**Title Page**

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

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Key words

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**Abstract**

Globally rare pitch pine (*Pinus rigida*) is thought to depend on intermittent fire, which encourages reproduction and niche preservation. At Mt. Desert Island in Acadia National Park (ME, USA) a major, stand-replacing conflagration enveloped a portion of the island in 1947; since then there has been no recurrence of fire. Other populations have been unaffected by fire disturbance for over one hundred and twenty years. Despite the absence of fire, pitch pine persists at Mt. Desert Island, suggesting that other environmental drivers may be as or more important than fire in that system. We examined the influence of fire history and topography on individual trees in four separate stands at Mt. Desert Island. Generally, topography was found to be a more important driver of leaf and plant level traits than fire history, with individuals possessing greater stress tolerance traits at high elevation. We attribute this to changes in topographical and soil characteristics along the gradient. These results challenge the suggestion that fire is the primary driver of pitch pine persistence at Mt. Desert Island and indicate that pitch pine has the capacity to thrive across a wider array of environments. These results can serve to better understand and manage this species in an ever-changing future world.

**Introduction**

On Mt. Desert Island at Acadia National Park in Maine USA, pitch pine (*Pinus rigida*), the most northerly member of the southern yellow pines (Plain *et al*. 1987), dwell at the edge of their northeastern range (Fig. 1) in heathland-pine barren communities. Over millennia, their 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 (Fig. 1; Pyne 2019). Ferocious winds whipped the fire into a frenzy and, notwithstanding efforts to subdue it, persevered for nearly two weeks. Since that time, fire suppression has been used to avoid a repetition of the tragic consequences from that fire. Interestingly, in ensuing decades, tree pyrogenic adaptations have diminished, perhaps as the result of phenotypic plasticity, shifting away from 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).

Recent history of pitch pine population success in fire-suppressed locations such as Mt. Desert Island defies a theory that fire (natural or proscribed) 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 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, including slope and aspect, 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 aspects of the soil environment, including soil carbon as well as macro and micro nutrient concentrations. Following previous studies, we expected to find less soil carbon (DeBano 1998), greater alkali cations (Certini 2005) and increased solubilized minerals (Caldwell and Richards 1989) in soils which experienced the 1947 fire. We predicted that there would be greater soil carbon at low elevations due to thermal exfoliation (as explained by Shakesby and Doerr 2006) or a failure of fire to remove pyrogenic carbon in former fire zones (Doerr *et al.* 2018). We also measured soil water retention, which we expected to be greater at sites that experienced the 1947 fire, as pyrogenic carbon is known to increase soil water retention (Licht and Smith, 2020). Beyond that, we anticipated higher soil water retention at low elevations due to flat terrain (alleviating erosion mechanics).

We hypothesized that topographical and fire history-driven changes to the growth environment would manifest in changes in leaf- and plant-level traits. We expected that stress induced by topographical features and low soil water retention at high elevation would lead to increased intrinsic water use efficiency (iWUE; Wang *et al.* 2017), as a stress tolerance response. We also hypothesized a reduction in leaf nutrients at high elevation, mimicking likely reductions in the soil. In addition, there was the prospect that fire history might alleviate these stress indicators, as a result of increased soil nutrients and water retention. At the plant level, we predicted plants would be smaller in height and DBH, have narrower canopy, and be more sparsely clustered (greater distance between conspecific neighbors) at high elevation, again as a result of the topography- and soil-induced stress. We expected to find smaller trees in areas that had experienced the 1947 fire due to age, but that the height difference would be less at high elevation due to stress-reducing effects of fire on the soil environment, an effect that would be more beneficial if higher elevation sites were less fertile.

**Methods**

*Study sites*

We investigated fifteen pitch pine specimens at each of four sites at Mt. Desert Island (Fig. 2, Tab. 1), factorially crossed in a fire history (Miller *et al*. 2017) by elevation design: (1) Wonderland trail at an average of 17.83 m elevation (low elevation, outside the footprint of the 1947 fire), (2) Gorham cliffs at an average of32.95 m (low elevation, within the footprint), (3) St. Sauveur trail at an average of171.72 m (high elevation, outside the footprint) and (4) South Cadillac trailat an average of 279.95 m (high elevation within the footprint). Elevation differences were more stark at St. Sauveur and South Cadillac trail transects. Soils at all four sites were overlain with rapidly drying needle duff, porous, and comprised of acidic hornblende granite or Ellsworth schist (Day *et al.* 2005). In addition they were uniformly shallow (varying between 0.7-2.5 cm), homogeneous, and low in fertility (Butak 2014). In some cases, sampling was limited by time, weather and site access yielding uneven sample accumulations. Our analytical methods were designed to deal with uneven sample sizes (see Statistical Analysis section below).

*Topographic features*

A Kodak Trimble Juno 3B was used to obtain horizontal resolution of data plotted using between five and seven satellite telecommunication vehicles to maintain a maximum Position Dilution of Precision. These data were differentially corrected and have estimated accuracies in the horizontal and vertical direction of 2m, while selective availability was set to zero. Multiple satellite-configured GPS data (USGS 2m LIDAR 2010) determined coordinates for individual trees (Lubinski *et al*. 2003) as well as slope and aspect attributes using ArcGIS (version 10). Mapping of this type of data has been used in the past to compare physiography and recalcitrant chemical biogeography, particularly in fire prone contexts (Kolden and Weisberg 2007; Szpakowski and Jensen 2019).

*Soil Elements and Water Retention (SWR)*

Soils were excavated by hand trowel and soil probe (Accuproducts, Saline, MI, USA); soil C, N and C/N were calculated from elemental analysis. 70 mL soil samples were extracted at fifteen tree locations at four sites, from <10.5 cm (Oa-Ab) horizon above bedrock. In a laboratory 50 g H2O were added to each aliquot to assess net water retention as a subset of soil moisture evaporation (*ψ*g) to determine net evaporative loss or adsorption to surfaces. Soil water retention analysis was conducted according to the Fields method (Lichtand Smith 2018). Retention effects of gravitational and evaporation forces was made on a wet basis where Wm=g H2O **●** (g moist soil)-1 (Qi *et al.* 2018). We also used a set of #10-#140 mesh sieves (Advantech, Wisconsin, USA) to determine presence of close-to-the-surface fine charcoal particulate matter symptomatic of recalcitrant pyrogenic material at all four sites.

*Leaf Traits*

Maximizing seasonal data relative to active growth during the driest months of the summer was achieved by obtaining C isotopic data (δ13C) and N isotopic data (δ15N) of fully expanded leaves (needle cluster) of 15 individuals at each site. All individuals selected had stem diameter of the bole at breast height (DBH) greater than 13 cm. Sample fascicles (one per tree) were separated and dried for two days at 60 ◦C ground in a SPEX ball mill (Metuchen, NJ, USA), weighed to +/- 2 mg for leaf tissue and +/- 5 mg for soil using a Cole-Palmer (Vernon Hills, IL, USA) micro analytic balance and rolled in Costech (Valencia, CA, USA) 5 x 9 mm tin capsules. A Thermo Delta (Waltham, MA, USA) V+ IR-MS continuous flow isotope ratio mass spectrometer with a universal triple collector was used. Combustion gasses were separated on a gas chromatograph column, passed through a diluter and reference gas box, and introduced into the spectrometer. δ13C was used to indicate water use efficiency (iWUEδ13C) (Farquhar et al. 1989). Leaf tissue was obtained from excision of basal fascicle bundles at 1.06 m. 50 mL samples of needles were separated, cut and dried for two days at 60 ◦C. Then they were ground in a SPEX ball mill (Metuchen, NJ, USA), sieved to <10 mm, and <2 mL were fed to a Leco CN-2000 Carbon-Nitrogen Analyzer (Leco Corp., St. Joseph, MI) coupled with the spectrometer to determine C and N concentrations. 35 mL aliquots were submitted for standard plant tissue nutrient analysis using a TJA Model 975 AtomComp ICP-AES (Thermo Jarrell-Ash Corp., Franklin, MA). The method comprised submersion in a 5 mL trace-metal-grade HNO3 treatment, then refluxed on hot block at 80 ◦C for two hours and diluted to 25 mL with 0.4 micron PTFE syringe filters to access extractable macro and micro inorganics.

*Plant-level Traits*

We measured individual tree height, stem diameter of the bole at breast height (DBH) and canopy spread. Tree height was estimated using a plastic clinometer (Kager, Lunenberg, MA USA) and 30 m tape. DBH was measured at 1.06 m using an expandable cloth measuring tape. Canopy spread across the first nodal branch expanse below the crown was measured using calibration between two aluminum flags as a ground truth reference. This method was selected to sort out upper canopy spread x height differences where trees across all four stands, which exuded very similar height and DBH characteristics, dominated. Mean distances between sampled trees were calculated including up to five of the nearest, reproductively mature conspecific (within 5 m) neighbors (Churchill *et al.* 2013)—this clustering method served as a surrogate, but inverse, measure for stand density (Mosseler *et al*. 2004).

*Statistical Analysis*

All data were analyzed using a similar linear model structure with elevation as a continuous independent factor and presence of the 1947 fire (yes or no) as a categorical independent factor. The interaction between elevation and presence of the 1947 fire was also included as an independent factor in each model. In total, 25 models were fit with the following dependent variables: tree height (m), canopy spread (m), DBH (cm), mean distance between neighbors (m), foliar carbon (C, %), foliar nitrogen (N, %), foliar C/N (unitless), foliar δ13C (‰), foliar δ15N (‰), foliar aluminum (Al+, mg kg-1), foliar calcium (Ca2+; mg kg-1), foliar magnesium (Mg2+; mg kg-1), foliar phosphorus (P; mg kg-1), foliar potassium (K+; mg kg-1), foliar zinc (Zn; mg kg-1), soil C (%), soil N (%), soil C/N (unitless), soil Al+ (mg kg-1), soil Ca2+ (mg kg-1), soil Mg2+ (mg kg-1), soil P (mg kg-1), soil K+ (mg kg-1), soil Zn (mg kg-1), and soil water retention (mg kg-1). Tree height, canopy spread, DBH, foliar P, foliar K+, foliar Zn and soil C/N were log transformed to meet model assumptions of normality and heterogeneity of variances, while soil water retention was arcsin square root transformed to meet model assumptions. All linear models were fit using the ‘lm’ function in R (R Core Team 2019). Type II F-tests were used to determine the statistical significance of each factor in each model using the ‘Anova’ function in the ‘car’ package in R (Fox and Weisberg, 2019). Type II tests are robust to unbalanced designs (Langsrud 2003). Slopes and intercepts for plotting were determined using the ‘emmeans’ package in R (Lenth and Lenth 2018). Because aspect data is circular in nature, we analyzed aspect data using a Watson’s Two-Sample Test of Homogeneity as implemented in the R package ‘circular’ (Agostinelli and Lund 2017). Specifically, one-to-one comparisons were done between each site in all six possible combinations. All analyses were performed with R version 4.0.5 (R Core Team 2019).

**Results**

*Topographical features*

Watson’s two sample t-tests indicated that the individual aspects of all sites differed with respect to one another except for the two sites that experienced the 1947 fire (Gorham cliffs and South Cadillac Trail), which had similar aspects (Fig. 3 and Tab. 2). There was an interaction between slope and fire history (*F*1,56 = 108.1, *P* < 0.05) that indicated that the slope was greater for individuals at the low elevation site that experienced the 1947 fire (Gorham cliffs) than low elevation individuals that did not experience the fire (Wonderland), with the reverse being true at high elevation (Table 1).

*Soil elements and water retention*

Soil C concentrations were greater at lower elevations (*P* < 0.05), but were unaffected by fire history or their interaction (*P* > 0.05 in all cases, Fig. 4 and Tab. 3). Soil N and C/N did not vary with elevation, fire history, or their interaction (*P* > 0.05 in all cases, Fig. 4 and Tab. 3).

Soil Ca2+ decreased with elevation (*P* < 0.05, Fig. 5 and Tab. 4), regardless of fire history. Soil P, Mg2+, and Zn did not vary with elevation, fire history, or their interaction (Tab. 4). Fire accounted for a 48% reduction in K+ at fire-experienced sites (*P* < 0.05, Fig. 5 and Tab. 4), regardless of elevation. There was an interaction between fire history and elevation (*P* < 0.01, Tab. 4) that indicated that soil Al+ increased with elevation in sites that did not experience the 1947 fire and decreased with elevation at sites that did experience the 1947 fire (Fig. 5).

There was an interaction between elevation and fire history on soil water retention (SWR; *P* < 0.01, Fig. 4 and Tab. 3), driven by higher SWR at sites that experienced the 1947 fire at low elevation, an effect that was diminished at higher elevations (Fig. 4).

*Leaf isotopes and elements*

Trees at higher elevations experienced less negative δ13C (*P* < 0.01, Fig. 6 and Tab. 5), reflecting greater water use efficiency, regardless of fire history. There were no significant effect of fire history, elevation, or their interaction on δ15N (*P* > 0.05 in all cases, Fig. 6 and Tab. 5)*.*

Foliar C was greater in trees at sites that experienced the 1947 fire (*P* < 0.05, Fig. 6 and Tab. 5), regardless of elevation; however there was no effect of fire history, elevation, or their interaction on foliar N or C/N (P > 0.05 in all cases, Fig. 6 and Tab. 5).

Foliar Ca2+ was negatively impacted by increasing elevation (*P* < 0.001, Fig. 7 and Tab. 6), regardless of fire history. Our model indicated that foliar P was significantly higher at fire-involved sites (*P* < 0.01, Fig. 7 and Tab. 6), regardless of fire history. Foliar K+ was reduced by fire involvement at high elevations, but not low elevations (elevation x fire: *P* < 0.05, Fig. 8C and Tab. 6). Neither foliar Al+ nor Mg2+ differed by fire history, elevation, or their interaction (*P* > 0.05 in all cases; Fig. 7 and Tab. 6). Foliar Zn concentrations decreased with increasing elevation (*P* < 0.01, Fig. 7 and Tab. 6), regardless of fire history.

*Plant-level traits*

There was a significant interaction between fire and elevation on tree height (*P* < 0.01, Tab. 7), which indicated that historical fire presence had a negative impact on tree height at high, but not low, elevation (Fig. 8). Increasing elevation reduced DBH (P < 0.001; Fig. 8 and Tab. 7), regardless of fire history. Canopy spread was reduced at high elevation (*P* < 0.01, Fig. 8 and Tab. 7), regardless of fire history. Distance between neighbors was greater at high elevation sites (*P* < 0.001, Fig. 8 and Tab. 7), regardless of fire history.

**D****iscussion**

*Soil characteristics*

Soil fertility and water retention varied across our environmental gradient. We were curious about the influence of subsurface charcoal as a soil component in fire-exposed areas. At nearby, burned-over Cadillac Brook, below the heights of South Cadillac trail, earlier paleo (Lafon *et al.* 2014) and fossil indicator reports (Patterson *et al.* 1987; Verma and Jayakumar 2012) underscore the presence of charcoal. However, there were no significant changes in soil C with fire history, although there was a reduction at higher elevations.

Patel *et al.* (2019) studied soil N in several watersheds (drainages) below South Cadillac trail, at low to mid-elevation, to determine recalcitrant atmospheric deposition since the 1947 fire. Since fire is known to increase N losses there was an expectation of lower nitrogen at sites closer to the most intense burns, but they found no evidence for this (Patel *et al.* 2019). These are consistent with our findings. Fire also did not significantly influence any of the other soil nutrients we measured, despite strong topographical differences.

A previous pine barren study reported that pyrolysis (either natural or anthropogenic) increased SWR (Licht and Smith 2020) and we found support for this at low elevations at Mt. Desert. Interestingly, this occurred despite steeper slopes at one cliff site that experienced fire at low elevation, which we would have expected to reduce SWR.

*Leaf traits*

Intrinsic water use efficiency, indicated by δ13C, has been shown to increase in the presence of pyrolytic soil (Licht and Smith 2020). However, we found no effect of the 1947 fire on this trait. Instead, δ13C (and, thus water use efficiency) increased with elevation, supporting previous findings (Wang *et al.* 2017; Chen *et al*. 2017, Körner *et al.* 1986; Friend *et al.* 1989; Bresson *et al.* 2009). At Mt. Desert, where elevation gradients are a significant feature of the landscape, this response is indicative of plant stress tolerance response (to higher wind turbulence, low pressure, and more quickly drying soils) as a feature of upper elevation life (Wang *et al.* 2017).

We expected that an increase in elevation would drive increases in leaf nutrients, particularly leaf N, to support high elevation photosynthesis at low stomatal conductance, as has been shown and is expected from physiological theory (Wang *et al.* 2017). This was not the case. A reduction in some soil nutrients (e.g., Ca2+) may have played a role in this (Firn *et al.* 2019), but may also have been the effect of non-measured variables, such as nutrient mineralization.

Despite a lack of soil nutrient responses, we found that fire involvement significant increased foliar P, possibly as the result of greater P availability. However, this was not consistent with our soil analysis. Further studies are needed to understand the connection between fire involvement, topography, soil nutrients, and foliar nutrients at Mt. Desert Island. A closer examination of fungal processes (such as those conducted by Luo *et al*. 2017 following prescribed burns in New Jersey) may yield clearer findings (Dove and Hart 2017) necessary to understand the influence of mycorrhizae on pitch pine in disjunct populations.

*Plant-level traits*

Elevation was the primary driver of plant traits, resulting in smaller, less clustered trees at high versus low elevation. Interestingly, there was relatively little difference in these responses with fire involvement, which we expected to reduce clustering and tree size regardless of elevation due to effects on tree age. Tree cores taken near the sites we used suggest that trees located at sites outside of 1947 fire are likely 15-30 years older than trees withing the 1947 fire zone (Patterson *et al.* 2016). As such, we expected older and larger individuals at sites that did not experience the 1947 fire. In fact, this lack of difference may be an indicator of stimulation of pitch pine growth after fire, for instance as a result of reduced competition (Jordan *et al.* 2003). This might suggest that a shift back could further spur dispersal, but, despite a significant fuel buildup in the forests on the island, this would require a change in current management policies. Coupled with climate projections (Fernandez *et al.* 2015), we can predict potential ledge population enlargement is unlikely to occur as a function of anthropogenic intervention. Nonetheless, our findings in non-fire involved sites suggest that pitch pine can persist in the absence of fire. However, further studies are needed to examine how long this will last.

*Disturbance, climate factors and predictions for species status*

Until now, disturbances such as mechanical thinning and bioturbation (Abney *et al.* 2019), disease such as *Ploioderma lethale* (needle cast; Little and Garrett 1990), deer browsing and rodent damage (Ledig *et al.* 2013), and insect herbivory (Lesk *et al.* 2017) have not been management factors at Mt. Desert Island as they are in barrens elsewhere. Yet, a possibly catastrophic problem may occur due to a combination of a prolonged fire interval and increases in annual winter temperatures (Lesk *et al.* 2017)—namely the potential invasion within the next decade of an herbivore, Southern pine beetle (*Dendroctonus frontalis* or ‘SPB’). This herbivore has already paid a deadly visit to New Jersey and Long Island NY (Dodds *et al.* 2018). Unless its progress is deterred by predators like double checkered clerid (*Thanasimus dubius*; Coulson and Klepzig 2011), or some undetermined climate factor, pitch pines, along with understory plants, butterflies and moth members of the Acadia ecosystem, are vulnerable to predation (Lesk *et al.* 2017).

It is no doubt that a warming climate is having the greatest impact on island vegetative prospects, including the fortunes of pitch pine. Models project a negative impact on future vegetative status at Mt. Desert Island (Fernandez *et al.* 2015; Swanston *et al*. 2018). According to several studies (Day *et al*. 2005; Lee *et al*. 2019) warming climate impacts habitat suitability and pitch pine tendencies to consolidate, regenerate, or migrate. What has been clear for almost three decades is the effect of global climate change on physiological traits. Day *et al*. (2001) found an uptick in annual temperatures signaled increased leaf-air vapor pressure deficits that negatively impacted pitch pine stomatal conductance and limited gas exchange. In a related report, scientists found warming trends (Kunkel *et al* 2013) increased pitch pine reproductive difficulties (Ledig *et al*. 2015). These trends include weather-related effects such as episodic drought, harsh winds, and salt spray (Fernandez *et al.* 2015) as well as increased cold intolerance (Steiner and Berrang 1990). What is not clear is the extent to which tree plasticity (Day *et al.* 2014) will be shaped by a continuing rise in warming temperatures. What appears to be more certain is the prediction that pitch pine colonies will suffer due to a combination of diminished open space capacity, loss of enriched substrates and elimination of suitable habitats (Day *et al.* 2005). Our study indicates that pitch pine physiology may be more flexible than previously thought, as we find trait shifts and population persistence along a large topographical gradient. However, global changes are likely to present these populations with novel conditions that may override this flexibility. Future monitoring, manipulative, and modeling studies will be critical to ensure the future persistence of this important species.

## 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.** Circular plots indicating the aspect of individual trees at each site. Color of points indicates the fire history with red and blue indicating exposure and no exposure to the 1947 fire, respectively. For consistency with other plots, the shapes represent different sites. Circles, triangles, diamonds, and squares correspond to measurements at Gorham Cliffs, South Cadillac, St. Sauveur, and Wonderland, respectively (Table 1). Group letters were assigned using site-to-site Watson test comparisons, with different letters indicating significantly different aspects (Table 2).

**Figure 4.** 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 5.** 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 6.** Relationship between elevation and δ13C (A) and δ15N (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).

**Figure 7.** Relationship between elevation and foliar 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 8.** Relationship between elevation and canopy spread (A), diameter at breast height (DBH; B), distance between neighbors (C), and tree height (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).

## Data availability statement

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

## Author contributions

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

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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

Buma, B., Brown, C., Donato, D., Fontaine, J., and Johnstone, J. (2013). The impacts of changing disturbance regimes on serotinous plant populations and communities. *BioScience*, *63*(11), 866-876. doi.org/10.1525/bio.2013.63.11.5

Butak, Amanda L. (2014). Vegetation Composition, Structure, and Ecophysiology of Maritime Ledge Ecosystems. *Dissertation/Master’s Thesis*. Orono (ME): University of Maine. https://digitalcommons.library.umaine.edu/etd/2212

Caldwell, M. and J. Richards. (1989). Hydraulic lift: water efflux from upper roots improves effectiveness of water uptake by deep roots. *Oecologia, 79*, 1-5. doi.org/10.1007/BF00378231

Carlo, N., Renninger, H., Clark, K., and Schäfer, K. (2016). Impacts of prescribed fire on Pinus rigida Mill. in upland forests of the Atlantic Coastal Plain. *Tree Physiology*, *36*(8), 967-982. doi: 10.1093/treephys/tpw044

Certini, G. (2005) Effects of fire on properties of forest soils: a review. *Oecologia,* *143*, 1–10. doi.org/10.1007/s00442-004-1788-8

Chen, Z., Wang, G., and Jia, Y. (2017). Foliar d13C Showed No Altitudinal Trend in an Arid Region and Atmospheric Pressure Exerted a Negative Effect on Plant d13C, *Frontiers in Plant Science*, *8*, 1-9. https://doi.org/10.3389/fpls.2017.01070

Churchill, D., Larson, A., Dahlgreen, M., Franklin, J., Hessburg, P., and Lutz, J. A. (2013). Restoring forest resilience: from reference spatial patterns to silvicultural prescriptions and monitoring. *Forest Ecology and Management*, *291*, 442-457. https://doi.org/10.1016/j.foreco.2012.11.007

Conkey, L., Keifer, M., and Lloyd, A. (1995). Disjunct jack pine (Pinus banksiana Lamb.) structure and dynamics, Acadia National Park, Maine. *Ecoscience*, *2*(2), 168-176. doi.org/10.1080/11956860.1995.11682281

Coulson, R. and Klepzig, K. (2011). Southern Pine Beetle II. Gen. Tech. Rep. SRS-140. Asheville, NC: U.S. Department of Agriculture Forest Service, Southern Research Station. 153-160. doi.org/10.2737/SRS-GTR-140

Day, M., Greenwood, M., and White, A. (2001). Age-related changes in foliar morphology and physiology in red spruce and their influence on declining photosynthetic rates and productivity with tree age. *Tree Physiology*, *21*(16), 1195-1204. doi.org/10.1093/treephys/21.16.1195

Day, M., Schedlbauer, J., Livingston, Greenwood, M., White, M., and Brissette, J. (2005). Influence of seedbed, light environment, and elevated night temperature on growth and carbon allocation in pitch pine (*Pinus rigida*) and jack pine (*Pinus banksiana*) seedlings. *Forest Ecology and Management*, *205*(1), 59-71. doi.org/10.1016/j.foreco.2004.10.004

Day, M., Zazzaro, S., and Perkins, L. (2014). Seedling ontogeny and environmental plasticity in two co‐occurring shade‐tolerant conifers and implications for environment–population interactions. *American Journal of Botany*, *101*(1), 45-55. doi.org/10.3732/ajb.1300253

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

Dodds, K., Aoki, C., Arango-Velez, A., Cancelliere, J., D’Amato, A., DiGirolomo, M., *et al.* (2018). Expansion of southern pine beetle into northeastern forests: Management and impact of a primary bark beetle in a new region. *Journal of Forestry*, *116*(2), 178-191. doi.org/10.1093/jofore/fvx009

Doerr, S., Santin, C., Merino, A., Belcher, C., and Baxter, G. (2018). Fire as a removal mechanism of pyrogenic carbon from the environment: effects of fire and pyrogenic carbon characteristics. *Frontiers in Earth Science*, *6*, 127. doi: 10.3389/feart.2018.00127

Dove, N. and Hart, S. (2017) Fire Reduces Fungal Species Richness and In Situ Mycorrhizal Colonization: A Meta-Analysis. *Fire Ecology,* *13*, 37–65. doi: 10.4996/fireecology.130237746

Farquhar G., Ehleringer J., and Hubick K. (1989) Carbon Isotope Discrimination and Photosynthesis. *Annual Review of Plant Physiology and Plant Molecular Biology* 40, 503–537. doi: 10.1146/annurev.pp.40.060189.002443

Fernandez, I., Schmitt, C., Birkel, S., Stancioff, E., Pershing, A., Kelley, J., *et al.* (2015). Maine’s climate future: 2015 update. University of Maine, Orono, ME. 24 pp. doi: 10.13140/2.1.3356.4961

Firn, J., McGree, J.M., Harvey, E., Flores-Moreno, H., Schütz, M., Buckley, Y.M., *et al*. 2019. Leaf nutrients, not specific leaf area, are consistent indicators of elevated nutrient inputs. *Nature Ecology & Evolution*, *3*(3), 400-406. doi: 10.1038/s41559-018-0790-1

Foereid, B., Lehmann, J., Wurster, C., and Bird, M. (2015). Presence of black carbon in soil due to forest fire in the New Jersey pine barrens. *Journal of Earth Science and Engineering,* *5*, 91–97. doi: 10.17265/2159-581X/2015.02.001

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

Friend, A., Woodward, F. and Switser, V. (1989). Field Measurements of Photosynthesis, Stomatal Conductance, Leaf Nitrogen and δ 13 C Along Altitudinal Gradients in Scotland. *Functional Ecology,* *3*, 117-122. doi: [10.2307/2389682](https://doi.org/10.2307/2389682)

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

Hanson, A. A. (2017). Distribution Patterns in Appalachian Table Mountain Pine and Pitch Pine Stands. Dissertation/Master’s Thesis. College Station (TX): Texas A&M University. <https://hdl.handle.net/1969.1/161568>

Howard, L. and Stelacio, M. (2011). Fire and the development of high-elevation pitch pine communities in northeastern West Virginia. *Bulletin of the New Jersey Academy of Science*, *56*(2), 19-23.

Jordan, M., Patterson III, W. and Windisch, A. (2003). Conceptual ecological models for the Long Island pitch pine barrens: implications for managing rare plant communities. *Forest Ecology and Management*, *185*(1-2), 151-168. doi: 10.1016/S0378-1127(03)00252-4

Kolden, C. and Weisberg, P. (2007). Assessing accuracy of manually-mapped wildfire perimeters in topographically dissected areas. *Fire Ecology*, *3*(1), 22-31. doi: 10.4996/fireecology.0301022

Körner, C., Bannister, P. and Mark, A. (1986). Altitudinal variation in stomatal conductance, nitrogen content and leaf anatomy in different plant life forms in New Zealand. *Oecologia* 69, 577–88.

Kunkel, K., Stevens, L., Stevens, S., Janssen, S., Wuebbles, D. and Dobson, J. (2013). Regional climate trends and scenarios for the US national climate assessment: Part 1. Climate of the Northeast United States. NOAA technical report NESDIS 142-1. Washington, DC. 87 pp. Digital Commons, University of Nebraska.

Langsrud, Ø. (2003). ANOVA for unbalanced data: Use Type II instead of Type III sums of squares. *Statistics and Computing* *13***,**163–167. doi: 10.1023/A:1023260610025.

Lafon, C., Grissino-Mayer, H., Aldrich, S., DeWeese, G., Flatley, W., LaForest, L. *et al*. (2014). Three centuries of Appalachian fire history from tree rings. (SRS-199), 99-103. USDA, Southern Research Station.

Ledig, F., Hom, J., and Smouse, P. (2013). The evolution of the New Jersey pine plains. *American Journal of Botany*, *100*(4), 778-791. doi.org/10.3732/ajb.1200581

Ledig, F., Smouse, P., and Hom, J. (2015). Postglacial migration and adaptation for dispersal in pitch pine (Pinaceae). *American Journal of Botany*, *102*(12), 2074-2091. doi: 10.3732/ajb.1500009

Lee, C., Robinson, G., Robinson, I., and Lee, H. (2019). Regeneration of pitch pine (Pinus rigida) stands inhibited by fire suppression in Albany Pine Bush Preserve, New York. *Journal of Forestry Research*, *30*(1), 233-242. doi: 10.1007/s11676-018-0644-3

Lenth, R. and Lenth, M. (2018). Package ‘lsmeans’. *The American Statistician*, *34*(4), 216-221. http://glmmadmb.r-forge.r-project.org/repos

Lesk, C., Coffel, E., D'Amato, A., Dodds, K., and Horton, R. (2017). Threats to North American forests from southern pine beetle with warming winters. *Nature Climate Change,* *7*, 713–717. doi: 10.1038/nclimate3375

Licht, J. and Smith, N. (2018). The influence of lignocellulose and hemicellulose biochar on photosynthesis and water use efficiency in seedlings from a Northeastern US pine-oak ecosystem. *Journal of Sustainable Forestry*, *37*(1), 25-37. doi: 10.1080/10549811.2017.1386113

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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