

# Does fire regime influence life history traits of jack pine in the southern boreal forest of Québec, Canada?

Christopher H. Briand · Dylan W. Schwilk ·  
Sylvie Gauthier · Yves Bergeron

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**Abstract** In the southern boreal forest of Québec, jack pine (*Pinus banksiana* Lamb.) stands occur in two habitat units, mainland and island. These two habitats have historically experienced different fire regimes. Infrequent lethal fires characterize the mainland, while frequent non-lethal and infrequent lethal fires characterize the islands. Previous studies have shown that highly serotinous jack pine trees tend to dominate on the mainland, while intermediate and non-serotinous trees are more abundant on the islands. A comparison

of morphological characters describing tree form, cone morphology and reproductive output was made on 14 mainland and 10 island stands in an effort to determine if they exhibited variation consistent with variation in fire regime and serotiny. Generally, mean values of the morphological and reproductive characters measured did not vary between the two habitats, nor did bark allometry. Live crown height to tree height ratio, as a function of tree age, and cone number as a function of tree height varied between the habitats. Relatively old mainland trees had a shorter crown in relation to tree height than their island counterparts. Cone number increased faster with tree height for island versus mainland trees. Island trees exhibited earlier reproduction than did mainland trees: in the island habitat the percentage of cone bearing trees (55 %) in the youngest age class (<21 years) was significantly greater than in the mainland habitat (34 %). Mainland populations were fire-resilient with a high degree of serotiny. Island populations behave like fire-resistant/fire-surviving species with a low degree of serotiny and earlier reproductive investment.

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C. H. Briand (✉)  
Department of Biological Sciences, Salisbury University,  
Salisbury, MD 21801-6837, USA  
e-mail: chbriand@salisbury.edu

D. W. Schwilk  
Department of Biological Sciences, Texas Tech  
University, Lubbock, TX 79409-3131, USA  
e-mail: dylan.schwilk@ttu.edu

S. Gauthier  
Natural Resources Canada, Canadian Forest Service,  
Laurentian Forestry Center, Box 3800, Sainte-Foy,  
QC G1V 4C7, Canada  
e-mail: Sylvie.Gauthier@RNCAN-NRCAN.gc.ca

Y. Bergeron  
Chaire Industrielle en Aménagement Forestier Durable  
(NSERC-UQAT-UQAM), Université du Québec en  
Abitibi-Témiscamingue, 445 Boulevard de l'Université,  
Rouyn-Noranda, QC J9X 5E4, Canada  
e-mail: Yves.Bergeron@uqat.ca

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## Introduction

Pines in fire-prone environments fall generally into one of two groups: those in surface-fire regimes that

survive fire through thick bark, greater mature height, and self-pruning of dead branches, and those in crown-fire regimes that have more flammable architectures and are easily killed by fire, but have serotinous cones (McCune 1988; Keeley 2012). Fire-adapted traits in pines are believed to have arisen in the early Cretaceous, between 126 and 89 Ma (He et al. 2012). Schwilk and Ackerly (2001) have placed these strategies into an evolutionary context and argued that they have resulted from a repeated pattern of correlated evolution between the “fire-surviving” and the “fire-embracing” strategies that comprise suites of structural and life history traits. This pattern of trait variation holds across species in the genus, but the extent to which it applies to intra-specific variation is less well known and existing data are contradictory.

Intra-specific variation in life history characters has been reported to co-vary with fire intensity and interval between fires, but the intra-specific trait correlations have not always matched the inter-specific pattern among pine species (e.g. Climent et al. 2004). In some serotinous species, the level of serotiny is related to fire frequency and severity (Good and Good 1975; Givnish 1981; Cowling and Lamont 1985; Muir and Lotan 1985a, b; Gauthier et al. 1996). In areas of lethal fires, trees may exhibit precocious reproduction and a greater investment in reproduction at the expense of vegetative growth (Good and Good 1975; Givnish 1981; Muir and Lotan 1985a; Ledig et al. 2013). In addition to shifts in mean trait values in response to fire regime, there is evidence that species growing in different fire regimes may exhibit differences in ontogenetic patterns of investment to defense or reproduction (Jackson et al. 1999; Schwilk et al. 2013). Such shifts in age-related bark thickness and self-pruning may be adaptations to fire regime.

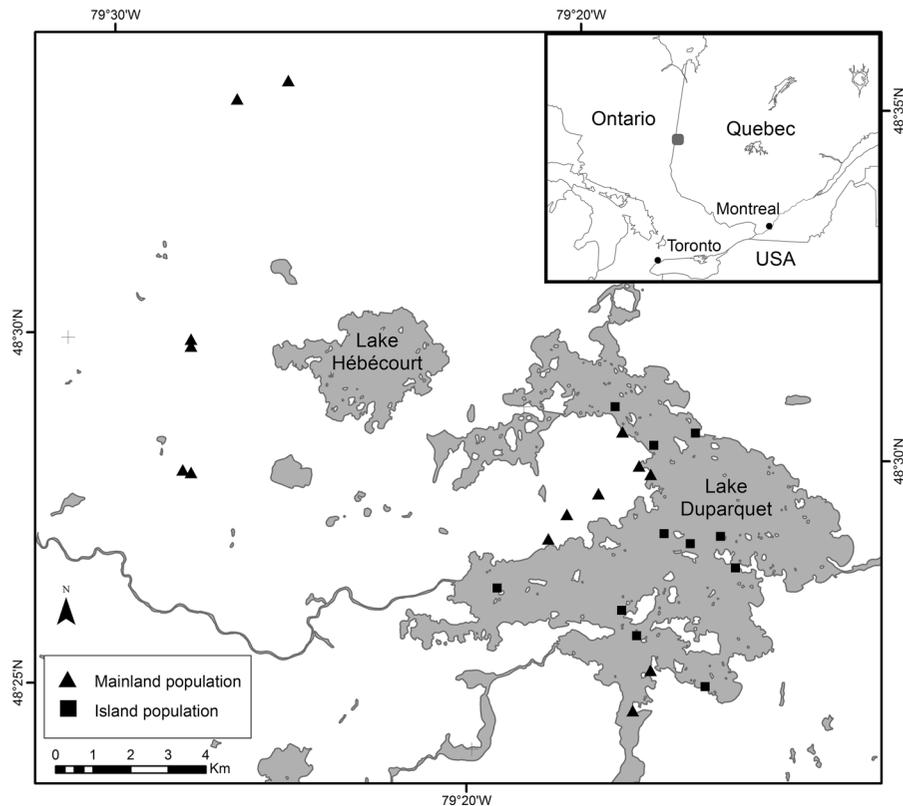
Jack pine (*Pinus banksiana*) is generally placed in the “fire resilient” (McCune 1988) or “fire embracing” (Schwilk and Ackerly 2001) category: populations persist through lethal fires in the form of an aerial seed bank stored in serotinous cones on the parent trees, with seed release following heat-induced cone opening. Jack pine may, however, bear only serotinous cones, non-serotinous (open) cones, or a mixture of both (Gauthier et al. 1993, 1996). Small trees typically bear only non-serotinous cones and the mature expression of the level of serotiny occurs only when trees reach a diameter at breast height (DBH) of about 10 cm (Gauthier et al. 1993).

In jack pine, the level of serotiny is strongly linked to fire regime. For example, Radeloff et al. (2004) reported that at its southern limit in Wisconsin, serotiny was highest in forest stands that experience infrequent lethal fires and lowest in savannah stands that experience more frequent non-lethal fires. A similar situation exists in the southern boreal forest of Québec, where jack pine is found in mainland and island stands, each exhibiting distinct fire regimes (Bergeron 1991; Dansereau and Bergeron 1993; Drobyshev et al. 2010). Stands on the mainland, which experience infrequent lethal fires exhibited higher serotiny levels (74 %) than those on islands (62 %), which experience infrequent lethal and frequent non-lethal fires (Gauthier et al. 1996). This natural variation was used to explore the effect of fire regime on variation in other traits. We examined phenotypic morphological variation in naturally occurring jack pine stands, to determine if: (1) fire regime differences result in differences in vegetative and reproductive morphology, (2) trade-offs exist between reproductive output and vegetative growth, and (3) there are differences in the timing of sexual maturity between the mainland and island stands. We hypothesize that island trees will exhibit faster height growth, greater self-pruning, greater bark thickness, and precocious reproduction in order to increase their survival due to the high probability of fire occurrence.

## Materials and methods

### Study area and sampling

The study area was in the southern part of the boreal forest, in the region of Lake Duparquet, Abitibi-Témiscamingue, Québec (48°30'N, 79°20'W). This region is dominated by balsam fir (*Abies balsamea*). Other important components of the forest included black spruce (*Picea mariana*), white spruce (*Picea glauca*), paper birch (*Betula papyrifera*), jack pine (*P. banksiana*) and trembling aspen (*Populus tremuloides*) (Bergeron and Bouchard 1984). Although the climate was humid continental, with mean annual precipitation of 889.8 mm (643.5 mm of rain and 246.3 mm of snow, Environment Canada 2013), the sites were relatively xeric as the substrate was composed of exposed bedrock or thin morainic deposits (Gauthier et al. 1993). In the vicinity of Lake Duparquet, Québec, mainland stands of jack pine are



**Fig. 1** Map of the study area, showing the mainland (*filled triangle*) and island (*filled square*) jack pine stands sampled, Lake Duparquet region

subjected to infrequent fires of lethal severity ( $0.009\text{--}0.130$  fires per  $100\text{ km}^2\text{ year}^{-1}$ ). These fires generally burn areas  $>100$  ha, with the average time between fires ranging from 150 to 205 years and with non-stand replacing fires very rare (Gauthier et al. 1996). Island stands are subject to a complex fire regime of both infrequent lethal and frequent non-lethal fires ( $0.300\text{--}0.870$  fires per  $100\text{ km}^2\text{ year}^{-1}$ ). These fires, however, tend to be smaller than those on the mainland ( $<100$  ha burned, presumably due to the lake acting as a fire break), with an average fire interval of 35 years. The higher frequency of low-intensity fires on the islands is the result of warmer and drier conditions there during the fire season, and more frequent lightning strikes on the lake than the surrounding mainland (48 vs. 6.3 lightning strikes  $100\text{ km}^2\text{ year}^{-1}$ ) (Drobyshev et al. 2010).

Fourteen mainland and 10 island stands were sampled in 1987 and 1988 (Fig. 1). The stands were pure jack pine or mixed stands with jack pine co-occurring with black spruce. Jack pine density did not

vary between the habitats ( $t = 0.23$ ,  $P = 0.822$ ), averaging  $1092 \pm 159$  ( $\pm$ SE) stems  $\text{ha}^{-1}$  on the mainland and  $1148 \pm 191$  stems  $\text{ha}^{-1}$  on the islands (data from Gauthier et al. 1993). Also the age of the sampled trees did not vary between habitats ( $t = 0.95$ ,  $P = 0.341$ ), averaging  $65.9 \pm 4.1$  (range: 5–222 years) on the mainland and  $60.1 \pm 4.2$  (range: 5–180 years) on the islands. Stand age was strongly correlated with time since the last fire of lethal intensity ( $r = 0.900$ ,  $P < 0.0001$ ; data log-transformed). For further information about fire history, see Gauthier et al. (1993).

In each stand, 20 points were systematically located using the point-centred quarter method (Cottam and Curtis 1956), and the two nearest jack pines in two different quarters at each point selected. These trees were cored for age determination, their DBH was measured, and the presence/absence of mature seed cones was recorded. A subset of 10 trees per stand was selected and felled ( $n = 238$ ). For these trees, height, crown length, and diameter were determined. Self-

pruning was estimated as the ratio of live crown length to height. We also recorded the number of mature one-year-old seed cones (reached maturity during the sampling season) on the terminal 50 cm of each 1st and 2nd order axis. The axes were ordered in a centrifugal fashion, starting with the trunk. Bark thickness was measured, using a bark gauge, at the four cardinal points on a subset (3–8) of the felled trees ( $n = 125$ ). Ten cones were collected from each felled tree, and their length, diameter, and fresh weight (FW) were determined. In order to facilitate cone opening, the cones were placed in an oven at 70 °C for 2 h. We determined the number of seeds per cone and the FW of the total number of seeds per cone, and average seed weight per cone was calculated. For bark thickness and all cone characters, mean values for each tree were used in the analyses.

### Statistical analysis

In order to account for the influence of age, the log-linear relationship between each character ( $Y$ ) and age ( $X$ ) was modeled with analysis of covariance (ANCOVA), and variation of slopes and intercepts between the mainland and island habitats was tested. As the number of trees per stand ( $n = 10$ ) was low and age and size variation was relatively low within stands (most stands established following a single fire), all the trees for each habitat were pooled.

The relationship between the number of cones and DBH, height, crown length, and crown diameter was also determined using Poisson regression to test if any trade-off(s) occurred between reproductive output and vegetative growth (nlme package in R; Pinheiro et al. 2013). The ratio of live crown height to tree height and the effect of habitat were analysed using beta regression (Ferrari and Cribari-Neto 2004; Simas et al. 2010; Cribari-Neto and Zeileis 2010).

A hierarchy of log-linear models (Bishop et al. 1975) was used to determine if the percentage of trees bearing cones was independent of habitat, while controlling for tree age. The three main effects included were habitat, age class, and cone occurrence. For this analysis, data from a large data set of 941 trees were used. Differences between habitats within age classes, with respect to cone bearing were explored using  $\chi^2$  analysis. Statistical analyses were performed using R (R Core Team 2013), Minitab™ Release 13.1 and SAS/STAT™ Release 6.03.

## Results

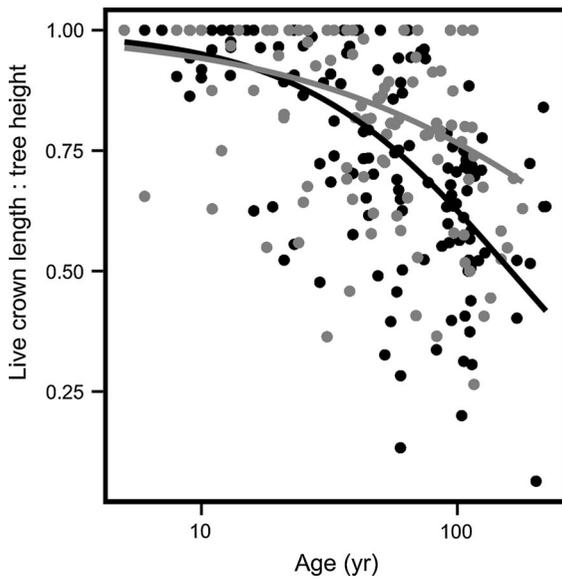
### Vegetative and reproductive morphology

In both habitats, there were significant positive log-linear relationships between the following variables and age: DBH, height, bark thickness, crown length, and diameter. There were also significant negative log-linear relationships between the following variables and age: cone diameter (mainland only) and total seed FW. Cone length and individual seed FW exhibited no relationship with age regardless of habitat. The relationship between DBH, height, bark thickness, and total seed FW and age did not vary between habitats ( $P > 0.05$ ). There was however, evidence that the relationship between crown diameter and age varied between habitats (ANCOVA,  $F_{3,120} = 39.2$ , overall  $P < 0.0001$ ; slopes are significantly different,  $F_1 = 6.384$ ,  $P = 0.0122$ ). The data showed considerable overlap between habitats and the two regressions intersected at 65 years, making these results difficult to interpret in an ecological context.

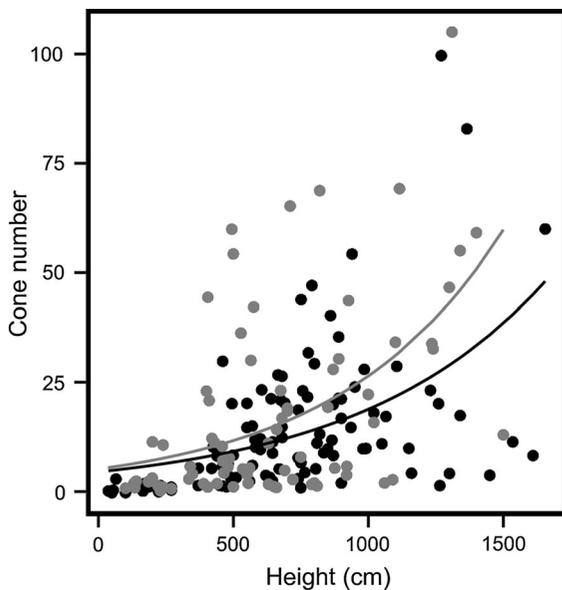
The ratio of live crown length to height (a measure of self-pruning) decreased at a greater rate in the mainland habitat with increasing tree age (Fig. 2; beta regression habitat effect  $P = 0.0298$ ). Young island and mainland trees did not differ greatly in live crown ratios, but relatively old mainland trees had a shorter crown in relation to tree height than their island counterparts. One must be cautious in interpreting this, however, because age accounted for only about 50 % of the variation in live crown ratio (beta regression pseudo  $r^2 = 0.25$ ).

### Reproductive output

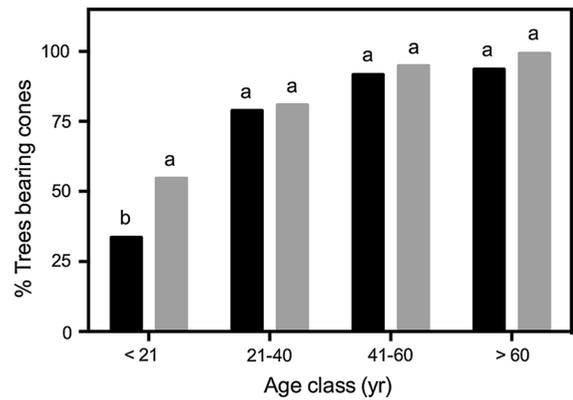
In both the mainland and island habitats, there were significant effects of tree age and size on cone production. Older and larger trees produced more cones on a yearly basis (significant effect of age, height, crown diameter, and crown volume on number of cones according to Poisson regression, all  $P < 0.001$ ). Cone production rose faster with tree height for island trees than for mainland trees (Fig. 3, Poisson regression, height by habitat interaction  $P = 0.0455$ ). This relationship held true for trees <1,200 cm, <900 cm, and <800 cm tall or when the model was forced through the origin.



**Fig. 2** Live crown height to tree height ratio as a function of tree age for jack pine at Lake Duparquet. The *black curve* represents the beta regression model fit for mainland trees, while the *gray curve* represents the beta regression for island trees. Log-likelihood is 366,  $df = 5$  (pseudo  $r^2 = 0.25$ ). The effect of age was significantly different according to habitat ( $P = 0.0298$ )



**Fig. 3** Cone number as a function of tree height for jack pine at Lake Duparquet. The *black curve* represents the Poisson regression model fit for mainland trees, while the *gray curve* represents the regression for island trees. The effect of height was significantly different according to habitat ( $P = 0.0455$ )



**Fig. 4** Distribution of trees bearing female cones by age class for jack pine in the mainland (*black bars*) and island (*gray bars*) habitats of Lake Duparquet. Values with the same letters within an age class are not significantly different ( $\chi^2$  analysis,  $P \leq 0.05$ )

When controlling for age differences between habitats on the frequency of trees bearing cones, there was a significant effect of habitat on the presence/absence of cones on a tree ( $G_1^2 = 11.75$ ,  $P = 0.001$ ). Chi square analysis indicated that, in the youngest age class (<21 years), the percentage of cone bearing trees in the island habitat (55 %) was greater than in the mainland habitat (34 %). No differences were, however, apparent between habitats in the older age classes (Fig. 4).

**Discussion**

Jack pine was established in the Duparquet region of Québec *c.* 8,000 years ago, following deglaciation (Carcaillet et al. 2001). Despite the fact that gene flow between the mainland and adjacent islands was high (Gauthier et al. 1992), consistent with other pines (e.g. Epperson and Allard 1989; Parker et al. 2001), past work has demonstrated that mainland populations have higher serotiny levels than island populations (Gauthier et al. 1996). We found, however, only subtle differences in vegetative growth and reproductive timing among trees in these two habitats.

The previously reported differences in serotiny were attributed to differences in fire regime between islands and the mainland (Gauthier et al. 1996). Although one cannot rule out either plastic responses

to different environmental conditions or selection in response to factors other than fire, the strong association of serotiny with fire regime and evidence for strong heritability in serotiny (Hernández-Serrano et al. 2014), suggests that either fire regime or some interaction of fire regime and population size (relative immaturity risk) is a plausible explanation for these population differences. Partially serotinous species may release seed in the absence of fire, especially during drier conditions (e.g. Espelta et al. 2011). Although we cannot rule out plastic effects on cone development, Gauthier et al. (1996) determined serotiny in the lab using closed cones subjected to heating and not by counting open and closed cones in the field, therefore the measurements of serotiny were not influenced directly by climatic differences between island and mainland.

The fire survival life history strategy is generally characterized by greater self-pruning of dead branches and less flammable architectures (Schwilk and Ackerly 2001). As trees aged, self-pruning increased at a more rapid rate among mainland trees (Fig. 2). We had hypothesized that island trees would exhibit greater self-pruning particularly when young in order to survive more frequent low-intensity fires; this was not the case. Past work has shown genetic variation in onset of reproduction and in reproductive allocation among pine populations (Santos-del-Blanco et al. 2010, Climent et al. 2008). In response to frequent lethal fires, trees might also exhibit a greater investment in reproduction at the expense of vegetative growth. We found no evidence to support this theory, because the relationship between reproductive output and overall tree size, as measured by DBH, height, crown diameter and length, did not vary significantly between mainland and island habitats.

Although fire-cued seedbanks such as those produced by serotiny provide a clear selective advantage under some fire regimes, serotiny also presents costs. In addition to any cost of delayed reproduction, serotiny may have direct costs to an individual tree in requiring structural and vascular support of cones (Midgley 2000); we therefore expect variation in serotiny level across species and habitats (Enright et al. 1998). In serotinous pines, the effect of fire regime on other adaptive traits is very much species dependent. In lodgepole pine (*P. contorta*), where a detailed study of the relationship between life history traits and serotiny was made, no relationship was

found between fire frequency, tree size, and reproductive output (Muir and Lotan 1985a). This is in agreement with our results for jack pine. Tree height in pitch pine (*P. rigida*) was, however, inversely correlated with the frequency of lethal fires in the New Jersey Pine Barrens (Good and Good 1975; Givnish 1981; Ledig et al. 2013). Extensive common garden experiments conducting over 36 years by Ledig et al. (2013) confirmed that dwarf pitch pine from the Pine Plains are an ecotype that has evolved in response to fire frequency, in contrast with earlier conclusions (Fang et al. 2006) that differences in height, growth, and stem habit between dwarf and normal stature pitch pine were primarily plastic responses to their growth environment.

As jack pine is often killed by fire, especially during major conflagrations, it should optimize the probability of being reproductively mature at the time of the next fire (Clark 1991) to minimize “immaturity risk” (Keeley et al. 1999). In both the mainland and island habitats, reproduction began early, with mature seed cones present on trees as young as 6 years. As these cones require 3 years from initiation to seed maturation (Ho 1991), seed cones would have been initiated on some trees at 3 years of age. Other serotinous pines also exhibit precocious reproduction (Ne’eman et al. 2004; Tapias et al. 2004; Ledig et al. 2013).

In contrast with the broad pattern across pine species that finds serotiny positively correlated with precocious reproduction (Schwilk and Ackerly 2001), a higher proportion of island trees were found to be reproductively active (excluding pollen cone formation for which no data were collected) in the youngest age class (<21 years) and cone production rose more rapidly with tree height in island than mainland trees (Figs. 3 and 4). Thus, the island fire regime of frequent low severity and infrequent high severity fires is selecting for earlier reproductive maturity. Unlike pitch pine (Good and Good 1975; Ledig et al. 2013), early reproduction in jack pine was not coupled with the presence of high levels of cone serotiny. In jack pine, young island trees may have a greater chance than their mainland counterparts of being killed before they reach reproductive maturity. This results from the mixed fire regime and the relatively high frequency, when compared to the mainland, of low severity fires. A similar pattern was reported by de Gouvenain and Delgadillo (2012) in serotinous Tecate cypress (*Hesperocyparis forbesii*). Although low severity fires are

generally non-lethal to larger trees, they may kill seedlings and small saplings. Early seed production would thus be beneficial in the island habitat and would take advantage of the relatively high frequency of small gaps. Overall, the probability of seeds from non-serotinous trees establishing themselves is lower than that for serotinous trees. Sexual maturation in the mainland habitat may be delayed without diminishing the probability of reproducing. On the mainland, recruitment into gaps is uncommon and seed is stored for many years in the canopy. Seeds from serotinous trees are released “en masse” after a lethal fire, which also prepares the seed bed, opens the canopy, and reduces competition by destroying surrounding vegetation. The best seedbeds for jack pine post-fire are mineral soil and surviving *Sphagnum* (Greene et al. 2004).

A major limitation of our field approach is that phenotypic variation observed between mainland and island habitats may result from different genotypes, plastic responses to varying environmental conditions or a combination of the two (Kruuk 2004). For example, field determination of serotiny in Aleppo pine (*Pinus halepensis*) was highly influenced by environmental conditions, with a higher proportion of cones opening during drier years (Espelta et al. 2011). Common garden experiments such as Ledig et al. (2013) and Hernández-Serrano et al. (2014) would allow us to more clearly elucidate whether the phenotypic differences we observed between the mainland and islands truly represent evolutionary adaptations to these environments. Additionally, any ecotypic differences may be responses to selection pressures other than fire (e.g. Bertz and Brewer 2013). In our study, it is quite possible that the absolute population size differences and the isolation of the island population from nearby seed sources following fire may contribute to selection for precocious reproduction on islands.

McCune (1988) classified jack pine as a fire-resilient species, describing fire-resilient species as those that possess a “high degree of cone serotiny, small seed, and precocious reproduction.” Fire-resistant species, on the other hand tend to be “tall, with thick bark, long needles, and thick twigs.” Serotiny and crown trait differences across habitats are consistent with the trait variation axis described for the genus as a whole. Mainland populations are classically fire-resilient with a high degree of serotiny. On the other

hand, island populations exhibit a lower degree of serotiny; yet have earlier reproductive maturity. The mixed and unpredictable fire regime experienced by these island populations may create an environment where early reproduction is advantageous even within the partially non-serotinous recruitment strategy.

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