine barren communities. Over millennia, their persistence (ability to remain

35 in a particular setting) is defined by frequent fire disturbance that regulates competition, removes post-fire

36 pyrogenic carbon (C) from the soil and drives the radiation of fire adaptations. Among the most

37 significant fire adaptations are serotinous cones (which typically open only when fire engulfs the tree),

38 thickened bark to withstand scorching, and epicormic sprouting along branches and trunk (Little 1953).

39 On Mt. Desert in 1947 an intense October fire started in a dump just west of Bar Harbor, on the east side

40 of the island (Fig. 1; Pyne 2019). Ferocious winds whipped the fire into a frenzy and, notwithstanding

41 efforts to subdue it, persevered for nearly two weeks. Since that time, fire suppression has been used to

42 avoid a repetition of the tragic consequences from that fire. Interestingly, in ensuing decades, tree

43 pyrogenic adaptations have diminished, perhaps as the result of phenotypic plasticity, shifting away from

44 cone serotiny (Conkey *et al*. 1995; Jordan *et al*. 2003). As there is less pressure to produce seeds that

45 survive in the midst of a fire (Givnish 1981), there may also be less need for thick bark or epicormic

46 sprouting (Renninger *et al.* 2013). Past studies have speculated that tree defenses are shifting from fire

47 resiliency to traits that may help deal with other abiotic conditions such as warmer temperatures and

48 increasing summer drought (Day *et al.* 2005; Buma *et al.* 2013).

49

50 Recent history of pitch pine population success in fire-suppressed locations such as Mt. Desert Island

51 defies a theory that fire (natural or prescribed) is likely a requirement every six to twenty-five years for

52 pine barren well-being (Jordan *et al*. 2003). While fire responses have been studied previously (Foereid *et*

53 *al.* 2015; Carlo *et al.* 2016; Neill *et al.* 2007), there is a critical need to understand other factors that might

54 be influencing pitch pine persistence in the absence of fire at Mt. Desert Island.

55

56 Here, we address one such factor, topography, that has not yet been thoroughly assessed at Mt. Desert in

57 comparison with fire history (Parshall and Foster 2002; Fig. 2). Specifically, we use four populations that

58 lie along a topographical and fire history gradient (Fig. S1) as proxies for more than a dozen other

59 colonies, to examine the effects of elevation, aspect and slope (Bolstad and Stowe 1994) on soil, leaf, and

60 plant-level traits. The four populations were chosen to represent a factorial combination of elevation (high

61 or low) and fire history (having experienced the 1947 stand-clearing fire or not). First, we characterize

62 differences in topographical features, including slope and aspect, given that these are likely important

63 non-elevation topographical drivers of the traits examined (Howard and Stelacio 2011; Hanson 2017;

64 Nowacki and Abrams 2008). We then explore aspects of the soil environment, including soil carbon as

65 well as macro and micro nutrient concentrations. Following previous studies, we expected to find less soil

66 carbon (DeBano 1998), greater alkali cations (Certini 2005) and increased solubilized minerals (Caldwell

67 and Richards 1989) in soils which experienced the 1947 fire. We predicted that there would be greater

68 soil carbon at low elevations due to thermal exfoliation (as explained by Shakesby and Doerr 2006) or a

69   failure of fire to remove pyrogenic carbon in former fire zones (Doerr *et al.* 2018). We also measured soil

70   water retention, which we expected to be greater at sites that experienced the 1947 fire, as pyrogenic

71   carbon is known to increase soil water retention (Licht and Smith, 2020). Beyond that, we anticipated

72   higher soil water retention at low elevations due to flat terrain (alleviating erosion mechanics).

73

74   We hypothesized that topographical and fire history-driven changes to the growth environment would

75   manifest in changes in leaf- and plant-level traits. We expected that stress induced by topographical

76   features and low soil water retention at high elevation would lead to increased intrinsic water use

77   efficiency (iWUE; Wang *et al.* 2017), as a stress tolerance response. We also hypothesized a reduction in

78   leaf nutrients at high elevation, mimicking likely reductions in the soil. In addition, there was the prospect

79   that fire history might alleviate these stress indicators, as a result of increased soil nutrients and water

80   retention. At the plant level, we predicted plants would be smaller in height and DBH, have narrower

81   canopy, and be more sparsely clustered (greater distance between conspecific neighbors) at high

82   elevation, again as a result of the topography- and soil-induced stress. We expected to find smaller trees

83   in areas that had experienced the 1947 fire due to age, but that the height difference would be less at high

84   elevation due to stress-reducing effects of fire on the soil environment, an effect that would be more

85   beneficial if higher elevation sites were less fertile.

86

87   **Methods**

88   *Study sites*

89   We investigated pitch pine specimens at each of four sites at Mt. Desert Island (Fig. 2, Tab. 1, Tab. S1),

90   factorially crossed in a fire history (Miller *et al*. 2017) by elevation design: (1) Wonderland trail at an

91   average of 17.83 m elevation (low elevation, outside the footprint of the 1947 fire), (2) Gorham cliffs at

92   an average of 32.95 m (low elevation, within the footprint), (3) St. Sauveur trail at an average of 171.72 m

93   (high elevation, outside the footprint) and (4) South Cadillac trail at an average of 279.95 m (high

94   elevation within the footprint). Elevation differences were more stark at St. Sauveur and South Cadillac

95   trail transects. Soils at all four sites were overlain with rapidly drying needle duff, porous, and comprised

96   of acidic hornblende granite or Ellsworth schist (Day *et al.* 2005). In addition they were uniformly

97   shallow (varying between 0.7-2.5 cm), homogeneous, and low in fertility (Butak 2014). In some cases,

98   sampling was limited by time, weather and site access yielding uneven sample accumulations (see sample

99   size for each measured variable in Tab. S1). Our analytical methods were designed to deal with uneven

100   sample sizes (see Statistical Analysis section below).

101

Topographic features

103 A Kodak Trimble Juno 3B was used to obtain horizontal resolution of data plotted using between five and

104 seven satellite telecommunication vehicles to maintain a maximum Position Dilution of Precision. These

105 data were differentially corrected and have estimated accuracies in the horizontal and vertical direction of

106 2m, while selective availability was set to zero. Multiple satellite-configured GPS data (USGS 2m

107 LIDAR 2010) determined coordinates for individual trees (Lubinski *et al*. 2003) as well as slope and

108 aspect attributes using ArcGIS (version 10). Mapping of this type of data has been used in the past to

109 compare physiography and recalcitrant chemical biogeography, particularly in fire prone contexts

110 (Kolden and Weisberg 2007; Szpakowski and Jensen 2019).

111

112 *Soil Elements and Water Retention (SWR)*

113 Soils were excavated by hand trowel and soil probe (Accuproducts, Saline, MI, USA); soil C, N and C/N

114 were calculated from elemental analysis. 70 mL soil samples were extracted at fifteen tree locations at

115 four sites, from <10.5 cm (O_a-A_b) horizon above bedrock. In a laboratory 50 g H_2O were added to each

116 aliquot to assess net water retention as a subset of soil moisture evaporation (ψ_g) to determine net

117 evaporative loss or adsorption to surfaces. Soil water retention analysis was conducted according to the

118 Fields method (Licht and Smith 2018). Retention effects of gravitational and evaporation forces was

119 made on a wet basis where W_m=g H_2O ● (g moist soil)$^{-1}$ (Qi *et al.* 2018). We also used a set of #10-#140

120 mesh sieves (Advantech, Wisconsin, USA) to determine presence of close-to-the-surface fine charcoal

121 particulate matter symptomatic of recalcitrant pyrogenic material at all four sites.

122

123 *Leaf Traits*

124 Maximizing seasonal data relative to active growth during the driest months of the summer was achieved

125 by obtaining C isotopic data ($\delta^{13}C$) and N isotopic data ($\delta^{15}N$) of fully expanded leaves (needle cluster) of

126 15 individuals at each site. All individuals selected had stem diameter of the bole at breast height (DBH)

127 greater than 13 cm. Sample fascicles (one per tree) were separated and dried for two days at 60 °C ground

128 in a SPEX ball mill (Metuchen, NJ, USA), weighed to +/- 2 mg for leaf tissue and +/- 5 mg for soil using

129 a Cole-Palmer (Vernon Hills, IL, USA) micro analytic balance and rolled in Costech (Valencia, CA,

130 USA) 5 x 9 mm tin capsules. A Thermo Delta (Waltham, MA, USA) V+ IR-MS continuous flow isotope

131 ratio mass spectrometer with a universal triple collector was used. Combustion gasses were separated on a

132 gas chromatograph column, passed through a diluter and reference gas box, and introduced into the

133 spectrometer. $\delta^{13}C$ was used to indicate water use efficiency (iWUE$_{\delta^{13}C}$) (Farquhar et al. 1989). Leaf

134 tissue was obtained from excision of basal fascicle bundles at 1.06 m. 50 mL samples of needles were

135 separated, cut and dried for two days at 60 °C. Then they were ground in a SPEX ball mill (Metuchen, NJ,

136   USA), sieved to <10 mm, and <2 mL were fed to a Leco CN-2000 Carbon-Nitrogen Analyzer (Leco

137   Corp., St. Joseph, MI) coupled with the spectrometer to determine C and N concentrations. 35 mL

138   aliquots were submitted for standard plant tissue nutrient analysis using a TJA Model 975 AtomComp

139   ICP-AES (Thermo Jarrell-Ash Corp., Franklin, MA). The method comprised submersion in a 5 mL trace-

140   metal-grade HNO_3 treatment, then refluxed on hot block at 80 °C for two hours and diluted to 25 mL with

141   0.4 micron PTFE syringe filters to access extractable macro and micro inorganics.

142

143   *Plant-level Traits*

144   We measured individual tree height, stem diameter of the bole at breast height (DBH) and canopy spread.

145   Tree height was estimated using a plastic clinometer (Kager, Lunenberg, MA USA) and 30 m tape. DBH

146   was measured at 1.06 m using an expandable cloth measuring tape. Canopy spread across the first nodal

147   branch expanse below the crown was measured using calibration between two aluminum flags as a

148   ground truth reference. We measured from the first nodal branch expanse because crown shapes were

149   relatively consistent across sites at the first node. Mean distances between sampled trees were calculated

150   including up to five of the nearest, reproductively mature conspecific (within 5 m) neighbors (Churchill *et*

151   *al.* 2013)—this clustering method served as a surrogate, but inverse, measure for stand density (Mosseler

152   *et al*. 2004).

153

154   *Statistical Analysis*

155   All data were analyzed using a similar linear model structure with elevation as a continuous independent

156   factor (i.e., a covariate) and presence of the 1947 fire (yes or no) as a categorical independent factor (i.e.,

157   grouping factor). The interaction between elevation and presence of the 1947 fire was also included as an

158   independent factor in each model. Mathematically, this can be shown as:

159

160    $Y = \beta_0 + \beta_1(\text{elevation}) + \beta_2(\text{fire history}) + \beta_3(\text{elevation*fire history}) + \varepsilon$

161

162   where Y is the response variable, β_0 is the model intercept, β_1 is the slope of the effect of elevation (a

163   continuous variable or covariate), β_2 is the slope of the effect of fire history (a categorical or grouping

164   variable with two levels), β_3 is the slope of the interaction between elevation and fire history, and ε is an

165   error term. In total, 25 models were fit with the following dependent variables: tree height (m), canopy

166   spread (m), DBH (cm), mean distance between neighbors (m), foliar carbon (C, %), foliar nitrogen (N,

167   %), foliar C/N (unitless), foliar $\delta^{13}C$ (‰), foliar $\delta^{15}N$ (‰), foliar aluminum (Al^+, mg kg^{-1}), foliar calcium

168   (Ca^{2+}; mg kg^{-1}), foliar magnesium (Mg^{2+}; mg kg^{-1}), foliar phosphorus (P; mg kg^{-1}), foliar potassium (K^+;

169   mg kg^{-1}), foliar zinc (Zn; mg kg^{-1}), soil C (%), soil N (%), soil C/N (unitless), soil Al^+ (mg kg^{-1}), soil Ca^{2+}

170   (mg kg^{-1}), soil Mg^{2+} (mg kg^{-1}), soil P (mg kg^{-1}), soil K$^+$ (mg kg^{-1}), soil Zn (mg kg^{-1}), and soil water

171   retention (mg kg^{-1}). Tree height, canopy spread, DBH, foliar P, foliar K$^+$, foliar Zn and soil C/N were log

172   transformed to meet model assumptions of normality and heterogeneity of variances, while soil water

173   retention was arcsin square root transformed to meet model assumptions. All linear models were fit using

174   the 'lm' function in R (R Core Team 2019). Type II F-tests were used to determine the statistical

175   significance of each factor in each model using the 'Anova' function in the 'car' package in R (Fox and

176   Weisberg, 2019). Type II tests are robust to unbalanced designs (Langsrud 2003; Tab. S1). Slopes and

177   intercepts for plotting were determined using the 'emmeans' package in R (Lenth and Lenth 2018).

178   Because aspect data is circular in nature, we analyzed aspect data using a Watson's Two-Sample Test of

179   Homogeneity as implemented in the R package 'circular' (Agostinelli and Lund 2017). Specifically, one-

180   to-one comparisons were done between each site in all six possible combinations. All analyses were

181   performed with R version 4.0.5 (R Core Team 2019).

182

183   **Results**

184   *Topographical features*

185   Watson's two sample t-tests indicated that the individual aspects of all sites differed with respect to one

186   another except for the two sites that experienced the 1947 fire (Gorham cliffs and South Cadillac Trail),

187   which had similar aspects (Fig. S2 and Tab. 2). There was an interaction between slope and fire history

188   ($F_{1,56} = 108.1$, $P < 0.05$) that indicated that the slope was greater for individuals at the low elevation site

189   that experienced the 1947 fire (Gorham cliffs) than low elevation individuals that did not experience the

190   fire (Wonderland), with the reverse being true at high elevation (Table 1).

191

192   *Soil elements and water retention*

193   Soil C concentrations decreased with increasing elevation ($P < 0.05$), but were unaffected by fire history

194   or their interaction ($P > 0.05$ in all cases, Fig. 3 and Tab. 3). Soil N and C/N did not vary with elevation,

195   fire history, or their interaction ($P > 0.05$ in all cases, Fig. 3 and Tab. 3).

196

197   There was an interaction between elevation and fire history on soil water retention (SWR; $P < 0.01$, Fig. 3

198   and Tab. 3), driven by higher SWR at sites that experienced the 1947 fire at low elevation, an effect that

199   was diminished at higher elevations (Fig. 3).

200

201   There was an interaction between fire history and elevation ($P < 0.01$, Tab. 4) that indicated that soil Al$^+$

202   increased with elevation in sites that did not experience the 1947 fire and decreased with elevation at sites

203   that did experience the 1947 fire (Fig. 4). Soil Ca^{2+} decreased with elevation ($P < 0.05$, Fig. 4 and Tab. 4),

204   regardless of fire history. Fire accounted for a 48% reduction in K^+ at fire-experienced sites ($P < 0.05$,

205   Fig. 4 and Tab. 4), regardless of elevation. Soil P, Mg^{2+}, and Zn did not vary with elevation, fire history,

206   or their interaction (Tab. 4).

207

208   *Leaf isotopes and elements*

209   Trees at higher elevations experienced less negative $\delta^{13}C$ ($P < 0.01$, Fig. 5 and Tab. 5), reflecting greater

210   water use efficiency, regardless of fire history. There were no significant effect of fire history, elevation,

211   or their interaction on $\delta^{15}N$ ($P > 0.05$ in all cases, Fig. 5 and Tab. 5).

212

213   Foliar C was greater in trees at sites that experienced the 1947 fire ($P < 0.05$, Fig. 5 and Tab. 5),

214   regardless of elevation; however there was no effect of fire history, elevation, or their interaction on foliar

215   N or C/N ($P > 0.05$ in all cases, Fig. 5 and Tab. 5).

216

217   Foliar Ca^{2+} was negatively impacted by increasing elevation ($P < 0.001$, Fig. 6 and Tab. 6), regardless of

218   fire history. Our model indicated that foliar P was significantly higher at fire-involved sites ($P < 0.01$, Fig.

219   6 and Tab. 6), regardless of fire history. Foliar K^+ was reduced by fire involvement at high elevations, but

220   not low elevations (elevation x fire: $P < 0.05$, Fig. 6 and Tab. 6). Neither foliar Al^+ nor Mg^{2+} differed by

221   fire history, elevation, or their interaction ($P > 0.05$ in all cases; Fig. 6 and Tab. 6). Foliar Zn

222   concentrations decreased with increasing elevation ($P < 0.01$, Fig. 6 and Tab. 6), regardless of fire

223   history.

224

225   *Plant-level traits*

226   There was a significant interaction between fire and elevation on tree height ($P < 0.01$, Tab. 7), which

227   indicated that historical fire presence had a negative impact on tree height at high, but not low, elevation

228   (Fig. 7). Increasing elevation reduced DBH ($P < 0.001$; Fig. 7 and Tab. 7), regardless of fire history.

229   Canopy spread was reduced at high elevation ($P < 0.01$, Fig. 7 and Tab. 7), regardless of fire history.

230   Distance between neighbors was greater at high elevation sites ($P < 0.001$, Fig. 7 and Tab. 7), regardless

231   of fire history.

232

233   **Discussion**

234   *Soil characteristics*

235   Soil fertility and water retention varied across our environmental gradient. We were curious about the

236   influence of subsurface charcoal as a soil component in fire-exposed areas. At nearby, burned-over

237   Cadillac Brook, below the heights of South Cadillac trail, earlier paleo (Lafon *et al.* 2014) and fossil

238   indicator reports (Patterson *et al.* 1987; Verma and Jayakumar 2012) underscore the presence of charcoal.

239   However, there were no significant changes in soil C with fire history, although there was a reduction at

240   higher elevations. The reduction in soil C also coincided with a reduction in soil Ca^{2+} and, at fire exposed

241   sites, soil Al^+ at high elevations. Further studies at more sites that track environmental variables across the

242   elevational gradient at Mt. Desert Island would be useful for helping to understand the mechanisms

243   driving this variation.

244

245   Patel *et al.* (2019) studied soil N in several watersheds (drainages) below South Cadillac trail, at low to

246   mid-elevation, to determine recalcitrant atmospheric deposition since the 1947 fire. Since fire is known to

247   increase N losses there was an expectation of lower nitrogen at sites closer to the most intense burns, but

248   they found no evidence for this (Patel *et al.* 2019). These are consistent with our findings. Fire also did

249   not significantly influence any of the other soil nutrients we measured, despite strong topographical

250   differences.

251

252   A previous pine barren study reported that pyrolysis (either natural or anthropogenic) increased SWR

253   (Licht and Smith 2020) and we found support for this at low elevations at Mt. Desert. Interestingly, this

254   occurred despite steeper slopes at one ledge site that experienced fire at low elevation, which we would

255   have expected to reduce SWR.

256

257   *Leaf traits*

258   Intrinsic water use efficiency, indicated by $\delta^{13}C$, has been shown to increase in the presence of pyrolytic

259   soil (Licht and Smith 2020). However, we found no effect of the 1947 fire on this trait. Instead, $\delta^{13}C$ (and,

260   thus water use efficiency) increased with elevation, supporting previous findings (Wang *et al.* 2017; Chen

261   *et al.* 2017, Körner *et al.* 1986; Friend *et al.* 1989; Bresson *et al.* 2009). At Mt. Desert, where elevation

262   gradients are a significant feature of the landscape, this response is indicative of plant stress tolerance

263   response (to higher wind turbulence, low pressure, and more quickly drying soils) as a feature of upper

264   elevation life (Wang *et al.* 2017).

265

266   We expected that an increase in elevation would drive increases in leaf nutrients, particularly leaf N, to

267   support high elevation photosynthesis at low stomatal conductance, as has been shown and is expected

268   from physiological theory (Wang *et al.* 2017). This was not the case. A reduction in some soil nutrients

269   (e.g., Ca^{2+}) may have played a role in this (Firn *et al.* 2019), but may also have been the effect of non-

270   measured variables, such as nutrient mineralization.

271

272   Despite a lack of soil nutrient responses, we found that fire involvement significant increased foliar P,

273   possibly as the result of greater P availability. However, this was not consistent with our soil analysis.

274   Further studies are needed to understand the connection between fire involvement, topography, soil

275   nutrients, and foliar nutrients at Mt. Desert Island. A closer examination of fungal processes (such as

276   those conducted by Luo *et al*. 2017 following prescribed burns in New Jersey) may yield clearer findings

277   (Dove and Hart 2017) necessary to understand the influence of mycorrhizae on pitch pine in disjunct

278   populations where glaciated soils prevail.

279

280   *Plant-level traits*

281   Elevation was the primary driver of plant traits, resulting in smaller, less clustered trees at high versus low

282   elevation. Interestingly, there was relatively little difference in these responses with fire involvement,

283   which we expected to reduce clustering and tree size regardless of elevation due to effects on tree age.

284   Tree cores taken near the sites we used suggest that trees located at sites outside of 1947 fire are likely 15-

285   30 years older than trees withing the 1947 fire zone (Patterson *et al.* 2016). As such, we expected older

286   and larger individuals at sites that did not experience the 1947 fire. In fact, this lack of difference may be

287   an indicator of stimulation of pitch pine growth after fire, for instance as a result of reduced competition

288   (Jordan *et al.* 2003). This might suggest that a shift back could further spur dispersal, but, despite a

289   significant fuel buildup in the forests on the island, this would require a change in current management

290   policy. Coupled with climate projections (Fernandez *et al.* 2015), we can predict potential ledge

291   population enlargement is unlikely to occur as a function of anthropogenic intervention. Nonetheless, our

292   findings in non-fire involved sites suggest that pitch pine can persist in the absence of fire. However,

293   further studies are needed to examine how long this will last.

294

295   *Disturbance, climate factors and predictions for species status*

296   Until now, disturbances such as mechanical thinning and bioturbation (Abney *et al.* 2019), disease such

297   as *Ploioderma lethale* (needle cast; Little and Garrett 1990), deer browsing and rodent damage (Ledig *et*

298   *al.* 2013), and insect herbivory (Lesk *et al.* 2017) have not impacted management at Mt. Desert Island as

299   in barren islands elsewhere. Yet, a possibly catastrophic problem may occur due to a combination of a

300   prolonged fire interval and increases in annual winter temperatures (Lesk *et al.* 2017)—namely the

301   potential invasion within the next decade of an herbivore, Southern pine beetle (*Dendroctonus frontalis* or

302   'SPB'). This herbivore has already paid a deadly visit to New Jersey and Long Island NY (Dodds *et al.*

303   2018). Unless its progress is deterred by predators like double checkered clerid (*Thanasimus dubius*;

304   Coulson and Klepzig 2011), or some undetermined climate factor, pitch pines, along with understory

305   plants, butterflies and moth members of the Acadia ecosystem, are vulnerable to predation (Lesk *et al.*

306   2017).

307

308   It is no doubt that a warming climate is having the greatest impact on island vegetative prospects,

309   including the fortunes of pitch pine. Models project a negative impact on future vegetative status at Mt.

310   Desert Island (Fernandez *et al.* 2015; Swanston *et al*. 2018). According to several studies (Day *et al*.

311   2005; Lee *et al*. 2019) warming climate impacts habitat suitability and pitch pine tendencies to

312   consolidate, regenerate, or migrate. What has been clear for almost three decades is the effect of global

313   climate change on physiological traits. Day *et al*. (2001) found an uptick in annual temperatures signaled

314   increased leaf-air vapor pressure deficits that negatively impacted pitch pine stomatal conductance and

315   limited gas exchange. In a related report, scientists found warming trends (Kunkel *et al* 2013) increased

316   pitch pine reproductive difficulties (Ledig *et al*. 2015). These trends include weather-related effects such

317   as episodic drought, harsh winds, and salt spray (Fernandez *et al.* 2015) as well as increased cold

318   intolerance (Steiner and Berrang 1990). What is not clear is the extent to which tree plasticity (Day *et al.*

319   2014) will be shaped by a continuing rise in warming temperatures. What appears to be more certain is

320   the prediction that pitch pine colonies will suffer due to a combination of diminished open space capacity,

321   loss of enriched substrates and elimination of suitable habitats (Day *et al.* 2005). Our study indicates that

322   pitch pine physiology may be more flexible than previously thought, as we find trait shifts and population

323   persistence along a large topographical gradient. However, global changes are likely to present these

324   populations with novel conditions that may override this flexibility. Future monitoring, manipulative, and

325   modeling studies will be critical to ensure the future persistence of this important species.

326

327 **Table 1.** Mean topographic features for individuals at each site.

Site	1947 Fire	Type	Latitude (°)	Longitude (°)	Elevation (m)	Slope (°)	Aspect (°)	Compass
Gorham Cliffs	Yes	Cliff	44.328	-68.185	31.7	31.9	151.5	SE
South Cadillac	Yes	Ledge	44.333	-68.224	284.0	9.4	138.1	SE
St. Sauveur	No	Cliff/Ledge	44.311	-68.326	182.0	13.3	262.6	W
Wonderland	No	Flat/Hilly	44.237	-68.316	16.3	3.7	208.1	S

328
329
330 **Table 2.** Watson's Two Sample Test of Homogeneity results for aspect at each site.*

	Gorham Cliffs	St. Sauveur	South Cadillac
Wonderland	t = 0.259 *	t = 0.288 **	t = 0.194 *
Gorham cliffs		t = 0.385 **	t = 0.166 *ns*
St. Sauveur			t = 0.519 ***

331 *Key: t = test statistic, *ns* = not significant, * = P < 0.05, ** = P < 0.01, *** = P < 0.001, P = P-value.
332
333
334 **Table 3.** Analysis of variance results for the linear models with soil carbon (C), nitrogen (N), and C/N, and soil water retention (SWR).*

	Soil C			Soil N			Soil C/N			SWR		
	df	F	P	df	F	P	df	F	P	df	F	P
Elevation	1	4.675	**0.040**	1	0.190	0.667	1	3.853	*0.062*	1	2.503	0.122
Fire	1	2.718	0.111	1	0.260	0.615	1	1.493	0.235	1	12.400	**0.001**
Elevation x Fire	1	0.404	0.530	1	1.153	0.295	1	2.771	0.110	1	12.981	**0.001**
Residuals	27			22			22			36		

335 * P-values < 0.05 are bolded. Sample sizes for each variable can be found in Table S1. Elevation in the model was a continuous variable (i.e., covariate) and fire
336 was a categorical variable (i.e., grouping variable) with two levels (exposure to 1947 fire and no exposure to 1947 fire). Key: df = degrees of freedom, F = F-
337 value, P = P-value.
338
339
340

341 **Table 4.** Analysis of variance results for the linear models with soil aluminum (Al$^+$), calcium (Ca^{2+}), potassium (K$^+$), magnesium (Mg^{2+}), phosphorus (P), and
342 zinc (Zn).*

	df	Soil Al$^+$ F	Soil Al$^+$ P	Soil Ca^{2+} F	Soil Ca^{2+} P	Soil K$^+$ F	Soil K$^+$ P	Soil Mg^{2+} F	Soil Mg^{2+} P	Soil P F	Soil P P	Soil Zn F	Soil Zn P
Elevation	1	1.342	0.257	6.729	**0.015**	2.284	0.142	2.525	0.124	2.829	0.104	2.079	0.161
Fire	1	0.032	0.860	0.041	0.840	6.664	**0.016**	0.254	0.618	1.015	0.323	0.082	0.776
Elevation x Fire	1	7.851	**0.009**	0.135	0.716	0.100	0.755	0.224	0.640	0.065	0.801	2.883	0.101
Residuals	27												

343 * P-values < 0.05 are bolded and < 0.1 are italicized. Sample sizes for each variable can be found in Table S1. Elevation in the model was a continuous variable
344 (i.e., covariate) and fire was a categorical variable (i.e., grouping variable) with two levels (exposure to 1947 fire and no exposure to 1947 fire). Key: df =
345 degrees of freedom, F = F-value, P = P-value.
346
347 **Table 5.** Analysis of variance results for the linear models with foliar δ^{13}C and δ^{15}N, carbon (C), nitrogen (N), and C/N.*

	δ^{13}C df	δ^{13}C F	δ^{13}C P	δ^{15}N df	δ^{15}N F	δ^{15}N P	Foliar C df	Foliar C F	Foliar C P	Foliar N df	Foliar N F	Foliar N P	Foliar C/N df	Foliar C/N F	Foliar C/N P
Elevation	1	9.786	**0.003**	1	0.787	0.379	1	0.148	0.702	1	0.983	0.326	1	1.639	0.206
Fire	1	1.369	0.247	1	2.857	*0.097*	1	4.053	**0.049**	1	1.156	0.287	1	0.425	0.517
Elevation x Fire	1	0.227	0.636	1	1.831	0.182	1	0.001	0.981	1	1.020	0.317	1	1.707	0.197
Residuals	51			51			56			52			52		

348 * P-values < 0.05 are bolded and < 0.1 are italicized. Sample sizes for each variable can be found in Table S1. Elevation in the model was a continuous variable
349 (i.e., covariate) and fire was a categorical variable (i.e., grouping variable) with two levels (exposure to 1947 fire and no exposure to 1947 fire). Key: df =
350 degrees of freedom, F = F-value, P = P-value.
351
352 **Table 6.** Analysis of variance results for the linear models with foliar aluminum (Al$^+$), calcium (Ca^{2+}), potassium (K$^+$), magnesium (Mg^{2+}), phosphorus (P), and
353 zinc (Zn).*

	df	Foliar Al$^+$ F	Foliar Al$^+$ P	Foliar Ca^{2+} F	Foliar Ca^{2+} P	Foliar K$^+$ F	Foliar K$^+$ P	Foliar Mg^{2+} F	Foliar Mg^{2+} P	Foliar P F	Foliar P P	Foliar Zn F	Foliar Zn P
Elevation	1	0.341	0.563	13.302	**0.001**	3.158	*0.084*	2.557	0.119	0.012	0.914	8.007	**0.008**
Fire	1	0.021	0.887	0.843	0.365	4.071	*0.051*	0.507	0.481	8.309	**0.007**	0.050	0.824
Elevation x Fire	1	0.187	0.668	0.088	0.769	4.863	0.034	0.377	0.543	0.407	0.527	1.458	0.235
Residuals	36												

354 * P-values < 0.05 are bolded and < 0.1 are italicized. Sample sizes for each variable can be found in Table S1. Elevation in the model was a continuous variable
355 (i.e., covariate) and fire was a categorical variable (i.e., grouping variable) with two levels (exposure to 1947 fire and no exposure to 1947 fire). Key: df =
356 degrees of freedom, F = F-value, P = P-value.

357
358 **Table 7.** Analysis of variance results for the linear models with slope, tree height, canopy spread, diameter at breast height (DBH), and distance between
359 neighbors.*

	Canopy Spread			DBH			Distance Between Neighbors			Tree Height		
	df	F	P	df	F	P	df	F	P	df	F	P
Elevation	1	7.948	**0.008**	1	13.724	**0.001**	1	21.148	**<0.001**	1	3.451	*0.071*
Fire	1	0.012	0.914	1	1.100	0.301	1	1.418	0.248	1	0.097	0.757
Elevation x Fire	1	0.068	0.795	1	3.022	*0.091*	1	0.468	0.502	1	6.593	**0.015**
Residuals	*36*			*36*			*20*			*36*		

360 * P-values < 0.05 are bolded and < 0.1 are italicized. Sample sizes for each variable can be found in Table S1. Elevation in the model was a continuous variable
361 (i.e., covariate) and fire was a categorical variable (i.e., grouping variable) with two levels (exposure to 1947 fire and no exposure to 1947 fire). Key: df =
362 degrees of freedom, F = F-value, P = P-value, DBH = diameter at breast height.
363

Figure legends

Figure 1. Location of pitch pine populations on Mt. Desert Island used in this study. "H" and "L" indicate high and low elevation populations, respectively, within (orange) and outside (green) the 1947 fire extent. More information about the populations can be found in Table 1.

Figure 2. Topographical maps showing the location of pitch pine individuals (blue dots) within each studied population on Mt. Desert Island. Areas in orange represent areas exposed to the 1947 fire.

Figure 3. Relationship between elevation and soil carbon (A), soil nitrogen (B), soil carbon/nitrogen (C) and soil water retention (D). Color of points and trendlines indicates the fire history with red and blue indicating exposure and no exposure to the 1947 fire, respectively. The trendlines indicate the modeled responses from the linear regression models. Only significant ($P < 0.05$ trends are shown. Black lines indicate relationships that are similar across fire history groups and blue and red lines indicate a difference in trends between fire history groups. Stars, triangles, diamonds, and squares correspond to measurements at Gorham Cliffs (GOR), South Cadillac (SCT), St. Sauveur (STS), and Wonderland (WON), respectively (Table 1).

Figure 4. Relationship between elevation and soil aluminum (A), calcium (B), potassium (C), magnesium (D), phosphorus (E), and zinc (F). Color of points and trendlines indicates the fire history with red and blue indicating exposure and no exposure to the 1947 fire, respectively. The trendlines indicate the modeled responses from the linear regression models. Only significant ($P < 0.05$ trends are shown. Black lines indicate relationships that are similar across fire history groups and blue and red lines indicate a difference in trends between fire history groups. Stars, triangles, diamonds, and squares correspond to measurements at Gorham Cliffs (GOR), South Cadillac (SCT), St. Sauveur (STS), and Wonderland (WON), respectively (Table 1).

Figure 5. Relationship between elevation and $\delta^{13}C$ (A) and $\delta^{15}N$ (B), foliar carbon (C), foliar nitrogen (D), and foliar carbon/nitrogen (E). Color of points and trendlines indicates the fire history with red and blue indicating exposure and no exposure to the 1947 fire, respectively. The trendlines indicate the modeled responses from the linear regression models. Only significant ($P < 0.05$ trends are shown. Black lines indicate relationships that are similar across fire history groups and blue and red lines indicate a difference in trends between fire history groups. Stars, triangles, diamonds, and squares correspond to measurements at Gorham Cliffs (GOR), South Cadillac (SCT), St. Sauveur (STS), and Wonderland (WON), respectively (Table 1).

398

399 **Figure 6.** Relationship between elevation and foliar aluminum (A), calcium (B), potassium (C),
400 magnesium (D), phosphorus (E), and zinc (F). Color of points and trendlines indicates the fire history
401 with red and blue indicating exposure and no exposure to the 1947 fire, respectively. The trendlines
402 indicate the modeled responses from the linear regression models. Only significant ($P < 0.05$ trends are
403 shown. Black lines indicate relationships that are similar across fire history groups and blue and red lines
404 indicate a difference in trends between fire history groups. Stars, triangles, diamonds, and squares
405 correspond to measurements at Gorham Cliffs (GOR), South Cadillac (SCT), St. Sauveur (STS), and
406 Wonderland (WON), respectively (Table 1).

407

408 **Figure 7.** Relationship between elevation and canopy spread (A), diameter at breast height (DBH; B),
409 distance between neighbors (C), and tree height (D). Color of points and trendlines indicates the fire
410 history with red and blue indicating exposure and no exposure to the 1947 fire, respectively. The
411 trendlines indicate the modeled responses from the linear regression models. Only significant ($P < 0.05$
412 trends are shown. Black lines indicate relationships that are similar across fire history groups and blue and
413 red lines indicate a difference in trends between fire history groups. Stars, triangles, diamonds, and
414 squares correspond to measurements at Gorham Cliffs (GOR), South Cadillac (SCT), St. Sauveur (STS),
415 and Wonderland (WON), respectively (Table 1).

416

417 **Data availability statement**
418 Data used in this article can be found at the following repository:
419 https://github.com/SmithEcophysLab/mtDesertIsland_Pinusrigida (DOI: 10.5281/zenodo.4663255).

420

421 **Author contributions**
422 JL and NGS conceived the work. JL, RM, and NGS contributed substantially to the interpretation of the
423 data and to drafting the manuscript, gave final approval of the version submitted, and agreed to be
424 accountable for all aspects of the work. Questions related to the accuracy or integrity of any part of the
425 work are appropriately investigated and resolved. JL carried out sample collection and field
426 measurements, conducted soil water retention tests and prepared samples for EA-IRMS analysis. NS
427 performed C/N foliar analysis. NGS and RM conducted statistical analyses and formulated figures and
428 tables.

429

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