Hedging at the rear edge: intraspecific trait variability drives the trajectory of marginal populations in a widespread boreal tree species

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Abstract

1. Rear-edge populations at the warm margin of species distribution are small, isolated and face environmental conditions at the limit of species bioclimatic envelope. Intraspecific phenotypic variation contributing to the persistence of peripheral populations is expected to become increasingly important under future climate conditions in order to avoid local extirpation where range shifts lag behind climate change velocity.

2. We investigated the putative role of intraspecific phenotypic variation for the maintenance of rear-edge populations of fire-prone jack pine (*Pinus banksiana*), an obligate pyriscent boreal species. We assessed whether variation in cone serotiny is associated with the population trajectory of marginal stands located south of the boreal biome, in the temperate forest where natural wildfires are infrequent and unpredictable. To this end, we estimated stand-scale serotiny, minimal age and tree size structure in 26 jack pine stands from the rear edge (n = 17 sites) and the core (n = 9 sites) of the species' range in eastern Canada.

3. On average, rear-edge jack pine populations are less serotinous albeit more variably compared to range-core populations where serotiny is more uniformly high. Rear-edge stands are generally older and display reverse J-shape tree size structure indicative of a multi-aged demographic equilibrium, whereas range-core stands are younger and show a unimodal stand structure depicting a single aging cohort generally lacking interfire recruitment. Eco-evolutionary dynamics shifts from a dependency on wildfires in range-core populations to stands that can regenerate and persist without recurrent fires at the rear edge, where stand-scale serotiny reaches values below 85%.

4. Synthesis: Unlike range-core populations, rear-edge jack pine populations can locally rely on a dual life-history strategy to ensure both steady recruitment during fire-free intervals and successful

postfire regeneration. This capacity to cope with infrequent and unpredictable fire regime should increase the resilience and resistance of jack pine populations as global changes alter fire dynamics of the boreal forest. More generally, unique intraspecific phenotypic variation in rear-edge populations contributes to long-term species persistence in marginal environmental conditions that might scale up with global changes. The conservation of rear-edge populations and their genetic legacy appears crucial for the resilience of species.

Introduction

Populations located at the geographical margins of species distribution usually face environmental conditions at the limit of the species' physiological and ecological tolerance (Brown, 1984; Lesica & Allendorf, 1995). Such marginal populations are generally smaller and more isolated from one another than those located in the core of the range (Vucetich & Waite, 2003; Kawecki, 2008; Sexton *et al.*, 2009). As a result of limited gene flow, increased genetic drift, and local adaptation to heterogeneous microclimates, peripheral populations are expected to be genetically distinct, displaying low intrapopulation genetic diversity but high differentiation with respect to core populations (Hampe & Petit, 2005; Eckert *et al.*, 2008; de Lafontaine *et al.*, 2013). Because marginal populations lie at ecological and geographical forefronts, they should readily experience novel environments and corresponding evolutionary pressures in a changing climate (Nadeau & Urban, 2019; Vilà-Cabrera *et al.*, 2019). As a result, peripheral populations might exhibit a high degree of phenotypic variation in traits conferring a fitness advantage in currently peculiar marginal conditions that may become increasingly widespread under future climates (Hampe & Petit, 2005; Rehm *et al.*, 2015). Populations at the range edges thus seem to be disproportionately important for the long-term persistence and eco-evolutionary dynamics of widespread species in the face of global changes (Lesica & Allendorf, 1995; Hampe & Petit, 2005; Rehm *et al.*, 2015).

In response to climate change, natural populations must migrate into newly available environments eventually leading to a shift of the species range, face extirpation due to poor demographic performance such as a failure to regenerate, or persist *in situ* by locally adapting to altered ecosystems (Davis & Shaw, 2001; de Lafontaine *et al.*, 2018). These responses should be amplified in range-margin populations (Nadeau & Urban, 2019). Specifically, cold-edge populations are expected to expand towards higher latitudes or altitudes under global warming (Rehm *et al.*, 2015), whereas population collapse and species range retraction should be exacerbated in warmer areas of the geographical distribution, *i.e.*, at the rear edge (Hampe & Petit,

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2005). Contrary to these simple biogeographical predictions, several empirical studies revealed that distributional shifts of many plant species currently lag behind climate change velocity (*e.g.*, Loarie *et al.*, 2009; Chen *et al.*, 2011; Zhu *et al.*, 2012; Corlett & Westcott, 2013; Lenoir *et al.*, 2020) and expected rear-edge populations contraction is often being challenged (*e.g.*, Doak & Morris 2010; Bertrand *et al.*, 2011; Cavin & Jump, 2017; Granda *et al.*, 2018; Vilà-Cabrera *et al.*, 2019). A high degree of locally adapted traits hindering fitness declines in range-edge populations might contribute to range stasis and thus partly explain these discrepancies (Rehm *et al.*, 2015; Nadeau & Urban, 2019). Yet, the contribution of adaptive evolution has long been ignored or minimized in predictive models of the potential impact of anthropogenic climate change on the biota (Davis & Shaw, 2001; Jump & Peñuelas, 2005, Hoffmann & Sgrò, 2011). Recent studies now emphasize the critical role played by local adaptation and phenotypic variation enabling long-term maintenance of populations in the face of climate change (Alberto *et al.*, 2013; Valladares *et al.*, 2014; de Lafontaine *et al.*, 2018; Nadeau & Urban, 2019; Walter *et al.*, 2020; Bisbing *et al.*, 2021).

Intraspecific phenotypic variation might occur through local adaptation and phenotypic plasticity (Gienapp *et al.*, 2008; Valladares *et al.*, 2014). Local adaptation promotes genetic divergence among populations facing contrasted environments through a combination of reduced gene flow between isolated populations and strong selection pressures favoring phenotypes that best fit local conditions (Lenormand, 2002; Kawecki & Ebert, 2004; Alberto *et al.*, 2013). While adaptive evolution is a property of populations, phenotypic plasticity allows a given individual (genotype) to express different phenotypes according to local environmental conditions without the need for evolutionary changes. Ultimately, plasticity also has a genetic basis and selection for greater adaptive plasticity under a changing climate can enable local populations to better track environment fluctuations (Via & Lande, 1985; Ghalambor *et al.*, 2007; Lande, 2014; Hendry, 2016; Chevin & Hoffmann, 2017). For instance, in places where environmental conditions are variable and unpredictable such as at the edge of species range, it might be advantageous for a population

to produce multiple phenotypes for the same trait, especially if the recruitment of new individuals is highly dependent on that trait (Olofsson *et al.*, 2009). Whether adaptive or plastic, phenotypic variation contributing to the maintenance of peripheral populations is expected to become increasingly important under future climate conditions (Valladares *et al.*, 2014; Walter *et al.*, 2020). Identifying such key variable traits and assessing their impacts on the dynamics of range-edge populations will aid conservation efforts and improve forecasting accuracy about when and where locally adapted populations will be instrumental for species persistence (Rehm *et al.*, 2015). This research agenda is increasingly critical in high latitude environments such as the boreal belt and the arctic, where global anthropogenic warming is predicted to be at least twice as large as the global average (Smith *et al.*, 2015; Bush & Lemmen, 2019; IPCC, 2021). To address this pressing need, we sought to gain new insights into the potential role of intraspecific trait variability in the persistence of marginal populations of a transcontinental boreal species at the rear edge of its distribution.

Of all North American conifer species, jack pine (*Pinus banksiana* Lamb.) is the most adapted to wildfire. Hence, it is generally found in fire-prone environments integral to the boreal forest (Rowe & Scotter, 1973). Serotiny, defined as the prolonged storage of seeds in mature cones retained in the canopy, stands out as the most prominent adaptation of jack pine to recurrent fires (Cayford & McRae, 1983). Serotiny is a highly heritable trait found in many pine species (Pike, 2011; Ledig *et al.* 2013; Budde *et al.*, 2014; Hernández-Serrano *et al.*, 2014; Castellanos *et al.*, 2015). Out of 95 *Pinus* species examined by Lamont *et al.* (1991), 22 are serotinous but only six (including jack pine) are considered obligate pyriscent, meaning cones will only open in response to fire, implying that seed release and thus regeneration is strictly contingent on stand-replacing fire events (*i.e.*, semelparity). Serotiny confers fitness benefits in a fire-prone environment where the build-up of an aerial seed bank and massive release following a fire event trigger a high recruitment rate and rapid establishment of an even-aged, monospecific stand under favorable

postfire conditions, rich in resources and devoid of competition (Lamont *et al.*, 1991; Keeley *et al.*, 2011; Pausas, 2015; Lamont *et al.*, 2020). A shift in the fire regime triggered by climate change could result in a rapid extirpation of local serotinous populations (Buma *et al.*, 2013). However, intraspecific variability in serotiny has been reported across fire regime gradients in pines (Muir & Lotan, 1985; Gauthier *et al.*, 1996; Hernández-Serrano *et al.*, 2013) and other species (de Gouvenain *et al.*, 2019). If this phenotypic variation enables local populations to persist in fire-free environments, we might expect steady regeneration (*i.e.*, iteroparity) in old-growth, uneven-aged stands.

Rear-edge jack pine populations located in the temperate mixedwood forest are smaller, more isolated and experience less fire activity than their boreal conspecifics. The adverse fire regime of the rear edge is expected to become more widespread as the climate changes and induces an increase of less flammable broadleaf vegetation (Girardin *et al.*,. 2013; Walker *et al.*, 2020; Huang *et al.*, 2021). Here we assessed if and how variation in serotiny can contribute to the persistence of rear-edge jack pine populations experiencing an otherwise unfavorable fire environment. With respect to core boreal populations, we hypothesized lower mean serotiny due to reduced fire activity but higher intrapopulation variability reflecting less predictable fire events at the rear edge. If the variation in serotiny contributes to long-term persistence, we expected populations with low and/or variable level of serotiny to exhibit old-growth, uneven-sized stand structure with steady regeneration whereas highly serotinous populations should display even-sized stand structure lacking recent regeneration. In prolonged absence of fire, the former populations should be apt to persist locally and contribute to species maintenance in the face of climate change, while the latter will become increasingly vulnerable.

Methods

Biological model

Jack pine is a serotinous species ranging from the Atlantic coast to the east of the Canadian Rockies (Fig. 1a; Little, 1971). This shade intolerant species is generally found in monospecific, even-aged stands where a single cohort dates back to the last fire event (Rudolph & Laidly, 1990). It grows directly on mineral substrates (*e.g.*, rock outcrops, sandy soils), sometimes topped with a shallow organic layer (Charron & Greene, 2002). Like a few other species particularly well adapted to fire-prone environments, jack pine is an obligate pyriscent species because mature seeds are released exclusively when temperatures induced by fire are high enough to melt the protective resin layer of the cones (Lamont *et al*., 1991). This is not the case for moderately serotinous species (e.g. *Pinus halepensis*, Nathan *et al*., 1999; Tapias *et al*., 2001) for which older cones/fruits eventually dehisce because of maintenance cost or desiccation (Lamont *et al*., 1991; Cramer & Midgley, 2009; Espelta *et al*., 2011; Martín-Sanz *et al*., 2017; Lamont, 2021). Indeed, our field observations have reported a senescent 253-year-old jack pine still bearing only closed cones (pers. obs.). Where the mean fire return interval is less than an average individual's lifespan (ca. 60 to 165 years), this type of seed dormancy makes for a higher postfire establishment success, since fires eradicate competition and expose the mineral soil (Cayford & McRae, 1983; Rudolph & Laidly, 1990; Lamont *et al*., 1991; Lamont *et al.*, 2020). However, model simulations show that fire intervals > 220 years should eventually lead to local jack pine extirpation and replacement by shade tolerant species (Le Goff & Sirois, 2004). A few jack pine populations do not exhibit strict obligate pyriscence syndrome and are known to bear non-serotinous cones (seed release at maturity, Gauthier *et al*., 1996; Radeloff *et al*., 2004). It has been suggested that this distinctive feature might allow for some interfire recruitment in regions with low fire activity (Gauthier *et al*., 1993b, 1996; Lamont *et al*., 2020).

Study area and sample stands

In the growing season of 2019, we sampled 26 jack pine stands from the core (n = 9 study sites) and the rear edge (n = 17 sites) of the species' range in eastern Québec, Canada (47−51°N; 68−70°W; Fig. 1). The rear edge was studied exhaustively whereas reference sites from the core

area represent a haphazard sampling of typical boreal jack pine stands that were easily accessible by roads. All but three rear-edge sites are located on isolated rock outcrops and monadnocks surrounded by an agricultural matrix within the temperate mixedwood forest ecozone dominated by sugar maple (*Acer saccharum*), yellow birch (*Betula alleghaniensis*), and balsam fir (*Abies balsamea*). The other three sites in this area (*i.e.*, sites PAO, MIS-B, and BIC) were found on a shallow organic horizon overlaying weathering bedrock. Sites from the core area were located on well-drained sandy glacial deposits topped by a shallow organic horizon within the boreal forest, dominated by black spruce (*Picea mariana*), balsam fir, and paper birch (*Betula papyrifera*).

A spatial analysis of Québec's ecoforest map (MFFP, 2020) reveals that rear-edge jack pine stands are smaller, more isolated and occupy a lower share of the terrestrial landscape than those in the core of the range (Fig. 1b; Table 1). This confirms that our case study correctly captures the most salient biogeographical features expected from a valid core-periphery model in a dynamic range (Hampe & Petit, 2005; de Lafontaine *et al*., 2018). Erni *et al*. (2020) developed a fire regime zonation system for Canada, in which they identified 60 Fire Regime Units (FRUs) across Canada through a stepwise synthesis of fire regime metrics based on 1970–2016 fire records, environmental attributes such as topographic features and vegetation, literature review, and expert advice. They provide some attributes of FRUs that we report in Table 1. Rear-edge populations are located within FRU 4 characterized by a very low fire activity and virtually no natural wildfire (100% human ignition since 1970). In fact, Elzein *et al*. (2020) estimated a natural fire rotation period >1600 years in preindustrial forests of this area. By contrast, our range-core populations fall in FRU 11 and FRU 10 where fire frequency is higher, and most fires are naturally ignited by lightning (Fig. 1; Table 1). This comparison of fire activities corroborates the postulate that our peripheral populations actually experience contrasted environments and distinct evolutionary pressures with respect to core populations.

Field sampling and laboratory treatments

Serotiny was estimated at the stand scale by assigning up to 100 mature jack pine individuals per site to one of six serotiny levels. Each randomly-chosen tree was visually classified as class 0 (0% closed cones), class 1 (1−25% closed cones), class 2 (26−50% closed cones), class 3 (51−75% closed cones), class 4 (76−99% closed cones), or class 5 (100% closed cones) by a single observer, using binoculars when necessary. A cone was considered 'opened' when scales were conspicuously reflexed away from the cone axis. Non-serotinous jack pine cones dehisce upon reaching maturation (year 2). Hence, to ascertain that the phenotype was fully expressed, only mature (≥ 2 years) cones were included to assess serotiny. In the field, the coloration of these older cones (brown to grey) differs from cones of the current year (green to greenish brown). Whilst this index of 'apparent' serotiny is by far the most commonly used, Lamont (2021) argued that it might be biased as it represents a snapshot in time of the possible degree of 'inherent' serotiny. This problem is encountered mainly because most serotinous species bear cones/fruits that gradually dehisce with time, until all eventually open. However, this issue is largely alleviated for jack pine, in which we found the inverse relationship (*i.e.*, older cones require higher heat sum to dehisce with no loss of seed viability; Pelletier & de Lafontaine, 2023). Although we acknowledge potential limits to the chosen approach, it is simple, intuitive, time efficient, and it has been extensively used to assess serotiny in many pine species. As such, it allowed us to obtain reliable estimates by sampling several individuals from multiple sites using a proxy that can be readily compared to values found in the literature for other pines species. It thus appears as a useful and practical index of serotiny for our biological model.

To establish the stand structure, a plot of at least 500 m^2 was randomly positioned in each of the 26 jack pine stands. In sites where tree density was low, larger plots were used to sample at least 50 trees >2 cm. Within each plot, the diameter at breast height (DBH: 1.3 m above the ground) of each tree (>2 cm DBH) was measured with a tree caliper (Haglöf, Sweden) whereas jack pine

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saplings and seedlings (<2 cm DBH) were tallied. In each stand, 10 of the largest jack pine trees were cored as close to the collar as possible using a Pressler increment borer (Haglöf, Sweden). At the laboratory, all increment cores ($n = 237$) were finely sanded to make the xylem cells clearly visible at 45× magnification under a stereomicroscope (Olympus SZ61, Tokyo, Japan). Tree-rings were counted, and the age of the oldest sampled tree was used to estimate the minimum age for each stand. When cores missed the pith, ages were adjusted by adding the number of missing rings estimated with a geometric pith locator (mean age adjustment = 3.5 years; Applequist, 1958).

Data analysis

Serotiny at the stand-scale level was estimated as the average serotiny class-value over the 100 sampled trees reported as a percentage (between 0 and 100% serotiny). A linear mixed-effect model with Satterhwaite's method using R software package lmerTest with the sample sites as a random effect was used to test difference in the mean serotiny level between populations of the rear edge and the core of the range (Bates *et al*., 2015; Kuznetsova *et al*., 2017). Intrapopulation variability in serotiny was estimated as the coefficient of variation (CV) of serotiny classes across the 100 individual trees sampled within each site. Asymptotic test for the equality of CV (Feltz & Miller, 1996) implemented in the R package cvequality (Marwick & Krishnamoorthy, 2019) was used to test for significant differences in intrapopulation variability. False discovery rate (FDR) control (Benjamini & Hochberg, 1995) was performed to adjust p-values (to FDR adjusted q-values) for multiple pairwise CV comparisons. Then, to assess whether serotiny was significantly more variable within populations at the rear edge than in core populations regardless of mean serotiny value, CV obtained for each stand were compared between regions using a Kruskal-Wallis test. Further insight into the relationship between stand-scale serotiny level and variability of the trait was obtained by testing for a correlation between CV and means across all sample sites.

To assess a potential effect of the variation in serotiny on population trajectories, tree size structure models were computed for each site by plotting the number of jack pine individuals per 2-cm diameter classes. Seedlings and saplings were included in the 0-2 cm DBH class. All stand structures were reported on a per-hectare basis to allow comparisons among sites sampled with unequal plot size. A significant relationship between age and DBH at the rear edge and range core based on the 10 cored individuals per site (Fig. S1) indicates that the tree size structure models should provide an appropriate estimation of demographic trends in each region. Because obligate pyriscent species typically perform all their life cycle within a single fire cycle and tend to have short, nonoverlapping generations with synchronous recruitment (Pausas, 2015), tree size structure in populations of such species generally follows a unimodal distribution indicating an even-aged stand that regenerated in the years following the last fire event. Alternatively, we expected that serotiny would differ in marginal populations fostering their long-term persistence by means of continuous regeneration independent of fire. Tree diameter distribution in such old-growth stands – albeit of short-lived trees species (see Frelich & Reich, 2003) − should rather have a reverse J-shape indicating uneven-aged stands with steady regeneration and equal mortality rates among diameter classes across the entire range of diameters (Westphal *et al*., 2006). Whether unimodal or reverse J-shaped, the frequency of individuals in different size classes can best be described by a quadratic model. Hence for each study site, we fitted a three-parameters univariate quadratic polynomial function under the form

$$f(x) = \beta_2 x^2 + \beta_1 x + \beta_0$$

where $f(x)$ is the number of individuals per hectare, x is the lower value of each 2-cm size class, β_2 is the quadratic coefficient, β_1 is the linear coefficient, and β_0 is the y-intercept. In the context of tree diameter distribution, a positive linear coefficient with a negative quadratic coefficient and a low (*i.e.*, null to negative) intercept value describe a unimodal (hump-shaped) curve, whereas a

negative linear coefficient with a null to positive quadratic coefficient and a high intercept value depict a reverse J-shape. Parameters of the quadratic function computed at each site were averaged over each of the two regions (rear edge and range core) to generate composite quadratic models describing mean regional size structure (composite models, thereafter; de Lafontaine & Payette, 2010). To determine overall differences in the tree size structure of jack pine stands between rear-edge and core populations, significant differences between the parameters of the two composite models were tested using a Welch Two Sample *t*-test. Because of lower fire frequency (Table 1), jack pine forests at the rear edge are expected to be old-growth stands with minimum age older than those from the core of the range, which likely dates back to the last fire event. To ascertain that this is the case, we compared the minimum stand age between the two regions using a Welch Two Sample *t*-test. In order to assess the relative importance of serotiny on the shape of the stand structure and thus on demographic patterns, quadratic model parameters (β_2, β_1, and β_0) of each site were plotted as functions of stand-scale serotiny. Significant relations between quadratic function parameters and serotiny were then tested with simple linear regression models.

In order to assess spatial independence of the rear-edge populations that are spatially clustered with respect to range-core populations, we tested for spatial autocorrelation across rear-edge populations for stand-scale level of serotiny, intrapopulation variability in serotiny (CV), as well as each parameter of the quadratic model (β_2, β_1, and β_0) using Moran.I function of R software package ape (Paradis & Schliep, 2019). All statistical analyses (significance level $\alpha = 0.05$) were performed with the R statistical software version 4.1.1 (R Core Team, 2021).

Results

We estimated serotiny on a total of 2413 jack pine trees in 26 stands from two biogeographical regions characterized by contrasting fire regimes (Fig. 1, Tables 1 and 2). Our results indicate that, on average, stand-scale level of serotiny is lower in rear-edge populations compared to core

populations (Fig. 2a, Table 2; t = 2.68, df = 24, P = 0.013). Regardless of mean serotiny value, intrapopulation variability in serotiny differs significantly among jack pine stands ($P < 0.001$, asymptotic test for the equality of CV across all stands; Table S1 provides p-values and FDR adjusted q-values for each pairwise comparison) with populations at the rear edge generally being more variable than core populations (Fig. 2b, Table 2; χ^2 = 4.8, df = 1, P = 0.029). Hence, apart from three outlier sites, jack pine stands in the fire-free environment of the rear edge are less serotinous albeit more variably with respect to stands in the core of the range, where serotiny is consistently high in the fire-prone environment of the boreal forest. In stark contrast with all other rear-edge populations, jack pine individuals of site BIC are strongly and uniformly serotinous whereas the level of serotiny at sites JEL and CAS is low and variable, which is unlike other sites sampled from the core of the range (Fig. 2a, b, Tables 2 and S1). These three sites (BIC, JEL and CAS) are thus considered outliers because their patterns of serotiny strikingly differ from other sampling sites in their respective biogeographic region. A negative correlation between stand-scale serotiny level and the CV in serotiny (Fig. 2c; Pearson's r = -0.98, $P < 0.001$) indicates that, overall, highly serotinous stands show less intrapopulation variability in serotiny whereas weakly serotinous stands are more variable.

The quadratic models showed good fit with the empirical stand size structures (Fig. 3; Table 2). Of the 17 rear-edge stands, 14 follow a reverse J-shape diameter distribution with high intercept (β_0) value, negative linear coefficient (β_1) and null to positive quadratic coefficient (β_2). Sites MIS-B, PAO and especially outlier site BIC are notable exceptions to the reverse J-shape pattern generally found at the rear edge. By contrast, most range-core stands follow a unimodal tree size structure with a null to negative intercept, a positive linear coefficient and a negative quadratic coefficient. Outlier sites JEL and CAS represent exceptions to the proper hump-shaped pattern found in the other sites from the core of the range (Fig. 3; Table 2). The composite models describing mean regional size structures display a distinctive reverse J-shape pattern at the rear

edge in striking contrast with the overall unimodal distribution reported in the range of the core (Fig. 4). Statistical comparisons of composite model parameters (Table 2) reveal significant differences between rear-edge and range-core for all three parameters (β_2: $t_{\text{two-sided}} = 3.56$, df = 24, $P = 0.002$; β_1: $t_{\text{two-sided}} = 3.87$, df = 22, $P < 0.001$; β_0: $t_{\text{two-sided}} = 3.89$, df = 20, $P < 0.001$). The reverse J-shape diameter distribution patterns at the rear edge reflect populations in a demographic equilibrium state and not a recent establishment as indicated by the fact that jack pine stands in this region are significantly older than those from the core of the range (Fig. 5; $t_{\text{one-sided}} = 3.40$, df = 22, $P = 0.001$).

All three parameters of the quadratic model describing stand size structure vary with stand-scale level of serotiny (Fig. 6). The quadratic coefficients and intercepts decrease with serotiny (β_2: $r^2 = 0.26$, $P = 0.008$; β_0: $r^2 = 0.15$, $P = 0.05$). According to the linear model relating the quadratic coefficients (β_2) to serotiny, the x-intercept is 84.4 implying that stands with a serotiny level below 84% tend to have a positive quadratic coefficient (reverse J-shape) while those with serotiny level above this threshold should have a negative quadratic coefficient (unimodal; Fig. 6a). In our sampling, all sites from the rear edge (except outlier site BIC) fall below 84% serotiny whereas all sites from the core of the range (except outlier sites JEL and CAS) fall above the threshold. The intercept of the quadratic model (β_0) depicts the amount jack pine regeneration established in a stand. This parameter declines steadily with increasing serotiny and reaches zero (*i.e.*, no pre-established regeneration) at ca. 100% serotiny (Fig. 6c; x-intercept of the linear model between β_0 and serotiny = 103.4). The linear coefficients of the quadratic model increase with serotiny (β_1: $r^2 = 0.22$, $P = 0.015$) with a shift from negative to positive values around 90% serotiny (Fig. 6b). No evidence of spatial autocorrelation was found in the rear-edge data indicating they can be treated as independent observations despite their proximity (observed I $\pm$ standard deviation and corresponding p-values: stand-scale serotiny = 0.09 $\pm$ 0.12, $P = 0.19$; serotiny CV = 0.12 $\pm$ 0.11, P

$= 0.12$; $\beta_2 = -0.20 \pm 0.12$, $P = 0.27$; $\beta_1 = -0.18 \pm 0.12$, $P = 0.33$; $\beta_0 =$ observed I $\pm$ SD $= -0.16 \pm$ 0.12, $P = 0.42$).

Discussion

This study sets out to evaluate the potential role of intraspecific variation in serotiny for the long-term persistence of marginal jack pine stands at the rear edge of the species distribution. We expected lower and more variable serotiny in rear-edge compared to range-core populations, which would result in contrasted trajectories reflected by distinct patterns of tree size structures. Our results indicate that serotiny is indeed associated with stand location within the species' range, according to contrasted regional fire regime: fire-prone stands in the core of the range have a higher level of serotiny than rear-edge sites where wildfire frequency is low. Reduced serotiny at the rear edge of jack pine distribution was also reported by Radeloff *et al.* (2004) who studied pine barrens in northwestern Wisconsin, USA and found a broad latitudinal gradient in stand-level serotiny with lowest values in the south. Because natural (*i.e.*, lightning-ignited) wildfire activity at the rear edge of jack pine distribution is low and unpredictable compared to the core of the range (Lorimer, 1977; Erni *et al*., 2020; Elzein *et al*., 2020), our results suggests that stand-scale serotiny varies in response to historic (*i.e.*, preindustrial) fire regime. Such an association between fire regime and the level of serotiny in jack pine has also been suggested by Gauthier *et al.* (1993b, 1996), Radeloff *et al*. (2004), and Briand *et al.* (2015). These studies reported contrasted patterns of serotiny according to fire severity, whereby higher level of serotiny was found in pine forests that exhibited stand-replacing fires whereas the proportion of low serotiny trees increased with the occurrence of nonlethal surface fires. Similar fire−serotiny associations were found in other serotinous pine species such as *Pinus rigida* (Givnish, 1981), *P. contorta* (Schoennagel *et al.*, 2003), *P. halepensis*, and *P. pinaster* (Hernández-Serrano *et al.*, 2013), although none of these are considered obligate pyriscent species. As such, interfire regeneration in highly serotinous stands of these species might

be somewhat lower than within their less serotinous counterparts but should not be strictly prevented as expected in highly serotinous stands of obligate pyriscent taxa. For instance, Hernández-Serrano *et al*. (2013) used an approach roughly similar to ours to estimate apparent stand-scale serotiny and found that *P. halepensis* and *P. pinaster* populations under frequent crown fires have 53% and 29% median serotiny, respectively, whereas these levels decrease to 26% (*P. halepensis*) and 6% (*P. pinaster*) in populations where crown fires are rare (Pausas, 2015). These estimates are much lower than those we found in obligate pyriscent jack pine, in which the median stand-scale serotiny across fire-prone populations from the core of the range was 91%, only decreasing to 77% at the rear edge.

Yet, our results indicate that most rear-edge populations are uneven-aged stands in a demographic equilibrium state with steady interfire recruitment. The high intrapopulation variability in serotiny within these marginal populations might contribute to this trend. Thus far, the evolutionary consequences of contrasted fire regimes have mainly focused on the difference in mean trait value, without much consideration for intrapopulation variability in fire traits such as serotiny (Pausas, 2015; Romero & Ganteaume, 2020). Unpredictable and infrequent fire regimes could select for increased adaptive plasticity leading to higher variance of key fire-related traits within populations in environments that rarely burn, but very few empirical studies have yet explored this possibility (Pausas, 2015). Still, a few authors have reported higher local phenotypic variability of fire traits in populations from heterogeneous fire landscapes (Moreira *et al*., 2012; Hernández-Serrano *et al.*, 2013). For instance, Romero and Ganteaume (2020) found no difference in mean trait values for many structural and functional fire-related traits whereas the variance of serotiny differed between *Pinus halepensis* populations from contrasted fire regimes, with a greater range where fire activity is reduced. Our results suggest that fire regime can modulate mean serotiny value as well as its variability within jack pine stands. Higher trait variability has been reported in other species at range margins in response to environmental stress (Valladares *et al.*, 2014; Lázaro-

Nogal *et al*., 2015). For example, Volis *et al*. (1998) found higher variability in peripheral wild barley (*Hordeum spontaneum*) populations' response to water stress compared with core populations.

In jack pine, intraspecific variation in serotiny, both in terms of mean trait value and intrapopulation trait variability, results in contrasted population trajectories at the rear edge compared to the core of the range. Range core stands with high mean serotiny and a lower variance exhibit the typical 'fire embracer' syndrome. Such syndrome includes semelparous monopyric life cycle, short nonoverlapping generations, and synchronous fire-dependent recruitment (Pausas, 2015). As such, range core jack pine stands form even-aged cohorts following massive seed release after a stand replacing fire, which is reflected in our results by hump-shaped tree size structures. In absence of wildfire, these stands will age and senesce without regenerating and are thus eventually bound to extirpation (Le Goff and Sirois, 2004). Contrastingly, rear-edge stands with lower mean serotiny and a higher intrapopulation variance rather display uneven tree size structures (reverse J-shape) including older trees as well as pre-established regeneration indicative of a state of equilibrium with overlapping longer generations. At the rear edge, high intrapopulation variability in serotiny implies that some individuals retain the typical 'fire embracer' syndrome but other jack pine individuals with weak or intermediate serotiny are iteroparous and fire independent as they can regenerate in absence of lethal fires (Gauthier *et al.*, 1993b). These atypical individuals are instrumental to the long-term maintenance of jack pine populations in low and unpredictable fire environments of the rear-edge. Indeed, our results suggest that the shape of the stand structure shifts from a state of decline (i.e., aging cohort) to a state of equilibrium (i.e., steady recruitment) where mean stand-scale serotiny reaches values below *ca*. 85%, a threshold at which stand dynamics change from a strict dependency on wildfires to a stand that can regenerate and persist without recurrent fires.

However, because jack pine is an early successional shade-intolerant species, long-term persistence of the self-regenerating old-growth stands is only possible in sites virtually devoid of competition (Gauthier *et al.*, 1993b). As such, the presence of peripheral jack pine stands outside the boreal biome is generally limited to poor and shallow soils, such as those found on rock outcrops unfavorable to more competitive species (Conkey *et al*., 1995). In our study, jack pine regeneration remains quite limited at rear-edge sites MIS-B and PAO despite low and variable serotiny. These two stands are located on developed soils that allow the establishment of competitive species (fir, spruce) and does not favor the germination and establishment of jack pine seeds, which typically germinate on mineral substrates (Chrosciewicz, 1974; Cayford & McRae, 1983; Rudolph & Laidly, 1990). Serotiny and stand structure of outlier sites JEL, CAS (range core) and BIC (rear edge) contrast with the general pattern found in their respective geographical setting. These outlier populations could originate from translocated genetic material (from the rear-edge to the core or vice-versa) or they might have been submitted to a distinct local (i.e., site-specific) fire regime. Ongoing investigations relying on genetic markers and macrofossil charcoal analysis should help address these hypotheses and decipher the origin and dynamics of these specific outlier sites. Although no empirical studies have specifically investigated the effect of local edaphic conditions on jack pine serotiny, higher serotiny is generally reported in xeric compared to mesic sites (e.g., *Banksia menziessi*, *Pinus pinaster*, and *Pinus halepensis*), which is interpreted as an adaptation to higher probability of fires reaching the crown of small individuals growing in xeric conditions (Lamont *et al.*, 1994; Cowling & Lamont, 1985; Lamont, 2021). Our results and interpretations are conservative since most rear-edge jack pine populations with low, albeit variable serotiny were sampled on xeric sites. Thus, fire regime and not edaphic conditions appears as a key driver of variation in serotiny of jack pine stands. Furthermore, Lamont *et al*. (2020) reported that serotiny levels in *Banksia* species are unaffected by differences in growing conditions, attesting to the genetic basis of the level of serotiny. Nevertheless, other physiological and environmental factors could potentially act upon the opening temperature of serotinous jack pine cones, such as the

difference in resource allocation within individuals, cone position within the canopy, and tree size or age (Gauthier *et al.,* 1993a; Martín-Sanz *et al.,* 2017).

Still, serotiny is a highly heritable trait (Pike, 2011; Ledig *et al*. 2013; Budde *et al*., 2014; Hernández-Serrano *et al*., 2014; Castellanos *et al*., 2015) that dictates the fate of postfire or interfire regeneration and thus the reproductive success of jack pines contingent upon the fire regime. As such, it entails rapid local adaptive responses to different fire regimes (Lamont *et al*. 2020). Theory predicts that natural selection might foster evolutive strategies such as moderate level of serotiny if: 1) the interval between fires approaches the species' lifespan, 2) fire return intervals are unpredictable, 3) interfire seedling recruitment is possible 4) the fitness cost of serotiny creates a tradeoff between supporting structures and the number of seeds (Muir & Lotan, 1985; Enright *et al*., 1998; Lamont & Enright, 2000; Lamont *et al*. 2020). At the rear edge of jack pine distribution, natural wildfire return intervals are highly unpredictable but historically exceeded the mean lifespan of the species (Payette *et al*., 2017; Elzein *et al*., 2020) and rock outcrops with reduced competition support interfire jack pine seedlings establishment (Conkey *et al*., 1995). This meets conditions 1, 2 and 3. Additionally, Pelletier and de Lafontaine (2023) reported a higher viable seed count within cones from rear-edge stands compared to those from the core of the range. This suggests that maintaining higher serotiny could come at a cost in jack pine, likely reflecting a tradeoff between maintenance and reproductive output (*i.e.*, condition 4). Hence, local eco-evolutionary dynamics at the rear edge of jack pine distribution should favor reduced serotiny, even in this obligate pyriscent species. Accordingly, we found reduced serotiny but also higher intrapopulation variability in rear-edge populations, which suggests that, unlike range-core populations, peripheral populations can locally rely on a dual life-history strategy to cope with the unpredictable fire regime. Some seeds are released at cone maturity, allowing steady tree recruitment in prolonged fire-free periods, but the concurrent buildup of an aerial seed bank retained within pyriscent cones ensures fire-heat resistance and eventual postfire regeneration

(Enright *et al.*, 1998; Whelan *et al*., 1998; Goubitz *et al*., 2004; Cramer & Midgley, 2009). This suggests a diversified bet-hedging strategy whereby rear-edge individuals invest in multiple phenotypes at once to account for the unpredictability of the environment. Bet-hedging strategies imply that individuals can optimize fitness in stochastic environments by sacrificing mean fitness to reduce temporal variance in fitness (Olofsson *et al*., 2009; Childs, 2010; Simons, 2011). In case of a fire event, it is safe to assume that jack pine individuals from rear-edge populations exhibiting lower mean serotiny should have lower average fitness compared to their conspecifics from the core of the range that end up with a larger aerial seed bank. However, during fire-free periods that extend beyond average lifespan, fitness of the latter should decline steadily down to zero upon reaching population extinction (*i.e.*, >220 years without fire; Le Goff and Sirois, 2004). Over time, individual fitness should thus be less variable in rear-edge populations that can take advantage of the infrequent and unpredictable fire environment through steady regeneration regardless of fire occurrence.

The dual life-history strategy at the rear edge may increase the resilience and resistance of these jack pine populations to future disturbance regimes. This could prove necessary as fire regimes change due to global change throughout the boreal forest (Young *et al*., 2017; Hart *et al*., 2018). While range-core jack pine populations may benefit from higher fire hazard in a warmer and drier climate (Baltzer *et al*., 2021), the infrequent and unpredictable fire environment of the rear edge might extend to the southern boreal forest as less flammable broadleaf tree species shift north (Girardin *et al*., 2013; Walker *et al*., 2020; Huang *et al*., 2021). More generally, because they are already located at the warm margin of species distributions, rear-edge populations are the most imminently threatened by climate warming (Nadeau & Urban, 2019; Vilà-Cabrera *et al*., 2019). This threat is amplified by the loss and fragmentation of habitats due to anthropogenic land use, which puts further stress on the small and isolated rear-edge populations already restricted to a few available favorable sites. Our results suggest that intraspecific phenotypic variation in rear-edge

populations contributes to their long-term persistence in peculiar marginal environmental conditions that might scale up as climate changes. However, the persistence of rear-edge populations might be temporary as they may eventually fail to keep up with the pace of global change, resulting in collapses and the irremediable loss of their potentially unique gene pool (de Lafontaine *et al.*, 2013), including locally adapted alleles. The conservation of marginal rear-edge populations thus appears crucial for the resilience of widespread species (Lesica & Allendorf, 1995; Hampe & Petit, 2005; Rehm *et al*., 2015; Snell-Rood *et al*., 2018).

Conflict of Interest

The authors declare no conflict of interest.

Authors' contributions

EP and GdL conceived the ideas and designed methodology; EP, MC and GdL collected and analyzed the data; EP and MC led the writing of the manuscript under the supervision of GdL. All authors contributed critically to the drafts and gave final approval for publication.

Data availability statement

The data used in this manuscript will be archived in Dryad data repository when the paper is accepted for publication.

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Tables

Table 1. Biogeographical settings of range-core and rear-edge jack pine (*Pinus banksiana*) stands between longitudes 68 and 70 °W. Jack pine statistics are based on Québec's ecoforest map sheets 21N, 22C, 22F, and 22K (MFFP, 2020) and fire statistics are from Erni *et al.* (2020).

	Range core	Rear edge
Latitude (°N)	47.9−50.7	47.4−48.4
Proportion of the terrestrial landscape occupied by jack pine stands (%)	2.36	0.23
Mean jack pine patch area (ha)	19.8	7.3
Mean distance between each jack pine stand and its nearest neighbor (m)	750	1725
Fire regime unit (FRU; Erni *et al.*, 2020)	FRU 10 (north of 49.8°N) FRU 11 (south of 49.8°N)	FRU 4
Fire frequency (no.·Mha^{-1}·yr^{-1})	FRU 10: 0.64 FRU 11: 0.33	FRU 4: 0.03
Burn rate (% burnable area·yr^{-1})	FRU 10: 0.349 FRU 11: 0.149	FRU 4: 0.002
Fire ignition (%)	FRU 10: 23% human, 77% lightning FRU 11: 50% human, 50% lightning	FRU 4: 100% human

Note: Ecoforest map of the Fifth Decennial Inventory was produced by Québec's Ministry of Natural Resources and Forests (MFFP, 2020). Mapping of *Pinus banksiana* stands ≥ 4 ha relied on the photointerpretation of aerial photographs, based on taxa dominance and co-dominance in the forest cover (MFFP, 2020). Using QGIS 3.28, we analyzed a total of 12,585 polygons (jack pine stands ≥ 4ha) from ecoforest map sheets 21N, 22C, 22F, and 22K to compute the proportion of terrestrial landscape occupied by jack pine stands, mean patch area, as well as mean distance between each stand and its nearest neighbor. Fire ignition provides the distribution, in percent, of the number of recent fires (1970–2016) depending on the cause, whether anthropogenic (human) or natural (lightning). The median of each fire metric was calculated by year, using fire data ≥ 50 ha for 1970–2016, and these were then averaged to obtain one value per FRU (data from Erni *et al.*, 2020).

Table 2. Summary statistics and parameters of the quadratic model computed for each sampled jack pine (*Pinus banksiana*) stand. Geographical coordinates (lat: latitude, long: longitude), minimum age of the stand, stand-scale level of serotiny and intrapopulation variability in serotiny (CV: coefficient of variation) are indicated for each study site. Quadratic model coefficients (β_2: quadratic coefficient, β_1: linear coefficient, β_0: y-intercept), proportion of explained variance (r^2), and *p*-values are provided for each stand. Values in boldface are statistically significant ($P < 0.05$).

Study region	Study site	Lat (°N)	Long (°W)	Minimum stand age (years)	Serotiny level (%)	Serotiny CV (%)	β_2	β_1	β_0	r^2	*p*-value (model)
Rear	BIC	48.35	68.81	158	98.6	8.8	**-0.26**	**9.42**	-20.51	0.33	**0.0424**
Core	MAN	50.65	68.67	49	97.4	8.1	**-0.20**	4.77	46.34	0.39	**0.0187**
Core	KIN	49.08	69.26	134	95.8	14.9	-0.05	2.12	-4.21	0.18	0.2145
Core	LAB	49.26	69.75	92	95.6	16.4	**-0.12**	**3.93**	-2.35	0.46	**0.0074**
Core	GAI	50.11	68.80	52	93.4	14.0	**-0.06**	1.92	0.24	0.20	0.1618
Core	SAG	47.94	70.05	79	91.2	23.0	**-0.34**	**11.41**	-14.08	0.60	**0.0006**
Core	REN	48.23	69.87	78	90.0	28.0	**-0.09**	**3.78**	-12.71	0.33	**0.0389**
Core	BER	48.31	69.48	62	88.0	30.0	**-0.16**	**6.38**	-14.65	0.37	**0.0265**
Rear	STS	48.26	68.98	91	84.2	32.4	**0.58**	**-34.19**	**482.79**	0.68	**0.0001**
Rear	VIL	47.67	69.71	111	84.0	32.7	**0.12**	**-5.73**	**63.66**	0.44	**0.0100**
Rear	CAC	47.93	69.50	172	82.8	34.8	-0.02	-1.11	**54.64**	0.43	**0.0111**
Rear	PEL	47.42	69.91	133	81.4	36.5	-0.03	0.03	**42.36**	0.48	**0.0050**
Rear	RAR	47.62	69.76	130	80.2	40.2	0.30	**-18.58**	**279.96**	0.57	**0.0012**
Rear	PAO	47.49	69.99	100	79.4	40.7	**-0.14**	**4.83**	13.59	0.29	0.0682
Rear	RSG	47.59	69.78	116	78.4	40.6	0.12	-13.54	**295.76**	0.48	**0.0051**
Rear	RRR	47.61	69.76	136	77.0	45.0	**0.32**	**-21.13**	**335.85**	0.85	**<0.0001**
Rear	SPN	47.48	69.86	209	76.6	37.5	0.05	-5.57	**120.73**	0.53	**0.0023**
Rear	MIS-B	47.64	69.73	64	73.2	53.4	-0.10	2.58	18.11	0.33	**0.0388**
Rear	LGM	47.70	69.70	87	71.2	47.0	0.01	-3.51	**99.27**	0.63	**<0.0001**
Rear	EMB	47.53	69.84	115	70.4	49.4	0.01	**-4.98**	**144.32**	0.77	**<0.0001**
Rear	RAK	47.60	69.76	78	70.0	48.1	**0.25**	**-12.79**	**154.53**	0.83	**<0.0001**
Core	JEL	49.32	68.37	69	69.0	55.5	-0.01	-0.45	**23.70**	0.19	0.1909
Rear	MIS-A	47.64	69.73	80	69.0	56.8	**0.53**	**-29.53**	**391.52**	0.89	**<0.0001**
Core	CAS	48.64	69.17	63	66.6	57.7	0.02	-3.85	**105.40**	0.61	**<0.0001**
Rear	FOU	47.70	69.69	89	61.8	57.3	0.06	**-4.62**	**84.48**	0.75	**<0.0001**
Rear	PLO	47.57	69.79	138	58.9	68.0	**0.34**	**-16.59**	**181.77**	0.70	**<0.0001**
Rear-edge populations (mean)				118	76.3	42.9	0.13	-9.12	161.34	-	**-**
Range-core populations (mean)				75	87.4	27.5	-0.11	3.33	14.19	-	**-**

Figures
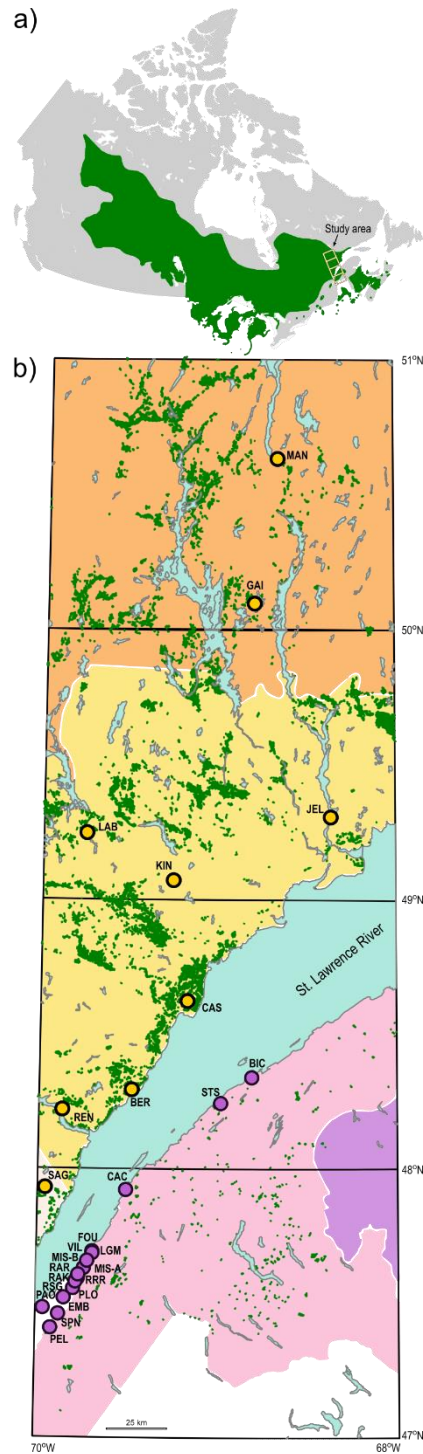
Figure 1. Location of sample sites and biogeographic setting of jack pine (*Pinus banksiana*). a) The study area in eastern Québec is shown within the transcontinental distribution of jack pine (green; Little, 1971). b) Circles indicate the location of rear-edge (purple) and range-core (yellow) sample sites. Green shapes indicate jack pine stands >4 ha according to Québec's ecoforest map sheets 21N, 22C, 22F and 22K (from south to north; MFFP, 2020). Different colors in the background represents different fire regime units (FRUs; Erni *et al.*, 2020), where pink is FRU 4, yellow is FRU 11, and orange is FRU 10 (salient features of the FRUs are provided in Table 1).

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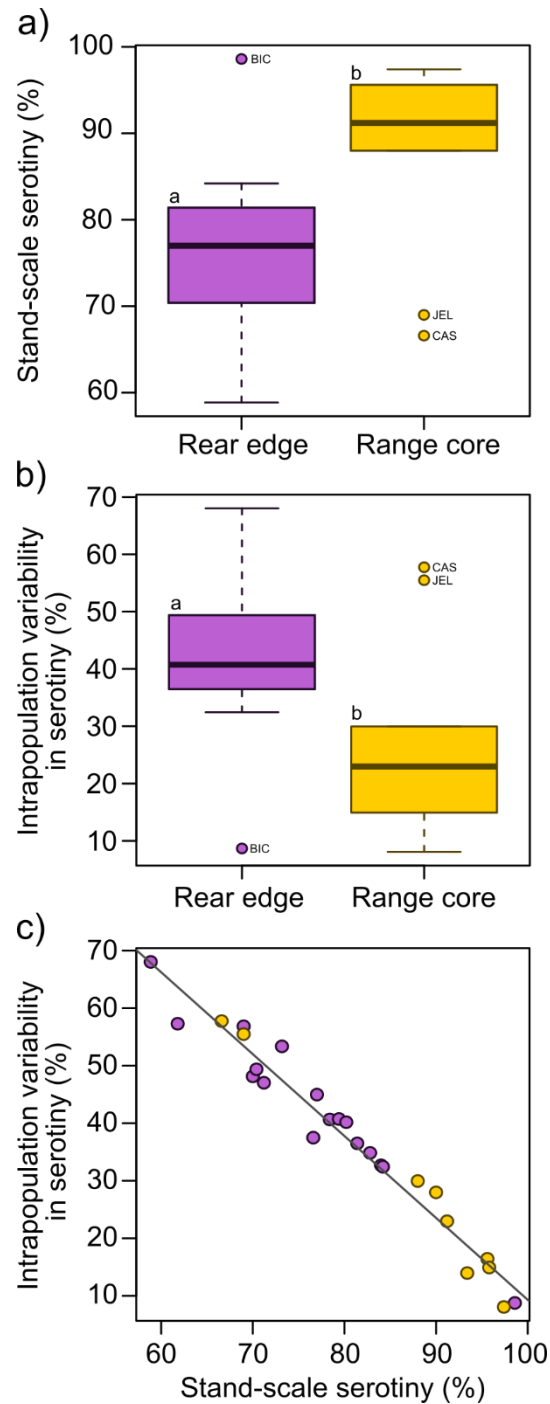
Figure 2. Intraspecific variation in serotiny among 26 jack pine (*Pinus banksiana*) stands including 17 rear-edge populations and 9 populations from the core of the range in eastern Québec. a) Comparison of stand-scale serotiny between rear-edge and core populations. b) Comparison of intrapopulation variability in serotiny between rear-edge and core populations. Boxplots indicate lower quartile, median, and upper quartile, and whisker length is $1.5 \times$ interquartile range. Different letters indicate statistically significant difference. c) Negative correlation between stand-scale serotiny and intrapopulation variability in serotiny. Rear-edge and range-core populations are shown in purple and yellow, respectively.
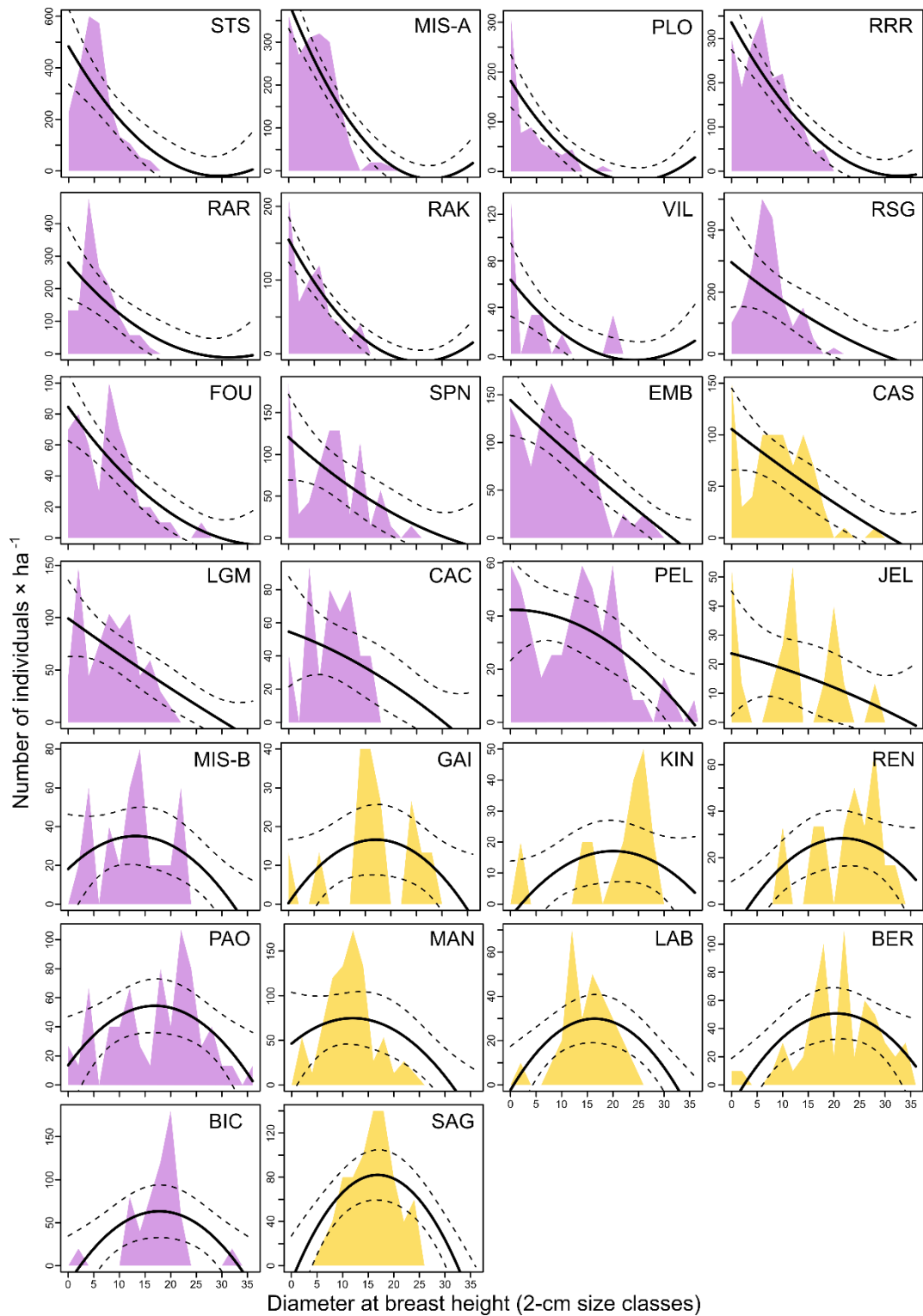
Figure 3. Empirical size structure and fitted quadratic model for 26 jack pine (*Pinus banksiana*) stands in eastern Québec. Colored polygons illustrate the actual number of individuals (per ha) in each 2-cm size class with rear-edge and range-core stands shown in purple and yellow, respectively. Solid and broken lines depict fitted quadratic models and 95% confidence intervals, respectively.

Plots are ordered from reverse J-shape (uneven sized) to unimodal (even sized). Parameters of the quadratic models are shown in Table 2.
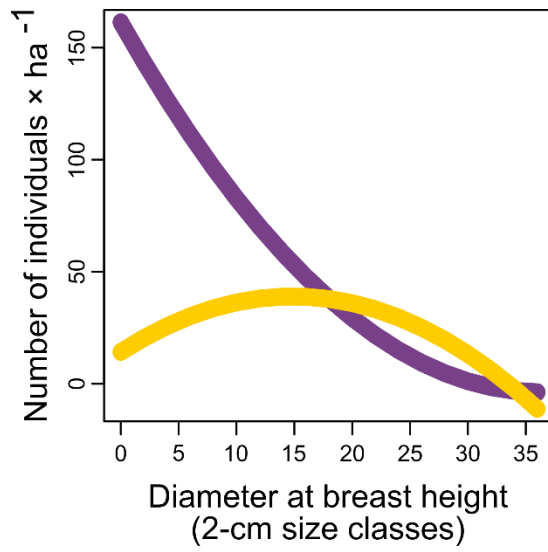
Figure 4. Composite quadratic models describing mean regional jack pine (*Pinus banksiana*) stand size structure at the rear edge (purple) and in the core of the range (yellow) in eastern Québec.
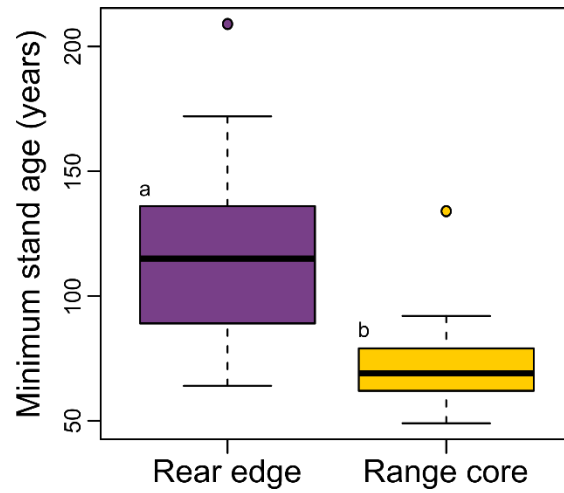
Figure 5. Comparison of minimum stand age between rear-edge and range-core jack pine (*Pinus banksiana*) forests in eastern Québec. Boxplots indicate lower quartile, median, and upper quartile, and whisker length is $1.5 \times$ interquartile range. Different letters indicate statistically significant difference.
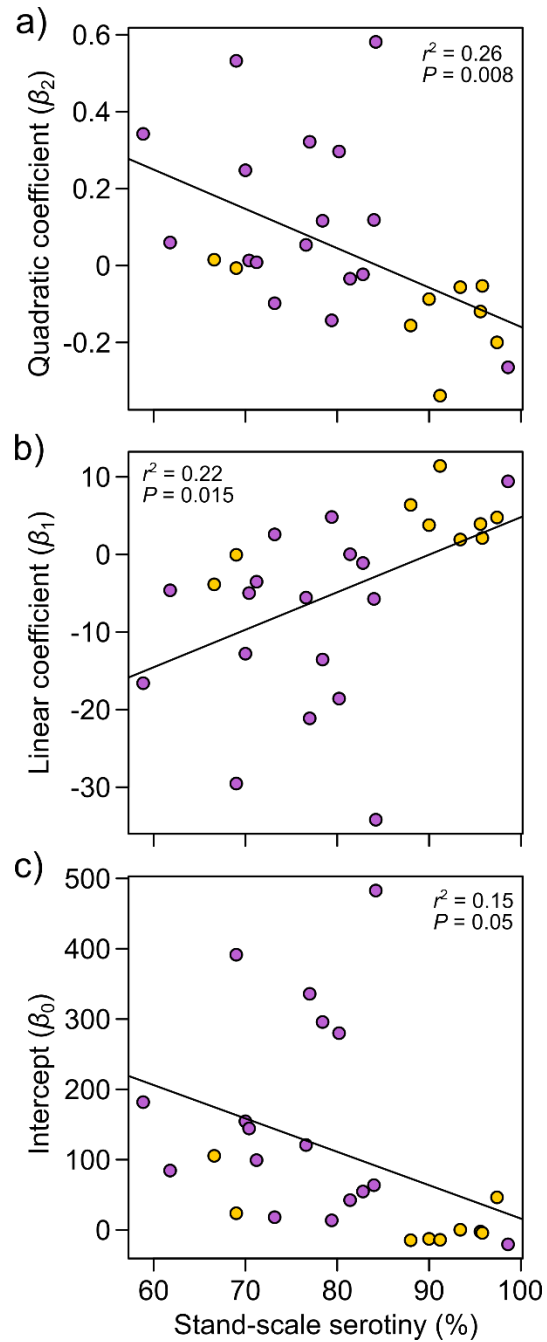
Figure 6. Parameters of the fitted quadratic model describing tree size structure − a) quadratic coefficients, b) linear coefficients, and c) intercepts − as a function of stand-scale serotiny in 26 jack pine (*Pinus banksiana*) stands in eastern Québec. Rear-edge and range-core populations are shown in purple and yellow, respectively.

Hedging at the rear edge: intraspecific trait variability drives the trajectory of marginal populations in a widespread boreal tree species

Table S1. Significance testing of pairwise differences in the level of intrapopulation variability in serotiny across 26 jack pine (*Pinus banksiana*) stands in eastern Québec. *P*-values (lower triangle) and false discovery rate (FDR) adjusted *q*-values (upper triangle) of pairwise asymptotic tests for the equality of the coefficients of variation (CV) of stand-level serotiny are shown in bold italics for statistically significant difference in variability between two sites or in grey boxes where the comparison is not significant. Rear-edge and core population names are shown in purple and yellow, respectively.

	PLO	FOU	MISA	RAK	EMB	LGM	MISB	RRR	RSG	PAO	SPN	RAR	PEL	CAC	VIL	STS	BIC	CAS	JEL	BER	REN	SAG	GAI	LAB	KIN	MAN
PLO		0.275	0.251	0.016	0.028	0.030	0.247	0.003	0.000	0.000	0.000	0.000	0.000	0.000	0.064	0.000	0.000	0.300	0.191	0.000	0.000	0.000	0.000	0.000	0.000	0.000
FOU	0.213		0.997	0.225	0.302	0.231	0.748	0.079	0.010	0.010	0.000	0.007	0.000	0.000	0.109	0.000	0.000	0.997	0.868	0.000	0.000	0.000	0.000	0.000	0.000	0.000
MISA	0.193	0.952		0.244	0.328	0.247	0.775	0.090	0.011	0.012	0.000	0.009	0.001	0.000	0.112	0.000	0.000	0.956	0.910	0.000	0.000	0.000	0.000	0.000	0.000	0.000
RAK	0.010	0.166	0.185		0.897	0.922	0.580	0.646	0.213	0.219	0.020	0.179	0.030	0.011	0.225	0.001	0.000	0.204	0.320	0.000	0.000	0.000	0.000	0.000	0.000	0.000
EMB	0.017	0.238	0.263	0.836		0.795	0.698	0.511	0.148	0.152	0.012	0.122	0.018	0.006	0.203	0.001	0.000	0.276	0.421	0.000	0.000	0.000	0.000	0.000	0.000	0.000
LGM	0.019	0.173	0.189	0.865	0.724		0.521	0.807	0.328	0.335	0.052	0.290	0.073	0.029	0.249	0.005	0.000	0.215	0.312	0.001	0.000	0.000	0.000	0.000	0.000	0.000
MISB	0.189	0.671	0.704	0.506	0.620	0.452		0.321	0.092	0.095	0.008	0.077	0.012	0.004	0.148	0.001	0.000	0.716	0.874	0.000	0.000	0.000	0.000	0.000	0.000	0.000
RRR	0.002	0.052	0.060	0.572	0.440	0.738	0.257		0.461	0.471	0.079	0.410	0.107	0.045	0.297	0.009	0.000	0.071	0.128	0.001	0.000	0.000	0.000	0.000	0.000	0.000
RSG	0.000	0.005	0.006	0.155	0.104	0.264	0.061	0.390		1.000	0.335	0.969	0.418	0.236	0.458	0.073	0.000	0.008	0.019	0.012	0.002	0.000	0.000	0.000	0.000	0.000
PAO	0.000	0.006	0.007	0.161	0.108	0.271	0.064	0.400	0.985		0.328	0.956	0.410	0.231	0.455	0.071	0.000	0.009	0.019	0.012	0.002	0.000	0.000	0.000	0.000	0.000
SPN	0.000	0.000	0.000	0.012	0.007	0.033	0.004	0.051	0.273	0.265		0.389	0.929	0.866	0.766	0.441	0.000	0.000	0.001	0.150	0.041	0.000	0.000	0.000	0.000	0.000
RAR	0.000	0.004	0.005	0.128	0.084	0.226	0.050	0.337	0.920	0.905	0.319		0.471	0.274	0.478	0.089	0.000	0.006	0.014	0.016	0.003	0.000	0.000	0.000	0.000	0.000
PEL	0.000	0.000	0.000	0.019	0.011	0.047	0.007	0.073	0.348	0.339	0.874	0.402		0.754	0.717	0.357	0.000	0.000	0.001	0.111	0.028	0.000	0.000	0.000	0.000	0.000
CAC	0.000	0.000	0.000	0.006	0.003	0.018	0.002	0.028	0.177	0.172	0.800	0.212	0.680		0.850	0.591	0.000	0.000	0.000	0.231	0.073	0.000	0.000	0.000	0.000	0.000
VIL	0.040	0.075	0.077	0.166	0.147	0.191	0.104	0.233	0.386	0.382	0.693	0.409	0.641	0.782		1.000	0.000	0.107	0.123	0.754	0.520	0.090	0.000	0.000	0.000	0.000
STS	0.000	0.000	0.000	0.001	0.000	0.003	0.000	0.005	0.047	0.045	0.369	0.059	0.291	0.519	0.971		0.000	0.000	0.000	0.540	0.236	0.003	0.000	0.000	0.000	0.000
BIC	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000		0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.483
CAS	0.236	0.950	0.903	0.148	0.215	0.157	0.637	0.045	0.005	0.005	0.000	0.003	0.000	0.000	0.072	0.000	0.000		0.824	0.000	0.000	0.000	0.000	0.000	0.000	0.000
JEL	0.137	0.804	0.850	0.255	0.351	0.248	0.812	0.089	0.011	0.012	0.000	0.008	0.001	0.000	0.086	0.000	0.000	0.756		0.000	0.000	0.000	0.000	0.000	0.000	0.000
BER	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.007	0.007	0.106	0.009	0.076	0.172	0.681	0.470	0.000	0.000	0.000		0.602	0.023	0.000	0.000	0.000	0.000
REN	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.001	0.025	0.001	0.017	0.047	0.449	0.178	0.000	0.000	0.000	0.531		0.097	0.000	0.000	0.000	0.000
SAG	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.059	0.002	0.000	0.000	0.000	0.014	0.066		0.000	0.003	0.000	0.000
GAI	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000		0.158	0.591	0.000
LAB	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.113		0.418	0.000
KIN	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.518	0.347		0.000
MAN	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.414	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	

Figure S1. Relationship between tree age and tree diameter at breast height (DBH) in jack pine (*Pinus banksiana*) stands from eastern Québec. Rear-edge and range-core populations are shown in purple and yellow, respectively. The relationship is based on the 10 c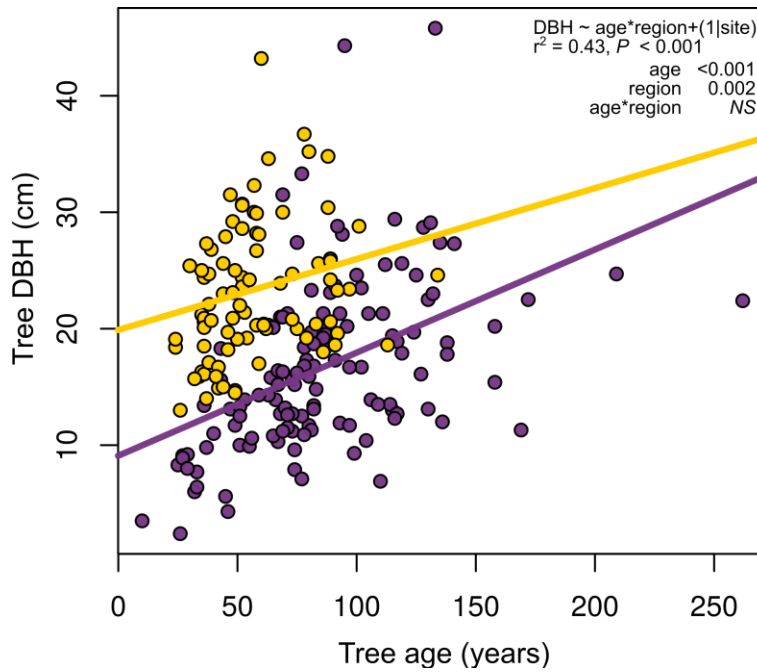ored trees per study site used to estimate the minimum age for each stand. The linear mixed model was computed with *lmer*() function in the R package *lmerTest*.