1 **Title Page**

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

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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 Pitch pine (*Pinus rigida*) is an evergreen 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 on the island have been unaffected by fire disturbance for over one

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

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

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

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

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

26 to 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. We anticipate pitch pine may

29 have the capacity to thrive across a wider array of environments although increasing summer and winter

30 warmth coupled with heightened moisture may limit persistence on the island. Our findings may be

31 applicable to other populations where fire is absent and where topography plays a similar role as it does

32 on Mt. Desert Island.

33

34 **Introduction**

On Mt. Desert Island at Acadia National Park in Maine USA, pitch pine (*Pinus rigida* Miller), the most northerly member of the southern yellow pines (Plain *et al*. 1987), dwell at the edge of their northeastern range (Fig. 1). Over millennia, pitch pine persistence (ability to remain in a particular setting) is defined by frequent fire disturbance that regulates competition, removes post-fire pyrogenic carbon (C) from the soil and drives the radiation of fire adaptations. Among the most significant fire adaptations are serotinous cones (which typically open only when fire engulfs the tree), thickened bark to withstand scorching, and epicormic sprouting along branches and trunk (Little 1953). On Mt. Desert in 1947 an intense October fire started in a dump just west of Bar Harbor, on the east side of the island that persisted for nearly two weeks (Fig. 1; Pyne 2019). Since that time, fire suppression has been used to avoid a repetition of the consequences from that fire. In ensuing decades, tree pyrogenic traits have been decreasingly observed (e.g., cone serotiny (Conkey *et al*. 1995; Jordan *et al*. 2003)). As there is less pressure to produce seeds that survive in the midst of a fire (Givnish 1981), there may also be less need for thick bark or epicormic sprouting (Renninger *et al*. 2013). Past studies have speculated that tree defenses are shifting from fire resiliency to traits that may help deal with other abiotic conditions such as warmer temperatures and increasing summer drought (Day *et al.* 2005; Buma *et al.* 2013). As a further sign of a shift away from a pyrolytic past, many pitch pine enclaves on the island anchor desertified communities highlighted by flora not necessarily associated with fire adaptation including *Sibbaldiopsis tridentata*, *Empetrum nigrum*, *Kalmia angustifolia*, *Hypercium perforatum,* and *Campanula rotundifolia.*

Recent history of pitch pine population success in fire-suppressed locations such as Mt. Desert Island defies a theory that fire (natural or prescribed) is likely a requirement every six to twenty-five years for pine barren well-being (Jordan *et al*. 2003). While fire responses have been studied previously (Foereid *et al.* 2015; Carlo *et al.* 2016; Neill *et al.* 2007), there is a critical need to understand other factors that might be influencing pitch pine persistence in the absence of fire at Mt. Desert Island.

Here, we address one such factor, topography, that has not yet been thoroughly assessed at Mt. Desert in comparison with fire history (Parshall and Foster 2002; Fig. 2). Specifically, we use four populations that lie along a graduated topographical and fire history gradient (Fig. S1) as proxies for more than a dozen other colonies, to examine the effects of elevation, aspect and slope (Bolstad and Stowe 1994) on soil, leaf, and plant-level traits. The four populations were chosen to represent a factorial combination of elevation (high or low) and fire history (having experienced the 1947 stand-clearing fire or not). First, we characterize differences in topographical features such as elevation; in addition, we probe slope and aspect data, given that these are likely important non-elevation topographical drivers of the traits examined (Howard and Stelacio 2011; Hanson 2017; Nowacki and Abrams 2008). We then explore

69 aspects of the soil environment, including soil carbon as well as macro and micro nutrient concentrations.

70 Following previous studies, we expected to find less soil carbon (DeBano 1998), greater alkali cations

71 (Certini 2005) and increased solubilized minerals (Caldwell and Richards 1989) in soils which

72 experienced the 1947 fire. We predicted that there would be greater soil carbon at low elevations due to

73 thermal exfoliation (as explained by Shakesby and Doerr 2006) or a failure of fire to remove pyrogenic

74 carbon in former fire zones (Doerr *et al.* 2018). We also measured soil water retention, which we

75 expected to be greater at sites that experienced the 1947 fire, as pyrogenic carbon is known to increase

76 soil water retention (Licht and Smith, 2020). Beyond that, we anticipated higher soil water retention at

77 low elevations due to flat terrain (alleviating erosion mechanics).

78

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

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

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

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

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

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

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

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

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

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

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

90 beneficial if higher elevation sites were less fertile.

91

92 **Methods**

93 *Study sites*

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

95 S1) as independent replicates, using a combination of systematic and cluster sampling methods with non-

96 fixed intervals between trees (1m to 4m) and non-fixed directionality (employing nine compass points).

97 The four populations of trees were factorially crossed in a fire history (Miller *et al.* 2017) by elevation

98 design: (1) Wonderland trail at an average of 17.83 m elevation (low elevation, outside the footprint of

99 the 1947 fire), (2) Gorham cliffs at an average of 32.95 m (low elevation, within the footprint), (3) St.

100 Sauveur trail at an average of 171.72 m (high elevation, outside the footprint) and (4) South Cadillac trail

101 at an average of 279.95 m (high elevation within the footprint). We found a funnel-like effect at St.

102 Sauveur and South Cadillac trail transects where larger clusters of pitch pine at lower elevation gave way

3

103 rapidly to much smaller groupings at higher elevation. While no coring was used to a determine a
104 dendrological metric for each cohort, we noted similarities in tree height and dbh, especially in fire-
105 present precincts (Gorham Cliffs and South Cadillac Trail), which underscored assumptions about similar
106 ages amongst the post-fire samples. Soils at all four sites were overlain with rapidly drying needle duff,
107 porous, and comprised of acidic hornblende granite or Ellsworth schist (Day *et al.* 2005). In addition they
108 were uniformly shallow (varying between 0.7-2.5 cm), homogeneous, and low in fertility (Butak 2014).
109 In some cases, sampling was limited by time, weather and site access yielding uneven sample
110 accumulations (see sample size for each measured variable in Tab. S1). Our analytical methods were
111 designed to deal with uneven sample sizes (see Statistical Analysis section below).
112
113 *Topographic features*
114 A Kodak Trimble Juno 3B was used to obtain horizontal resolution of data plotted using between five and
115 seven satellite telecommunication vehicles to maintain a maximum Position Dilution of Precision. These
116 data were differentially corrected and have estimated accuracies in the horizontal and vertical direction of
117 2m, while selective availability was set to zero. Multiple satellite-configured GPS data (USGS 2m
118 LIDAR 2010) determined coordinates for individual trees (Lubinski *et al*. 2003) as well as slope and
119 aspect attributes using ArcGIS (version 10). Mapping of this type of data has been used in the past to
120 compare physiography and recalcitrant chemical biogeography, particularly in fire prone contexts
121 (Kolden and Weisberg 2007; Szpakowski and Jensen 2019).
122
123 *Soil Elements and Water Retention (SWR)*
124 Soils were excavated by hand trowel and soil probe (Accuproducts, Saline, MI, USA); soil C, N and C/N
125 were calculated from elemental analysis. 70 mL soil samples were extracted at fifteen tree locations at
126 four sites, from <10.5 cm (O_a-A_b) horizon above bedrock. In a laboratory 50 g H_2O were added to each
127 aliquot to assess net water retention as a subset of soil moisture evaporation (ψ_g) to determine net
128 evaporative loss or adsorption to surfaces. Soil water retention analysis was conducted according to the
129 Fields method (Licht and Smith 2018). Retention effects of gravitational and evaporation forces was
130 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
131 mesh sieves (Advantech, Wisconsin, USA) to determine presence of close-to-the-surface fine charcoal
132 particulate matter symptomatic of recalcitrant pyrogenic material at all four sites.
133
134 *Leaf Traits*
135 Maximizing seasonal data relative to active growth during the driest months of the summer was achieved
136 by obtaining C isotopic data ($\delta^{13}C$) and N isotopic data ($\delta^{15}N$) of fully expanded leaves (needle cluster) of

137   15 individuals at each site. All individuals selected had stem diameter of the bole at breast height (DBH)

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

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

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

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

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

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

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

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

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

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

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

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

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

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

152   0.4 micron PTFE syringe filters to access extractable macro and micro inorganics.

153

154   *Plant-level Traits*

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

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

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

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

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

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

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

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

163   *et al*. 2004).

164

165   *Statistical Analysis*

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

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

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

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

170

171    $Y = \beta_0 + \beta_1(\text{elevation}) + \beta_2(\text{fire history}) + \beta_3(\text{elevation*fire history}) + \varepsilon$ (Eqn. 1)

172

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

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

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

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

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

178   %), foliar C/N (unitless), foliar δ^{13}C (‰), foliar δ^{15}N (‰), foliar aluminum (Al^+, mg kg^{-1}), foliar calcium

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

180   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+}

181   (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

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

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

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

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

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

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

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

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

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

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

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

193

194   **Results**

195   *Topographical features*

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

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

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

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

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

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

202

203   *Soil elements and water retention*

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

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

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

207

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

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

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

211

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

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

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

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

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

217   or their interaction (Tab. 4).

218

219   *Leaf isotopes and elements*

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

221   water use efficiency, regardless of fire history. There was no significant effect of fire history, elevation, or

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

223

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

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

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

227

228   Foliar Ca^{2+} was negatively correlated with elevation ($P < 0.001$, Fig. 6 and Tab. 6), regardless of fire

229   history. Our model indicated that foliar P was significantly higher at fire-involved sites ($P < 0.01$, Fig. 6

230   and Tab. 6), regardless of fire history. Foliar K^+ was lower at fire involved sites at high elevations, but not

231   low elevations (elevation x fire: $P < 0.05$, Fig. 6 and Tab. 6). Neither foliar Al^+ nor Mg^{2+} differed by fire

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

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

234

235   *Plant-level traits*

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

237   indicated that historical fire presence correlated with shorter trees at high, but not low, elevation (Fig. 7).

238 As elevation increased DBH was smaller (P < 0.001; Fig. 7 and Tab. 7), regardless of fire history. Canopy
239 spread was negatively correlated with elevation ($P < 0.01$, Fig. 7 and Tab. 7), regardless of fire history.
240 Distance between neighbors was greater at high elevation sites ($P < 0.001$, Fig. 7 and Tab. 7), regardless
241 of fire history.
242
243 **Discussion**
244 *Soil characteristics*
245 Soil fertility and water retention varied across our environmental gradient. We were curious about the
246 influence of subsurface charcoal as a soil component in fire-exposed areas. At nearby, burned-over
247 Cadillac Brook, below the heights of South Cadillac trail, earlier paleo (Lafon *et al.* 2014) and fossil
248 indicator reports (Patterson *et al.* 1987; Verma and Jayakumar 2012) underscore the presence of charcoal.
249 In our exploration for charcoal remnants, we found a small amount (<2mL) of charcoal fines (passing
250 through .25 mm sieve) across South Cadillac trail and none at the other three sites. This may explain the
251 lack of significant changes in soil C with fire history. However, there was a reduction in soil C with
252 increasing elevation. The reduction in soil C also coincided with a reduction in soil Ca^{2+} and, at fire
253 exposed sites, soil Al^+ at high elevations. Further studies at more sites that track environmental variables
254 across the elevational gradient at Mt. Desert Island (such as at Norumbega mountain, Champlain
255 mountain and the Precipice trailhead) would be useful in helping to understand the mechanisms driving
256 this variation.
257
258 Patel *et al.* (2019) studied soil N in several watersheds (drainages) below South Cadillac trail, at low to
259 mid-elevation, to determine recalcitrant atmospheric deposition since the 1947 fire. Since fire is known to
260 increase N losses there was an expectation of lower nitrogen at sites closer to the most intense burns, but
261 they found no evidence for this (Patel *et al.* 2019). These are consistent with our findings. Fire also did
262 not significantly influence any of the other soil nutrients we measured, despite strong topographical
263 differences.
264
265 A previous pine barren study reported that pyrolysis (either natural or anthropogenic) increased SWR
266 (Licht and Smith 2020) and we found support for this at low elevations at Mt. Desert. Interestingly, this
267 occurred despite steeper slopes at one ledge site that experienced fire at low elevation, which we would
268 have expected to reduce SWR.
269
270 While it is difficult to tease out the role of soil fertility in driving pine persistence with our data, the
271 relative lack of responsiveness to fire history might point to an increased role of soil fertility in driving

272 pitch pine persistence on Mt. Desert Island relative to other, more fire prone areas. Pitch pine is known to

273 be competitive in poor soils (Copenheaver *et al.* 2000). Further, cross-site evaluations would be helpful in

274 elucidating the relative role of fire and soil fertility in driving pitch pine persistence.

275

276 *Leaf traits*

277 Intrinsic water use efficiency, indicated by δ^{13}C, has been shown to increase in the presence of pyrolytic

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

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

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

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

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

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

284

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

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

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

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

289 measured variables, such as nutrient mineralization.

290

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

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

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

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

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

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

297 populations where glaciated soils prevail.

298

299 *Plant-level traits*

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

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

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

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

304 30 years older than trees withing the 1947 fire zone (Patterson *et al.* 2016). As such, we expected older

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

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

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

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

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

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

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

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

313

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

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

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

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

318   in barrens elsewhere (e.g., Myles Standish Forest in Plymouth, MA). Yet, a problem may occur in the

319   future due to a combination of a prolonged fire interval and increases in annual winter temperatures (Lesk

320   *et al.* 2017)—namely the potential invasion within the next decade of an herbivore, Southern pine beetle

321   (*Dendroctonus frontalis* or 'SPB'). This herbivore has already paid a deadly visit to New Jersey and Long

322   Island NY (Dodds *et al.* 2018). Unless its progress is deterred by predators like double checkered clerid

323   (*Thanasimus dubius*; Coulson and Klepzig 2011) or cooler winter temperatures, pitch pines, along with

324   understory plants, butterflies and moth members of the Acadia ecosystem, are vulnerable to predation

325   (Lesk *et al.* 2017).

326

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

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

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

330   2005; Lee *et al*. 2019) warming climate impacts habitat suitability and pitch pine tendencies to

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

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

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

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

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

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

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

338   2014) will be shaped by a continuing rise in temperatures and summer moisture. What appears to be more

339   certain is the prediction that pitch pine colonies will suffer due to a combination of diminished open space

340   capacity, loss of enriched substrates and elimination of suitable habitats (Day *et al.* 2005). Our study

341   indicates that pitch pine physiology may be more flexible than previously thought, as we find trait shifts

342   and population persistence along a large topographical gradient. However, global changes are likely to

343   present these populations with novel conditions that may override this flexibility. Further monitoring,

344   manipulative, and modeling studies will be critical to ensure the future persistence of this important

345   species.

346

347 **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

348
349
350 **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 ***

351 *Key: t = test statistic, *ns* = not significant, * = P < 0.05, ** = P < 0.01, *** = P < 0.001, P = P-value.
352
353
354 **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		

355 * 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
356 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-
357 value, P = P-value.
358
359
360

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 zinc (Zn).*

	df	Soil Al^+		Soil Ca^{2+}		Soil K^+		Soil Mg^{2+}		Soil P		Soil Zn	
		F	P	F	P	F	P	F	P	F	P	F	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												

* 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 (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 = degrees of freedom, F = F-value, P = P-value.

Table 5. Analysis of variance results for the linear models with foliar $\delta^{13}C$ and $\delta^{15}N$, carbon (C), nitrogen (N), and C/N.*

	$\delta^{13}C$			$\delta^{15}N$			Foliar C			Foliar N			Foliar C/N		
	df	F	P	df	F	P	df	F	P	df	F	P	df	F	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		

* 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 (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 = degrees of freedom, F = F-value, P = P-value.

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 zinc (Zn).*

	df	Foliar Al^+		Foliar Ca^{2+}		Foliar K^+		Foliar Mg^{2+}		Foliar P		Foliar Zn	
		F	P	F	P	F	P	F	P	F	P	F	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												

* 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 (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 = degrees of freedom, F = F-value, P = P-value.

377

378 **Table 7.** Analysis of variance results for the linear models with slope, tree height, canopy spread, diameter at breast height (DBH), and distance between
379 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*		

380 * 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
381 (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 =
382 degrees of freedom, F = F-value, P = P-value, DBH = diameter at breast height.
383

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; black line: $y = 24.40 - 0.046x$), soil nitrogen (B), soil carbon/nitrogen (C) and soil water retention (D; red line: $y = sin(0.69 – 0.0006x)^2 * 100$, blue line: : $y = sin(0.47 + 0.0004x)^2 * 100$). 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; red line: $y = exp(5.21 – 0.003x)$, blue line: $y = exp(4.49 + 0.003x)$), calcium (B; black line: $y = 785.2 - 2.02x$), 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; black line: $y = -29.2 + 0.005x$) 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

418   squares correspond to measurements at Gorham Cliffs (GOR), South Cadillac (SCT), St. Sauveur (STS),

419   and Wonderland (WON), respectively (Table 1).

420

421   **Figure 6.** Relationship between elevation and foliar aluminum (A), calcium (B; black line: $y = 1822.8 -$

422    $4.23x$), potassium (C), magnesium (D), phosphorus (E), and zinc (F; black line: $y = 3.72 - 0.0016x$).

423   Color of points and trendlines indicates the fire history with red and blue indicating exposure and no

424   exposure to the 1947 fire, respectively. The trendlines indicate the modeled responses from the linear

425   regression models. Only significant ($P < 0.05$ trends are shown. Black lines indicate relationships that are

426   similar across fire history groups and blue and red lines indicate a difference in trends between fire

427   history groups. Stars, triangles, diamonds, and squares correspond to measurements at Gorham Cliffs

428   (GOR), South Cadillac (SCT), St. Sauveur (STS), and Wonderland (WON), respectively (Table 1).

429

430   **Figure 7.** Relationship between elevation and canopy spread (A; black line: $y = 1.27 - 0.0024x$), diameter

431   at breast height (DBH; B; black line: $y = \exp(3.17 - 0.0023x)$), distance between neighbors (C; black line:

432    $y = 2.93 + 0.0035x$), and tree height (D; red line: $y = \exp(1.67 - 0.0030x)$, blue line: $y = \exp(1.25 +$

433    $0.0013x)$). Color of points and trendlines indicates the fire history with red and blue indicating exposure

434   and no exposure to the 1947 fire, respectively. The trendlines indicate the modeled responses from the

435   linear regression models. Only significant ($P < 0.05$ trends are shown. Black lines indicate relationships

436   that are similar across fire history groups and blue and red lines indicate a difference in trends between

437   fire history groups. Stars, triangles, diamonds, and squares correspond to measurements at Gorham Cliffs

438   (GOR), South Cadillac (SCT), St. Sauveur (STS), and Wonderland (WON), respectively (Table 1).

439

440   **Data availability statement**

441   Data used in this article can be found at the following repository:

442   https://github.com/SmithEcophysLab/mtDesertIsland_Pinusrigida (DOI: 10.5281/zenodo.4663255).

443

444   **Author contributions**

445   JL and NGS conceived the work. JL, RM, and NGS contributed substantially to the interpretation of the

446   data and to drafting the manuscript, gave final approval of the version submitted, and agreed to be

447   accountable for all aspects of the work. Questions related to the accuracy or integrity of any part of the

448   work are appropriately investigated and resolved. JL carried out sample collection and field

449   measurements, conducted soil water retention tests and prepared samples for EA-IRMS analysis. NS

450   performed C/N foliar analysis. NGS and RM conducted statistical analyses and formulated figures and

451   tables.

452

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References

Abney, R., Kuhn, T., Chow, A., Hockaday, W., Fogel, M., and Berhe, A. (2019). Pyrogenic carbon erosion after the Rim Fire, Yosemite National Park: The role of burn severity and slope. *JGR Biogeosciences* 124, 432–449. doi: 10.1029/2018JG004787

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

Bolstad, P. and Stowe, T. (1994). An evaluation of DEM accuracy: elevation, slope, and aspect. *Photogrammetric Engineering & Remote Sensing*, *60*(11), 1327-1332.

Bresson, C., Kowalski, A., Kremer, A., and Delzon S. (2009). Evidence of altitudinal increase in photosynthetic capacity: gas exchange measurements at ambient and constant CO2 partial pressures. *Annals of Forest Science, 66*, 505–505. doi: 10.1051/forest/2009027

484 Buma, B., Brown, C., Donato, D., Fontaine, J., and Johnstone, J. (2013). The impacts of changing

485   disturbance regimes on serotinous plant populations and communities. *BioScience*, *63*(11), 866-876.

486   doi.org/10.1525/bio.2013.63.11.5

487 Butak, Amanda L. (2014). Vegetation Composition, Structure, and Ecophysiology of Maritime Ledge

488   Ecosystems. *Dissertation/Master's Thesis*. Orono (ME): University of Maine.

489   https://digitalcommons.library.umaine.edu/etd/2212

490 Caldwell, M. and J. Richards. (1989). Hydraulic lift: water efflux from upper roots improves effectiveness

491   of water uptake by deep roots. *Oecologia, 79*, 1-5. doi.org/10.1007/BF00378231

492 Carlo, N., Renninger, H., Clark, K., and Schäfer, K. (2016). Impacts of prescribed fire on Pinus rigida

493   Mill. in upland forests of the Atlantic Coastal Plain. *Tree Physiology*, *36*(8), 967-982. doi:

494   10.1093/treephys/tpw044

495 Certini, G. (2005) Effects of fire on properties of forest soils: a review. *Oecologia, 143*, 1–10.

496   doi.org/10.1007/s00442-004-1788-8

497 Chen, Z., Wang, G., and Jia, Y. (2017). Foliar d^{13}C Showed No Altitudinal Trend in an Arid Region and

498   Atmospheric Pressure Exerted a Negative Effect on Plant d^{13}C, *Frontiers in Plant Science*, *8*, 1-9.

499   https://doi.org/10.3389/fpls.2017.01070

500 Churchill, D., Larson, A., Dahlgreen, M., Franklin, J., Hessburg, P., and Lutz, J. A. (2013). Restoring

501   forest resilience: from reference spatial patterns to silvicultural prescriptions and monitoring. *Forest*

502   *Ecology and Management*, *291*, 442-457. https://doi.org/10.1016/j.foreco.2012.11.007

503 Conkey, L., Keifer, M., and Lloyd, A. (1995). Disjunct jack pine (Pinus banksiana Lamb.) structure and

504   dynamics, Acadia National Park, Maine. *Ecoscience*, *2*(2), 168-176.

505   doi.org/10.1080/11956860.1995.11682281

506 Copenheaver C.A., White A.S. & Patterson III W.A. (2000) Vegetation development in a southern Maine

507   pitch pine-scrub oak barren. *Journal of the Torrey Botanical Society*, 19–32.

508   doi.org/10.2307/3088744

509 Coulson, R. and Klepzig, K. (2011). Southern Pine Beetle II. Gen. Tech. Rep. SRS-140. Asheville, NC:

510   U.S. Department of Agriculture Forest Service, Southern Research Station. 153-160.

511   doi.org/10.2737/SRS-GTR-140

512 Day, M., Greenwood, M., and White, A. (2001). Age-related changes in foliar morphology and

513   physiology in red spruce and their influence on declining photosynthetic rates and productivity with

514   tree age. *Tree Physiology*, *21*(16), 1195-1204. doi.org/10.1093/treephys/21.16.1195

515 Day, M., Schedlbauer, J., Livingston, Greenwood, M., White, M., and Brissette, J. (2005). Influence of

516   seedbed, light environment, and elevated night temperature on growth and carbon allocation in pitch

517   pine (*Pinus rigida*) and jack pine (*Pinus banksiana*) seedlings. *Forest Ecology and Management*,

518   *205*(1), 59-71. doi.org/10.1016/j.foreco.2004.10.004

519   Day, M., Zazzaro, S., and Perkins, L. (2014). Seedling ontogeny and environmental plasticity in two co-

520   occurring shade-tolerant conifers and implications for environment–population interactions. *American*

521   *Journal of Botany*, *101*(1), 45-55. doi.org/10.3732/ajb.1300253

522   DeBano, L., Neary, D., and Ffolliott, P. (1998). *Fire effects on ecosystems*. John Wiley & Sons.

523   Dodds, K., Aoki, C., Arango-Velez, A., Cancelliere, J., D'Amato, A., DiGirolomo, M., *et al.* (2018).

524   Expansion of southern pine beetle into northeastern forests: Management and impact of a primary

525   bark beetle in a new region. *Journal of Forestry*, *116*(2), 178-191. doi.org/10.1093/jofore/fvx009

526   Doerr, S., Santin, C., Merino, A., Belcher, C., and Baxter, G. (2018). Fire as a removal mechanism of

527   pyrogenic carbon from the environment: effects of fire and pyrogenic carbon characteristics.

528   *Frontiers in Earth Science*, *6*, 127. doi: 10.3389/feart.2018.00127

529   Dove, N. and Hart, S. (2017) Fire Reduces Fungal Species Richness and In Situ Mycorrhizal

530   Colonization: A Meta-Analysis. *Fire Ecology, 13*, 37–65. doi: 10.4996/fireecology.130237746

531   Farquhar G., Ehleringer J., and Hubick K. (1989) Carbon Isotope Discrimination and Photosynthesis.

532   *Annual Review of Plant Physiology and Plant Molecular Biology* 40, 503–537. doi:

533   10.1146/annurev.pp.40.060189.002443

534   Fernandez, I., Schmitt, C., Birkel, S., Stancioff, E., Pershing, A., Kelley, J., *et al.* (2015). Maine's climate

535   future: 2015 update. University of Maine, Orono, ME. 24 pp. doi: 10.13140/2.1.3356.4961

536   Firn, J., McGree, J.M., Harvey, E., Flores-Moreno, H., Schütz, M., Buckley, Y.M., *et al*. 2019. Leaf

537   nutrients, not specific leaf area, are consistent indicators of elevated nutrient inputs. *Nature Ecology*

538   *& Evolution*, *3*(3), 400-406. doi: 10.1038/s41559-018-0790-1

539   Foereid, B., Lehmann, J., Wurster, C., and Bird, M. (2015). Presence of black carbon in soil due to forest

540   fire in the New Jersey pine barrens. *Journal of Earth Science and Engineering, 5*, 91–97. doi:

541   10.17265/2159-581X/2015.02.001

542   Fox, J. and Weisberg, S. (2019) An R Companion to Applied Regression, Third Edition. *Sage*.

543   Friend, A., Woodward, F. and Switser, V. (1989). Field Measurements of Photosynthesis, Stomatal

544   Conductance, Leaf Nitrogen and δ 13 C Along Altitudinal Gradients in Scotland. *Functional*

545   *Ecology, 3*, 117-122. doi: 10.2307/2389682

546   Givnish, T. (1981). Serotiny, geography, and fire in the pine barrens of New Jersey. *Evolution*, pp.101-
547   123.

548   Hanson, A. A. (2017). Distribution Patterns in Appalachian Table Mountain Pine and Pitch Pine Stands.

549   *Dissertation/Master's Thesis.* College Station (TX): Texas A&M University.

550   https://hdl.handle.net/1969.1/161568

551 Howard, L. and Stelacio, M. (2011). Fire and the development of high-elevation pitch pine communities
552   in northeastern West Virginia. *Bulletin of the New Jersey Academy of Science*, *56*(2), 19-23.
553 Jordan, M., Patterson III, W. and Windisch, A. (2003). Conceptual ecological models for the Long Island
554   pitch pine barrens: implications for managing rare plant communities. *Forest Ecology and*
555   *Management*, *185*(1-2), 151-168. doi: 10.1016/S0378-1127(03)00252-4
556 Kolden, C. and Weisberg, P. (2007). Assessing accuracy of manually-mapped wildfire perimeters in
557   topographically dissected areas. *Fire Ecology*, *3*(1), 22-31. doi: 10.4996/fireecology.0301022
558 Körner, C., Bannister, P. and Mark, A. (1986). Altitudinal variation in stomatal conductance, nitrogen
559   content and leaf anatomy in different plant life forms in New Zealand. *Oecologia* 69, 577–88.
560 Kunkel, K., Stevens, L., Stevens, S., Janssen, S., Wuebbles, D. and Dobson, J. (2013). Regional climate
561   trends and scenarios for the US national climate assessment: Part 1. Climate of the Northeast United
562   States. NOAA technical report NESDIS 142-1. Washington, DC. 87 pp. Digital Commons,
563   University of Nebraska.
564 Langsrud, Ø. (2003). ANOVA for unbalanced data: Use Type II instead of Type III sums of
565   squares. *Statistics and Computing 13*, 163–167. doi: 10.1023/A:1023260610025.
566 Lafon, C., Grissino-Mayer, H., Aldrich, S., DeWeese, G., Flatley, W., LaForest, L. *et al*. (2014). Three
567   centuries of Appalachian fire history from tree rings. (SRS-199), 99-103. USDA, Southern Research
568   Station.
569 Ledig, F., Hom, J., and Smouse, P. (2013). The evolution of the New Jersey pine plains. *American*
570   *Journal of Botany*, *100*(4), 778-791. doi.org/10.3732/ajb.1200581
571 Ledig, F., Smouse, P., and Hom, J. (2015). Postglacial migration and adaptation for dispersal in pitch pine
572   (Pinaceae). *American Journal of Botany*, *102*(12), 2074-2091. doi: 10.3732/ajb.1500009
573 Lee, C., Robinson, G., Robinson, I., and Lee, H. (2019). Regeneration of pitch pine (Pinus rigida) stands
574   inhibited by fire suppression in Albany Pine Bush Preserve, New York. *Journal of Forestry*
575   *Research*, *30*(1), 233-242. doi: 10.1007/s11676-018-0644-3
576 Lenth, R. and Lenth, M. (2018). Package 'lsmeans'. *The American Statistician*, *34*(4), 216-221.
577   http://glmmadmb.r-forge.r-project.org/repos
578 Lesk, C., Coffel, E., D'Amato, A., Dodds, K., and Horton, R. (2017). Threats to North American forests
579   from southern pine beetle with warming winters. *Nature Climate Change, 7,* 713–717. doi:
580   10.1038/nclimate3375
581 Licht, J. and Smith, N. (2018). The influence of lignocellulose and hemicellulose biochar on
582   photosynthesis and water use efficiency in seedlings from a Northeastern US pine-oak ecosystem.
583   *Journal of Sustainable Forestry*, *37*(1), 25-37. doi: 10.1080/10549811.2017.1386113

584   Licht, J. and Smith, N. (2020). Pyrogenic Carbon Increases Pitch Pine Seedling Growth, Soil Moisture
585   Retention, and Photosynthetic Intrinsic Water Use Efficiency in the Field. *Frontiers in Forests and*
586   *Global Change*, *3*, 31. doi: 10.3389/ffgc.2020.00031

587   Little, S. (1953). Prescribed burning as a tool of forest management in the northeastern states. *Journal of*
588   *Forestry*, *51*, 496–500. doi: 10.1093/jof/51.7.496

589   Little, S. and Garrett, P. (1990). Pinus rigida Mill. pitch pine. *Silvics of North America*, *1*, 456-462.

590   Lubinski, S., Hop, K., and Gawler, S. (2003). US Geological Survey-National Park Service Vegetation
591   Mapping Program, Acadia National Park, Maine. *Project Report*. U.S. Department of Interior.

592   Luo, J., Walsh, E., Miller, S., Blystone, D., Dighton, J., and Zhang, N. (2017). Root endophytic fungal
593   communities associated with pitch pine, switchgrass, and rosette grass in the pine barrens ecosystem.
594   *Fungal. Biology*, *121*, 478–487. doi: 10.1016/j.funbio.2017.01.005

595   Miller, D., Castañeda, I., Bradley, R., and MacDonald, D. (2017). Local and regional wildfire activity in
596   central Maine (USA) during the past 900 years. *Journal of Paleolimnology*, *58*(4), 455-466.
597   doi.org/10.1007/s10933-017-0002-z

598   Mosseler, A., Rajora, O., and Major, J. (2004). Reproductive and genetic characteristics of rare, disjunct
599   pitch pine populations at the northern limits of its range in Canada. *Conservation Genetics*, *5*(5), 571-
600   583. doi.org/10.1007/s10592-004-1850-4

601   Neill, C., Patterson, W., and Crary, D. (2007). Responses of soil carbon, nitrogen and cations to the
602   frequency and seasonality of prescribed burning in a cape Cod oak-pine forest. *Forest Ecology and*
603   *Management*, *250*, 234–243. doi: 10.1016/j.foreco.2007.05.023

604   Nowacki, G. and Abrams, M. (2008). The demise of fire and "mesophication" of forests in the eastern
605   United States. *Bioscience, 58*, 123–138. doi: 10.1641/B580207

606   Parshall, T. and Foster, D. (2002). Fire on the New England landscape: regional and temporal variation,
607   cultural and environmental controls. *Journal of Biogeography*, *29*(10-11), 1305-1317.

608   Patel, K., Jakubowski, M., Fernandez, I., Nelson, S., and Gawley, W. (2019). Soil nitrogen and mercury
609   dynamics seven decades after a fire disturbance: a case study at Acadia National Park. *Water, Air, &*
610   *Soil Pollution*, *230*(2), 29. doi.org/10.1007/s11270-019-4085-1

611   Patterson III, W., Edwards, K., and Maguire, D. (1987). Microscopic charcoal as a fossil indicator of fire.
612   *Quaternary Science Reviews*, *6*(1), 3-23. doi.org/10.1016/0277-3791(87)90012-6

613   Patterson, T. R. Maxwell, S. Harley, G. L., Oliver, J. S., Speer, J. H., Collins, S., Downe, M., Gannon, B.,
614   Ma, L., Raso, C., Russell, C., Teets, A. (2016). Climate—Growth Relationships of *Pinus*
615   *rigida* (Mill.) at the Species' Northern Range Limit, Acadia National Park, ME. *Northeastern*
616   *Naturalist*, 23(4), 490-500. doi.org/10.1656/045.023.0406

617 Plain, A., Kuser, J., and Ledig, F. (1987). Provenance and Progeny Variation in Pitch Pine from the
618   Atlantic Coastal Plain. *Forest Science*, *33*(2), 558-564. doi: 10.1093/forestscience/33.2.558

619 Pyne, S. (2019). The Northeast: A Fire Survey. Tucson: University of Arizona Press.
620   doi.org/10.2307/j.ctvckq9kd

621 Qi, Z., Jingfang, S., and Wenwei, L. (2018). A survey about characteristics of soil water retention curve.
622   In *IOP Conference Series: Earth and Environmental Science* (Vol. 153, No. 6, p. 062076). IOP
623   Publishing.

624 Renninger, H., Clark, K., Skowronski, N., and Schäfer, K. (2013). Effects of a prescribed fire on water
625   use and photosynthetic capacity of pitch pines. *Trees*, *27*(4), 1115-1127. doi: 10.1007/s00468-013-
626   0861-5

627 Shakesby, R. and Doerr, S. (2006). Wildfire as a hydrological and geomorphological agent. *Earth-Science*
628   *Reviews*, *74*(3-4), 269-307. doi.org/10.1016/j.earscirev.2005.10.006

629 Steiner, K. and Berrang, P. (1990). Microgeographic adaptation to temperature in pitch pine progenies.
630   *American Midland Naturalist*, 292-300. doi.org/10.2307/2426557

631 Swanston, C., Brandt, L., Janowiak, M., Handler, S., Butler-Leopold, P., Iverson, L., *et al.* (2018).
632   Vulnerability of forests of the Midwest and Northeast United States to climate change. *Climate.*
633   *Change* 146, 103–116. doi: 10.1007/s10584-017-2065-2

634 Szpakowski, D. and Jensen, J. (2019). A review of the applications of remote sensing in fire ecology.
635   *Remote Sensing*, *11*(22), 2638. doi.org/10.3390/rs11222638

636 Verma, S. and Jayakumar, S. (2012). Impact of forest fire on physical, chemical and biological properties
637   of soil: A review. *Proceedings of the International Academy of Ecology and Environmental Sciences*,
638   *2* (3), 168.

639 Wang, H., Prentice, I., Davis, T., Keenan, T., Wright, I. and Peng, C. (2017) Photosynthetic responses to
640   altitude: an explanation based on optimality principles. *New Phytologist*, *213*, 976–982.
641   doi.org/10.1111/nph.14332