UQAR
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LA VARIABILITÉ PHÉNOTYPIQUE DU SÉROTINISME ET SON RÔLE SUR LA PERSISTANCE DU PIN GRIS À LA LIMITE SUD DE SON AIRE DE RÉPARTITION

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PAR

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RÉSUMÉ

Les populations à la marge chaude de l'aire de répartition d'une espèce sont souvent petites, isolées et à la limite de leur enveloppe bioclimatique/écologique. La variation phénotypique intraspécifique pourrait contribuer au maintien local des populations marginales, qui risquent l'extirpation lorsque leur capacité de migration est insuffisante pour suivre la vélocité des changements climatiques. Au Bas-Saint-Laurent, des populations marginales de pin gris persistent hors du biome boréal, malgré l'absence de feux naturels essentiels à l'ouverture des cônes sérotineux. Une variabilité du degré de sérotinisme pourrait expliquer cette persistance. Cette étude vise à évaluer les facteurs écologiques associés à la variabilité intraspécifique du sérotinisme à la limite sud de la répartition du pin gris et à déterminer l'effet de cette variabilité sur la trajectoire démographique des populations marginales. À cette fin, nous avons estimé le sérotinisme à l'échelle du peuplement, l'âge minimal et la structure de taille des arbres dans 26 peuplements de pin gris à la marge sud et au cœur de la répartition de l'espèce dans l'est du Canada. Nous avons ensuite déterminé le rôle potentiel de divers facteurs écophysiologiques sur la température d'ouverture de 1381 cônes et sur leur potentiel de régénération. Les populations marginales ont un degré de sérotinisme moindre et plus variable que celles au cœur de la répartition, permettant une régénération continue en plus d'un recrutement après-feu. Les cônes des peuplements marginaux s'ouvrent à des températures réduites qui augmentent avec leur âge, alors que les cônes des peuplements au cœur de la répartition s'ouvrent à une température plus élevée et constante. La viabilité des graines à la marge est constante peu importe l'âge des cônes (51% des graines viables), alors qu'elle diminue de 40% en 20 ans (passant de 70% à 30% de graines viables) en forêt boréale. Les populations marginales misent sur une double stratégie de reproduction (cônes ouverts et fermés) afin d'assurer une régénération adéquate avec ou sans feu, contrairement aux peuplements boréaux où tous les individus proviennent du dernier feu. Cette capacité à faire face à un régime de feux peu fréquents et imprévisibles devrait accroître la résilience des populations de pins gris alors que les changements globaux modifient la dynamique des feux de la forêt boréale.

Mots clés : adaptation locale, biome boréal, dynamique éco-évolutive, trajectoire démographique, stratégie de minimisation des risques, marge sud, populations marginales, régime de feu, *Pinus banksiana*, sérotinisme

ABSTRACT

Marginal populations at the rear edge of their distribution are often small, isolated, and at the limit of their bioclimatic or ecological envelope. Intraspecific phenotypic variation could contribute to the persistence of peripheral populations, which risk extirpation where range shifts lag behind climate change velocity. In the Lower Saint-Lawrence region, marginal jack pine populations persist outside the boreal biome, despite the virtual absence of wildfires necessary to the opening of its serotinous cones. An intraspecific variability in the degree of cone serotiny could contribute to such long-term persistence. This study aims to evaluate ecological factors associated with the intraspecific variability of serotiny at the rear edge of jack pine distribution and to determine the effect of this variability on the demographic trajectory of marginal populations. To this end, we estimated stand-scale serotiny, minimum age and tree size structure in 26 jack pine stands at the rear edge and at the core of the species distribution in Eastern Canada. We then assessed the potential role of various ecophysiological factors on the opening temperature of 1381 cones and on their regeneration potential. In rear-edge populations, cone serotiny is lower and more variable compared to range-core populations, which allows for a continuous recruitment as well as a postfire regeneration. Cones from marginal populations dehisce at a lower opening temperature, which increases with cone age. Cones from range-core stands open at a more constant, yet higher temperature. At the rear edge, seed viability remains invariable with cone age (51%), whereas it decreases from 70% to 30% in 20 years at the range core. Unlike semelparous range-core populations displaying a single aging cohort lacking interfire recruitment, rear-edge populations exhibit a dual life-history strategy that ensures both steady recruitment during fire-free intervals (iteroparity) and successful postfire regeneration. This capacity to cope with infrequent and unpredictable fire regime should increase the resilience of jack pine populations as global changes alter fire dynamics of the boreal forest.

Keywords: local adaptation, boreal biome, eco-evolutionary dynamics, demographical trajectory, bet-hedging, rear edge, marginal populations, fire regime, *Pinus banksiana*, serotiny

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Afin de bien informer les plans de conservation de la biodiversité, il est primordial d'évaluer correctement les réponses des écosystèmes terrestres face aux changements climatiques (Dawson *et al.*, 2011). Sur la base d'analyses paléopolliniques, la migration a longtemps été considérée comme la principale réponse des espèces végétales aux oscillations climatiques du Quaternaire (Huntley et Webb, 1989; Parmesan, 2006). Conséquemment, les prédictions actuelles quant à l'avenir des écosystèmes forestiers sont généralement basées sur le potentiel de migration des espèces qui leur permet de s'établir dans des environnements nouvellement favorables (p. ex., Woodall *et al.*, 2009; Chen *et al.*, 2011; Zhu, Woodall et Clark, 2012; Berteaux, 2014; Boisvert-Marsh, Périé et de Blois, 2014; Sittaro *et al.*, 2017). Ce potentiel de migration est particulièrement important pour les populations marginales, c'est-à-dire les populations qui se trouvent aux limites de l'aire de répartition des espèces. Certains auteurs proposent toutefois que les populations de plusieurs espèces végétales ne seront pas en mesure de migrer assez rapidement pour suivre la vélocité du réchauffement climatique, qui modifie rapidement les conditions environnementales de leurs écosystèmes (Zhu, Woodall et Clark, 2012; Sittaro *et al.*, 2017; Corlett et Westcott, 2013).

Dans l'hémisphère nord, les populations périphériques se situant à la limite sud des aires de leur répartition sont à la marge chaude de leur enveloppe climatique. Ces populations marginales et la diversité phénotypique/génétique qui s'y trouve localement sont voués à l'extinction si elles ne sont pas en mesure de s'établir assez rapidement plus au nord (Malcolm *et al.*, 2002). Cette menace est particulièrement inquiétante pour les écosystèmes forestiers du biome boréal qui se réchauffent deux fois plus rapidement que la moyenne globale (Bush et Lemmen, 2019). On reconnaît maintenant que l'extirpation des populations peut être évitée grâce aux interactions complexes entre les processus de migration et d'adaptation en réponse aux changements climatiques (Davis et Shaw, 2001; Aitken *et* al, 2008; de Lafontaine *et al.*, 2018). Toutefois, l'adaptation demeure encore rarement prise en compte lorsque la question des changements climatiques est discutée puisque son rôle dans le maintien des peuplements naturels est plutôt difficile à déterminer (Gienapp *et al.*, 2008; Hoffmann et Sgrò, 2011; Catullo, Ferrier et Hoffmann, 2015; Peterson, Doak et Morris, 2010).

La variabilité intraspécifique

Pourtant, la variabilité intraspécifique, due à l'adaptation locale et/ou la plasticité phénotypique, peut modifier considérablement les prédictions des déplacements des aires de répartition des espèces en réponse aux changements globaux (Benito Garzón *et al.*, 2011). Par exemple, les populations vulnérables de la marge chaude des aires de répartition peuvent persister à la limite de leur enveloppe environnementale grâce à cette variabilité, malgré l'effondrement attendu de ces populations (Hampe et Petit, 2005; Sexton *et al.*, 2009). Les populations marginales étant généralement petites et isolées les unes des autres, leur situation géographique favorise la dérive génétique à l'intérieur de ces populations et réduit le flux de gènes entre elles-mêmes et celles dans l'aire de répartition continue de l'espèce (Lesica et Allendorf, 1995; Vucetich et Waite, 2003; Hampe et Petit, 2005; Eckert *et al.*, 2008). Faisant face à un environnement qui n'est pas optimal à l'espèce, ces populations peuvent donc être soumises à de fortes pressions de sélection naturelle et présenter des adaptations locales aux conditions environnementales singulières (Davis et Shaw, 2001; Franks, Weber et Aitken, 2014; Nadeau et Urban, 2019). La plasticité phénotypique, c'est-à-dire la variation de phénotypes pour un même génotype en réponse à un changement environnemental, peut également jouer un rôle dans la persistance de ces populations marginales (Bradshaw, 1965). La plasticité phénotypique elle-même est sujette à la sélection et peut donc être plus ou moins grande pour une même espèce (Chevin et Lande, 2011; Chevin et Hoffmann 2017). En effet, des conditions environnementales imprédictibles et en changement peuvent promouvoir le développement d'une plus grande plasticité phénotypique avantageuse et qui reflète une adaptation des populations locales (Olofsson *et al.*, 2009). Dans certains cas, un environnement imprédictible d'une génération à l'autre peut mener au développement d'une stratégie de minimisation des risques (*bet-hedging)* chez les individus. Cette stratégie peut être conservatrice (c.-à-d. production de phénotypes assurés d'avoir une bonne valeur adaptative) ou diversifiée (c.-à-d. production d'une variété de phénotypes afin d'assurer la survie de certains individus quelles que soient les conditions futures; Seger et Brockmann, 1987). Ces deux stratégies de minimisation des risques entrainent la réduction de la variance de la valeur adaptative à long terme en sacrifiant la valeur adaptative moyenne à court terme (Childs *et al.*, 2010). La production d'une variété de phénotypes peut ainsi permettre une capacité de persistance accrue des populations marginales. Dans un environnement faisant face aux changements globaux, tel que les populations à la limite sud de la forêt boréale, la variabilité intraspécifique – adaptative ou plastique – des traits écophysiologiques peut s'avérer primordiale afin d'assurer la persistance locale des peuplements. Le cas échéant, il est possible que les populations marginales ne soient pas soumises à un processus d'extinction, mais représentent plutôt des populations démographiquement stables et bien adaptées localement aux conditions environnementales (Hampe et Petit, 2005).

Le pin gris comme modèle d'étude

En Amérique du Nord, le pin gris (*Pinus banksiana*, Lamb.) est l'espèce boréale transcontinentale la mieux adaptée aux fréquents feux de forêt (Rowe et Scotter, 1973). Typiquement, la dynamique des populations de cette espèce est largement déterminée par le sérotinisme. Ce trait adaptatif implique la capacité d'emmagasiner une banque de graines dans la canopée d'un peuplement grâce à des cônes fermés, ce qui fournit au pin gris un potentiel de régénération accru dans les conditions optimales suivant un feu. Le couvert végétal de la plupart des espèces compétitrices est alors brûlé et le sol minéral est exposé. Les cônes du pin gris s'ouvrent et libèrent leurs graines lorsque la couche de résine qui les protège est altérée par la température élevée du feu. Celles-ci se retrouvent alors dans des conditions favorables pour cette espèce intolérante à l'ombre, ayant un accès pratiquement total à la lumière (Lamont *et al.*, 1991). On peut donc typiquement observer des peuplements de pin gris à structure équienne (c.-à-d. composé d'individus de même âge), où tous les individus proviennent de la même cohorte suivant un feu. Une structure de tailles provenant de tels peuplements matures est donc en forme de « cloche », indiquant des individus d'âges semblables et peu de régénération (Figure 1a). À l'inverse, la structure de taille d'un peuplement stable et inéquienne (c.-à-d. composé d'individus de différents âges) est plutôt en « j-inversé », indiquant la présence de régénération ainsi que des individus d'âges variés (Figure 1b).

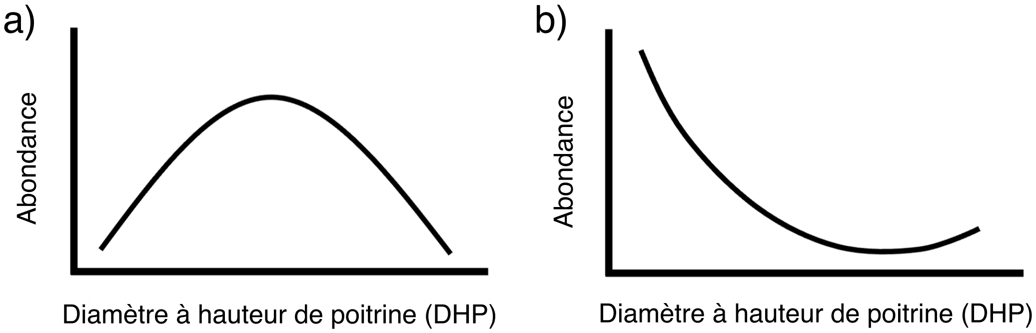

Figure 1. a) Structure de taille en « cloche » typique des populations matures de pins gris (peuplement équienne) b) Structure de taille en « j-inversé » (peuplement inéquienne).

En absence de feu sévère durant une période de plus de 220 ans, les peuplements de pins gris, n'ayant pas libéré leurs graines, sont généralement remplacés par des espèces plus tolérantes à l'ombre qui sont en mesure de s'établir sous un couvert végétal fermé (Le Goff et Sirois, 2004). Ce remplacement pourrait être évité grâce à la diminution du degré de sérotinisme (c.-à-d. la quantité de cônes fermés/quantité de cônes total), qui permet l’ouverture de certains cônes et donc la dispersion de graines malgré l’absence de feu. Certaines études ont démontré que le degré de sérotinisme semble varier selon la fréquence et la sévérité des feux de forêts, qui exercent une pression de sélection influençant la capacité de régénération et la trajectoire démographique des espèces sérotineuses (Lamont *et al.*, 1991). Un régime de feux de forêt naturels rares et imprévisibles marque la limite sud de l’aire de répartition du pin gris, à l’interface entre le nord de la forêt tempérée et le sud de la forêt boréale. Puisque le climat est peu propice aux feux naturels en forêt tempérée, la dynamique éco-évolutive des populations méridionales de pin gris pourrait dévier de celle documentée en milieu boréal. Or, les conditions de la marge sud pourraient se généraliser dans la partie sud de la forêt boréale au cours des prochaines décennies. En effet, même si le réchauffement climatique devrait créer des conditions propices aux feux dans la forêt boréale, la migration nordique d’espèces feuillues moins inflammables pourrait contribuer à réduire leur fréquence dans sa partie sud (Girardin *et al.*, 2013). Le sérotinisme étant un trait affectant directement le potentiel de régénération et donc la valeur adaptative des individus, le pin gris est un modèle idéal afin de déterminer le potentiel d’adaptation locale des populations marginales. Toutefois, il n’existe que peu de données probantes sur les mécanismes déterminant la variabilité du degré de sérotinisme chez le pin gris et l’effet de cette variabilité sur la démographie des peuplements (Gauthier, Bergeron et Simon, 1993; 1996).

La variabilité du degré de sérotinisme

Bien qu’un faible degré de sérotinisme ait été rapporté à divers endroits au sud de la forêt boréale, les facteurs qui déterminent la variabilité de ce trait chez le pin gris demeurent encore mal compris. Au Wisconsin, Radeloff *et al.* (2004) ont proposé qu’une faible fréquence de feux létaux et/ou une haute fréquence de feux de surface non-létaux dans les forêts préindustrielles auraient entraîné une diminution du degré de sérotinisme dans les populations marginales de pin gris. Suivant leur interprétation, les feux de surface réduisent la quantité de combustible disponible, ce qui diminue la température pouvant être atteinte lors des feux subséquents, empêchant ainsi la fonte de la résine des cônes (Heinselman, 1973; Muir et Lotan, 1985). Radeloff *et al.* (2004) proposent qu'une fréquence élevée de feux létaux, qui permettent la régénération des peuplements, est corrélée à un haut degré de sérotinisme. Dans l'ouest du Québec, la variabilité du sérotinisme chez le pin gris a également été associée à une différence dans le régime de feu entre les îles du Lac Duparquet et le continent (Gauthier, Bergeron et Simon, 1996; Briand *et al.*, 2015). Un degré de sérotinisme plus bas a été observé dans les peuplements soumis à des feux de surface non-létaux, alors que de fréquents feux de cimes létaux augmenteraient l'abondance d'individus plus sérotineux (Gauthier, Bergeron et Simon, 1996; Briand *et al.*, 2015). Ces résultats suggèrent que la fréquence des feux et leur sévérité représentent une importante pression de sélection sur ce trait écophysiologique directement relié à la reproduction. De plus, comme le sérotinisme est un trait phénotypique variable fortement héritable génétiquement (Pike, 2011; Wymore *et al.*, 2011), la fréquence du sérotinisme dans une population pourrait changer en seulement quelques générations (Radeloff *et al.*, 2004). Un faible niveau de sérotinisme pourrait donc représenter une réponse adaptative des peuplements soumis à un climat peu propice au feu (Lamont *et al.*, 1991). Ce lien entre la fréquence des feux de forêt et le degré de sérotinisme a également été observé chez le pin d'Alep (*Pinus halepensis*; Hernándo-Serrano *et al.*, 2013), le pin maritime (*Pinus pinaster*; Hernándo-Serrano *et al.*, 2013), le pin rigide (*Pinus rigida*; Givnish, 1981) et le pin tordu (*Pinus contorta*; Schoennagel *et al.*, 2003).

Outre cette association générale entre le régime de feu et le degré de sérotinisme, on connaît étonnamment peu les facteurs influençant l'ouverture des cônes du pin gris en absence de feu. On retrouve plus d'études effectuées sur la variabilité de ce trait chez le pin d'Alep, qui porte à la fois des cônes sérotineux et non sérotineux. Chez cette espèce, il a été déterminé que le coût de maintien des cônes sérotineux mène éventuellement à leur ouverture par sénescence (Martín-Sanz *et al.*, 2017). Spécifiquement, les vieux cônes entrent en compétition avec les plus jeunes pour l'allocation des ressources hydriques de l'arbre. Chez le pin d'Alep, il a donc été suggéré que l'ouverture des cônes plus âgés et plus secs était déclenchée par une exposition à une température inférieure à celle nécessaire pour ouvrir les cônes plus jeunes (Tapias *et al.*, 2001; Martín-Sanz *et al.*, 2017). Cette réponse à la disponibilité en eau du cône implique que le mécanisme d'ouverture des cônes dépend directement de leur taux d'humidité : les écailles d'un cône jeune et humide restent fermées et celles d'un cône plus vieux et sec tendent à s'ouvrir, même en absence de feu (Harlow, Côté et Day, 1964). Or, même si les cônes plus âgés pouvaient éventuellement s'ouvrir en absence de feu chez le pin gris, il est incertain que cela confère un avantage, puisque leurs graines sont moins viables que celles des cônes plus jeunes (Roe, 1963; Popovich, Demers et Gagnon, 1970; Jeffers, 1985). Chez le pin gris, Gauthier, Bergeron et Simon (1993) ont déterminé que la majorité des individus de moins de 7 cm de diamètre ne portent pas de cônes sérotineux, suggérant que la première cohorte d'arbres après-feu serait prédisposée à se régénérer rapidement, permettant de densifier le peuplement avec une deuxième cohorte avant l'établissement des espèces plus compétitives. De plus, ils rapportent que la proportion de cônes sérotineux augmente annuellement pour les arbres de 0 à 10 cm de diamètre et que l'expression du sérotinisme est à son maximum après 20 ou 30 ans. Ce délai permettrait la croissance rapide de l'effectif de la population dans les cas où peu d'individus auraient pu s'établir après feu. L'augmentation du sérotinisme avec l'âge des individus permet éventuellement de maintenir une banque de graine dans la canopée lorsque le couvert de la forêt devient trop dense pour l'établissement de plantules (Gauthier, Bergeron et Simon, 1993). De plus, Crossley (1956) a déterminé que les cônes du pin tordu sont exposés à une température plus grande lorsqu'ils sont positionnés plus près du sol, à une hauteur inférieure à 16,5 cm. Dû à ce gradient de température près du sol, les branches les plus basses des pins sérotineux pourraient porter des cônes ouverts (Crossley, 1956). L'ouverture serait alors causée par le rayonnement thermique du sol, qui permettrait d'atteindre une température suffisante pour faire fondre la résine des cônes du pin tordu (Lotan, 1964). Chez le pin gris, Gauthier, Bergeron et Simon (1993) ont observé plus de cônes ouverts sur les branches situées à moins de 2,6 m de hauteur chez les individus de plus de 10 cm de diamètre. Toutefois, ils ont attribué cette différence à l'âge plus élevé des branches basses plutôt qu'à la chaleur radiative du sol. En milieu naturel, l'effet de la radiation peut donc être confondu avec l'âge plus avancé des branches les plus basses qui pourrait également être la cause de l'ouverture hâtive de leurs cônes (Gauthier, Bergeron et Simon, 1993). En milieu contrôlé, l'énergie thermique déjà accumulée, plus grande chez les cônes près du sol, pourrait possiblement permettre leur ouverture après une plus faible exposition à la chaleur en laboratoire que les cônes sur des branches plus élevées.

Dans l'est du Québec, la limite sud de l'aire de répartition du pin gris se trouve à la transition entre la forêt boréale et la forêt décidue, dans la forêt mixte de la région du Bas-Saint-Laurent (Rudolph et Laidly, 1990). Les petites populations marginales de cette région sont moins nombreuses et plus isolées que dans le biome boréal. De plus, le cycle de feux naturels de ~1670 ans (Elzein *et al.*, 2020) y est considérablement plus long que celui de 150 à 200 ans en forêt boréale (Bouchard, 2015). Le climat et l'environnement au Bas-Saint-Laurent, peu propices aux feux de forêts naturels, représentent ainsi une pression de sélection qui pourrait favoriser un faible degré de sérotinisme. En retour, la possibilité de libérer les graines dès leur maturité pourrait permettre le recrutement continu du pin gris même en absence de feu et ainsi modifier la trajectoire démographique de l'espèce à sa marge sud en assurant la persistance de l'espèce à sa limite méridionale.

OBJECTIFS ET HYPOTHÈSES

Afin de mieux comprendre les réponses des écosystèmes boréaux aux changements climatiques, il est important de bien caractériser la dynamique écologique et évolutive des populations formant la limite sud du biome, soit la marge la plus susceptible au réchauffement. Nous proposons d'évaluer la variabilité du sérotinisme ainsi que d'autres traits phénotypiques reliés à la régénération des populations du pin gris au Bas-Saint-Laurent et de déterminer l'impact de cette variabilité sur la trajectoire démographique de ces populations (c.-à-d. déclin vs maintien). **L'hypothèse de travail est qu'un degré de sérotinisme réduit à la marge sud du pin gris reflète une adaptation permettant le maintien des populations malgré une faible activité de feu à la limite de l'enveloppe environnementale de l'espèce.**

Le **chapitre 1** de ce mémoire vise d'abord (1) à comparer le degré de sérotinisme des populations marginales au Bas-Saint-Laurent avec des populations de la forêt boréale afin de déterminer si le sérotinisme est réduit à limite sud de l'aire de répartition du pin gris.

Si l'ouverture des cônes reflète effectivement une adaptation au régime de feu, un faible degré de sérotinisme devrait permettre le maintien des populations dans les environnements soumis à une faible fréquence de feu. Dans ce cas, on s'attend à ce que la variabilité du degré de sérotinisme se traduise par des différences quant à la structure démographique des peuplements. À cette fin, le deuxième objectif du **chapitre 1** vise (2) à déterminer si la variabilité du sérotinisme est associée à la structure et la trajectoire démographique des peuplements (c.-à-d. déclin vs maintien) à la marge sud de sa répartition. Si le sérotinisme réduit confère un avantage face aux longs intervalles de feu au Bas-Saint-Laurent, on s'attend à observer des peuplements stables à structure inéquienne et incluant des jeunes arbres en régénération à la marge sud et des peuplements équiennes provenant d'une seule cohorte après feu dans au centre de l'aire de répartition géographique de l'espèce.

Dans le **chapitre 2**, cette étude vise finalement (3) à évaluer l'effet de divers facteurs physiologiques et environnementaux susceptibles d'influencer l'ouverture des cônes en absence de feu. La sénescence et le rayonnement thermique pourraient contribuer à l'ouverture prématurée des cônes sans toutefois représenter une adaptation au régime de feu. En absence prolongée de feu, une remobilisation des ressources vers les cônes plus jeunes pourrait entraîner l'ouverture des cônes plus âgés, libérant ainsi des graines moins viables. On s'attend alors à ce que les cônes plus âgés soient moins sérotineux et que leur capacité de germination soit réduite par rapport aux cônes plus jeunes. Dans les peuplements sur substrat rocheux, l'accumulation de chaleur près du sol pourrait déclencher l'ouverture des cônes en absence de feu. On s'attend alors à ce que les cônes provenant de branches plus basses s'ouvrent après une exposition moins grande à la chaleur que les cônes provenant de branches plus hautes en conséquence de l'énergie thermique déjà accumulée dans ces cônes depuis leur maturité. Chez les plus jeunes pins gris de petit diamètre à hauteur de poitrine (DHP), un délai de l'apparition du sérotinisme permettrait une densification du peuplement dans les années suivant un feu. On s'attend donc à une ouverture plus rapide lors d'une exposition à la chaleur des cônes provenant d'individus plus petits/jeunes.

MÉTHODE UTILISÉE

En associant la variabilité du sérotinisme sur le terrain et en laboratoire, cette étude permet d'élucider les causes d'ouverture des cônes de pin gris et de quelle façon ce potentiel d'ouverture diffère selon la localisation du peuplement dans l'aire de répartition de l'espèce et le régime de feux associé. Pour y arriver, le **chapitre 1** établit un degré de sérotinisme sur le terrain et évalue l'association entre sa variabilité et la structure de taille de 26 peuplements (17 sites marginaux et 9 sites boréaux) dans l'est du Canada. Le degré de sérotinisme apparent sur le terrain a été déterminé en classant 100 individus selon leur pourcentage de cônes fermés sur le nombre de cônes total dans leur couronne, en excluant les cônes immatures (<2 ans) et les cônes portés sur les branches mortes. Cette méthode permet une estimation rapide du degré de sérotinisme moyen d'un peuplement lorsque le nombre de sites échantillonnés est élevé. De plus, cette méthode est adéquate pour une espèce portant des cônes sérotineux qui restent indéfiniment sur les branches de l'arbre, tel le pin gris. La persistance des cônes de tous les âges dans l'arbre nous permet donc d'estimer un portrait global du degré de sérotinisme. La structure de taille a été estimée en mesurant tous les pins gris de plus de 2 cm de DHP et en dénombrant tous ceux ayant un DHP plus petit ou égal à 2 cm (régénération) dans une parcelle échantillon entre 500 et 1000 m^2, selon la densité du peuplement. Un modèle quadratique a été appliqué à chaque site pour décrire la forme de la structure de taille du peuplement. L'association entre le degré de sérotinisme et la structure de taille a été testée par des relations linéaires entre le sérotinisme et les trois paramètres des modèles quadratiques (composante linéaire, composante quadratique et ordonnée à l'origine).

Au **chapitre 2**, le degré de sérotinisme à chaque site a été mis en relation avec l'énergie thermique nécessaire pour ouvrir les cônes en milieu contrôlé. En laboratoire, le sérotinisme est évalué par l'exposition des cônes à différentes températures à l'étuve (48, 51, 54, 57, 60 et 63°C). La sélection de températures plutôt basses permet l'ouverture graduelle des cônes et ainsi une observation plus facile de la variabilité de ce phénomène, tout en conservant le potentiel de germination des graines. Le niveau d'ouverture des cônes a été évalué à chaque heure, alors que la température était graduellement augmentée de 3°C. Cette méthode permet de comparer la quantité d'énergie thermique accumulée nécessaire à l'ouverture des cônes en fonction de différentes variables physiologiques et environnementales. Cette variable réponse, nommée simplement *température d'ouverture*, représente l'énergie thermique accumulé par les cônes selon le temps passé aux différentes températures à l'étuve (température × temps). Tel que présumé initialement, le degré de sérotinisme moyen de la population est positivement corrélé avec la température d'ouverture : les données d'ouverture en laboratoire reflètent donc le potentiel d'ouverture des cônes selon le degré de sérotinisme observé en nature sur leur site respectif. En associant des facteurs physiologiques et environnementaux (âge de l'arbre, âge du cône, DHP, hauteur de la branche) avec l'énergie thermique nécessaire à l'ouverture des cônes en laboratoire, cette méthode nous permet d'approfondir nos connaissances sur la variabilité du sérotinisme chez le pin gris.

Ensemble, les deux chapitres permettent d'élucider les facteurs affectant la variabilité intraspécifique du sérotinisme, qu'ils soient spécifiques ou non à la limite sud de l'aire de répartition de l'espèce.

CHAPITRE 1

LA VARIABILITÉ INTRASPÉCIFIQUE DU SÉROTINISME MODULE LA TRAJECTOIRE DÉMOGRAPHIQUE DES POPULATIONS DE PINS GRIS À LA LIMITE SUD DE LA RÉPARTITION DE L'ESPÈCE

1.1 RÉSUMÉ EN FRANÇAIS DU PREMIER ARTICLE

1. Les populations formant la marge chaude de l'aire de répartition d'une espèce sont souvent petites, isolées et confrontées à des conditions environnementales à la limite de leur enveloppe bioclimatique. Ces populations périphériques pourraient être à risque d'extinction si leur capacité de migration est insuffisante pour suivre la vélocité des changements climatiques. Cependant, la variation phénotypique intraspécifique pourrait contribuer au maintien local de telles populations marginales.

2. Nous avons étudié le rôle potentiel de la variation intraspécifique du sérotinisme sur le maintien des populations à la marge sud du pin gris (*Pinus banksiana*), une espèce boréale généralement considérée pyriscente obligatoire dépendante des feux de forêt. Nous avons évalué l'association entre le sérotinisme et la trajectoire démographique de peuplements marginaux situés au sud du biome boréal, dans la forêt tempérée où les feux naturels sont peu fréquents et imprévisibles. À cette fin, nous avons estimé le sérotinisme à l'échelle du peuplement, l'âge minimal et la structure de taille des arbres dans 26 peuplements de pin gris à la marge sud (n = 17 sites) et au centre (n = 9 sites) de l'aire de répartition de l'espèce dans l'est du Canada.

3. En moyenne, les populations de pins gris à la marge sud ont un degré de sérotinisme moindre, quoique plus variable, par rapport aux populations du centre de l'aire de répartition où le degré de sérotinisme est plus uniformément élevé. Les peuplements de la marge sud sont généralement plus âgés et affichent une structure de taille d'arbre en forme de « J-inversé » indiquant un équilibre démographique typique des vieilles forêts, tandis que les peuplements du centre sont plus jeunes et présentent une structure de peuplement unimodale représentant une seule cohorte vieillissante dépourvue de recrutement entre les feux. La dynamique éco-évolutive passe d'une dépendance aux feux de forêt dans les populations du centre de l'aire de répartition à des peuplements qui peuvent se régénérer et persister sans feux récurrents à la marge sud, où le sérotinisme à l'échelle du peuplement atteint des valeurs généralement inférieures à 85 %.

4. Synthèse : Contrairement aux populations du centre de l'aire de répartition de l'espèce, les populations de pins gris à la marge sud misent sur une double stratégie de reproduction afin d'assurer à la fois un recrutement continu lors des longs intervalles sans feu et une régénération adéquate en cas de feu. Cette capacité à faire face à des régimes de feux peu fréquents et imprévisibles devrait augmenter la résilience et la résistance des populations de pins gris alors que les changements globaux modifient la dynamique des feux de la forêt boréale. De façon générale, une variation phénotypique intraspécifique accrue dans les populations à la marge chaude contribue à la persistance à long terme des espèces dans des conditions environnementales marginales qui pourraient s'intensifier avec les changements globaux. La conservation des populations marginales et de leur patrimoine génétique apparaît donc cruciale pour la résilience des espèces largement distribuées.

Mots-clés : adaptation locale, minimisation des risques, marge sud, populations marginales, trajectoire démographique, régime de feu, *Pinus banksiana*, sérotinisme

Cet article, intitulé « *Hedging at the rear edge: intraspecific trait variability drives demographical trajectory of marginal populations in a widespread boreal tree species* », sera soumis à la revue scientifique *Journal of Ecology*. En tant que première autrice, j'ai contribué à l'établissement des objectifs et hypothèses de travail, développé le protocole de recherche, exécuté la collecte de données et rédigé l'article. La seconde autrice Magali Couture a participé à la collecte et à l'analyse de données en plus d'assister à la rédaction de l'article. Mon directeur de recherche, Guillaume de Lafontaine, est le dernier auteur de cet article. Il a participé à toutes les étapes ayant permis la réalisation du projet, du développement de l'idée originale jusqu'à la révision de cet article. Les résultats préliminaires de cet article ont été présentés lors du congrès annuel du *Réseau de recherche international (IRN) Forêts froides* le 3 novembre 2020 et lors du colloque annuel du *Centre d'études nordiques* le 11 février 2021. Finalement, les résultats de cet article ont fait l'objet d'une présentation orale lors du 14e colloque annuel du *Centre d'étude de la forêt* le 11 mai 2021.

1.2 HEDGING AT THE REAR EDGE: INTRASPECIFIC TRAIT VARIABILITY DRIVES DEMOGRAPHICAL 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 demographical 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 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.

Keywords: local adaptation, bet-hedging, rear edge, marginal populations, demographic trajectory, fire regime, *Pinus banksiana*, serotiny

Introduction

Populations located at the geographical margins of species' range 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 high degree of phenotypic variation in traits conferring 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 appear 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 (Jackson & Overpeck, 2000; Davis & Shaw, 2001; Aitken *et al*., 2008; 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, whereas population collapse and species range recession should be exacerbated in warmer areas of the geographical distribution, *i.e.*, at the rear edge (Hampe & Petit, 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; Woodall *et al*., 2013) and expected rear-edge populations contraction is often being falsified (*e.g*., Doak & Morris 2010; Bertrand *et al*., 2011; Cavin & Jump, 2017; Granda *et al*., 2018; Vilà-Cabrera *et al*., 2019; Vizcaíno-Palomar *et al*., 2020). 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; Catullo *et al*., 2015; de Lafontaine *et al*., 2018; Benito Garzón *et al*., 2019; 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; Parchman *et al*., 2012; 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 buildup 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 lower fire activity than their boreal conspecifics. The unfavorable fire regime of the rear edge is expected to become more widespread as the climate changes. Indeed, although higher fire hazard is forecasted due to warmer and drier climate in the boreal forest (Wotton *et al.*, 2010), this is likely to be offset by an increase of less flammable broadleaf vegetation in a warmer climate (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 deleterious 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 (Figure 2a). 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; Figure 2b). 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 (Figure 2b; Table 1). This confirms that our case study correctly captures the most salient biogeographical features expected from a valid core-periphery model. According to the latest Canadian fire regime zonation system (Erni *et al.*, 2020), rear-edge populations are located within the fire regime unit 4 (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 (Figure 2b; 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, unpublished data). 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 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 ($n = 260$) were finely sanded to make the xylem cells clearly visible at 45× magnification under a stereomicroscope (Olympus SZ61, Tokyo, Japan). Trees-rings were counted and the maximal age of sampled trees were used to estimate a 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 demographical patterns, 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 (Figure S1) indicates that the tree size structure models should provide an appropriate estimation of demographical 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 (Welch, 1938). In order to assess the relative importance of serotiny on the shape of the stand structure and thus on demographical 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. All statistical analyses (significance level $\alpha = 0.05$) were performed with the R statistical software version 3.6.2 (R Core Team, 2019).

Results

We estimated serotiny on a total of 2413 jack pine trees in 26 stands from two biogeographical regions characterized by contrasting fire regimes (Figure 2b, 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 (Figure 3a, 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 (Figure 3b, Table 2; $\chi^2 = 4.8$, 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 (Figure 3a, 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 (Figure 3c; 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 (Figure 4; 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 (Figure 4; 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 (Figure 5). 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 (Figure 6; $t_{\text{one-sided}} = 3.40$, df = 22, $P = 0.001$).

All three parameters of the quadratic model describing stand size structure vary with stand-scale level of serotiny (Figure 7). 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; Figure 7a). 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 (Figure 7c; 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 (Figure 7b).

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 demographical trajectories reflected by distinct patterns of tree size structures. Our results indicate that serotiny is indeed associated with the marginality of the stands according to their 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 specie 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 demographical 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 demographical 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 cannot regenerate 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 are optimized on a mineral seedbed (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 (unpublished data) 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 range, 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 demographical 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).

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Table 1. Biogeographical settings of range-core and rear-edge jack pine (*Pinus banksiana*) stands between longitudes 68 and 70 °W. Fire statistics are based on 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 to nearest jack pine stand (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 (1970-2016)	FRU 10: 0.64 fire·Mha^{-1}·yr^{-1} FRU 11: 0.33 fire·Mha^{-1}·yr^{-1}	FRU 4: 0.03 fire·Mha^{-1}·yr^{-1}
Fire ignition (1970-2016)	FRU 10: 23% human, 77% lightning FRU 11: 50% human, 50% lightning	FRU 4: 100% human

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	68.81	48.35	158	98.6	8.8	**-0.26**	**9.42**	-20.51	0.33	**0.0424**
Core	MAN	68.67	50.65	49	97.4	8.1	**-0.20**	4.77	46.34	0.39	**0.0187**
Core	KIN	69.26	49.08	134	95.8	14.9	-0.05	2.12	-4.21	0.18	0.2145
Core	LAB	69.75	49.26	92	95.6	16.4	**-0.12**	**3.93**	-2.35	0.46	**0.0074**
Core	GAI	68.80	50.11	52	93.4	14.0	**-0.06**	1.92	0.24	0.20	0.1618
Core	SAG	70.05	47.94	79	91.2	23.0	**-0.34**	**11.41**	-14.08	0.60	**0.0006**
Core	REN	69.87	48.23	78	90.0	28.0	**-0.09**	**3.78**	-12.71	0.33	**0.0389**
Core	BER	69.48	48.31	62	88.0	30.0	**-0.16**	**6.38**	-14.65	0.37	**0.0265**
Rear	STS	68.98	48.26	91	84.2	32.4	**0.58**	**-34.19**	**482.79**	0.68	**0.0001**
Rear	VIL	69.71	47.67	111	84.0	32.7	**0.12**	**-5.73**	**63.66**	0.44	**0.0100**
Rear	CAC	69.50	47.93	172	82.8	34.8	-0.02	-1.11	**54.64**	0.43	**0.0111**
Rear	PEL	69.91	47.42	133	81.4	36.5	-0.03	0.03	**42.36**	0.48	**0.0050**
Rear	RAR	69.76	47.62	130	80.2	40.2	0.30	**-18.58**	**279.96**	0.57	**0.0012**
Rear	PAO	69.99	47.49	100	79.4	40.7	**-0.14**	**4.83**	13.59	0.29	0.0682
Rear	RSG	69.78	47.59	116	78.4	40.6	0.12	-13.54	**295.76**	0.48	**0.0051**
Rear	RRR	69.76	47.61	136	77.0	45.0	**0.32**	**-21.13**	**335.85**	0.85	**<0.0001**
Rear	SPN	69.86	47.48	209	76.6	37.5	0.05	-5.57	**120.73**	0.53	**0.0023**
Rear	MIS-B	69.73	47.64	64	73.2	53.4	-0.10	2.58	18.11	0.33	**0.0388**

Table 2. (continued).

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	LGM	69.70	47.70	87	71.2	47.0	0.01	-3.51	**99.27**	0.63	**<0.0001**
Rear	EMB	69.84	47.53	115	70.4	49.4	0.01	**-4.98**	**144.32**	0.77	**<0.0001**
Rear	RAK	69.76	47.60	78	70.0	48.1	**0.25**	**-12.79**	**154.53**	0.83	**<0.0001**
Core	JEL	68.37	49.32	69	69.0	55.5	-0.01	-0.45	**23.70**	0.19	0.1909
Rear	MIS-A	69.73	47.64	80	69.0	56.8	**0.53**	**-29.53**	**391.52**	0.89	**<0.0001**
Core	CAS	69.17	48.64	63	66.6	57.7	0.02	-3.85	**105.40**	0.61	**<0.0001**
Rear	FOU	69.69	47.70	89	61.8	57.3	0.06	**-4.62**	**84.48**	0.75	**<0.0001**
Rear	PLO	69.79	47.57	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	-	**-**

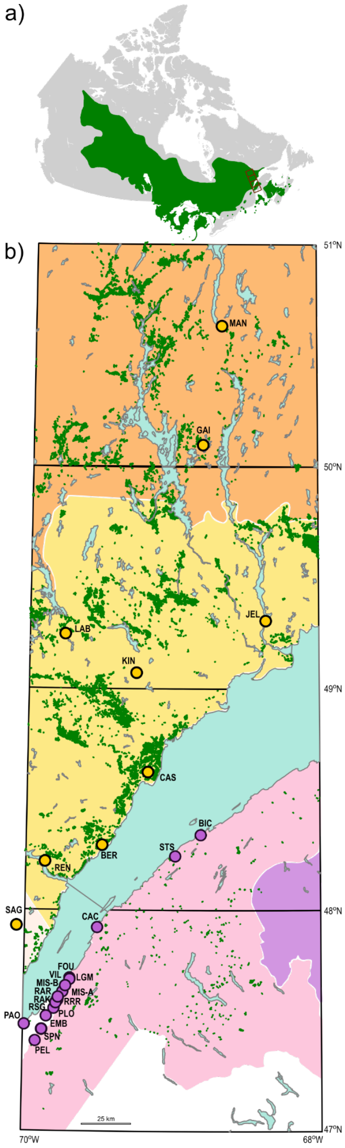

Figure 2. Location of sample sites and biogeographic setting of jack pine (*Pinus banksiana*). a) The study area in eastern Québec is shown within the transcontinental distribution of jack pine (green). b) Location of rear-edge and range-core sample sites are indicated by purple and yellow circles, respectively. 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).

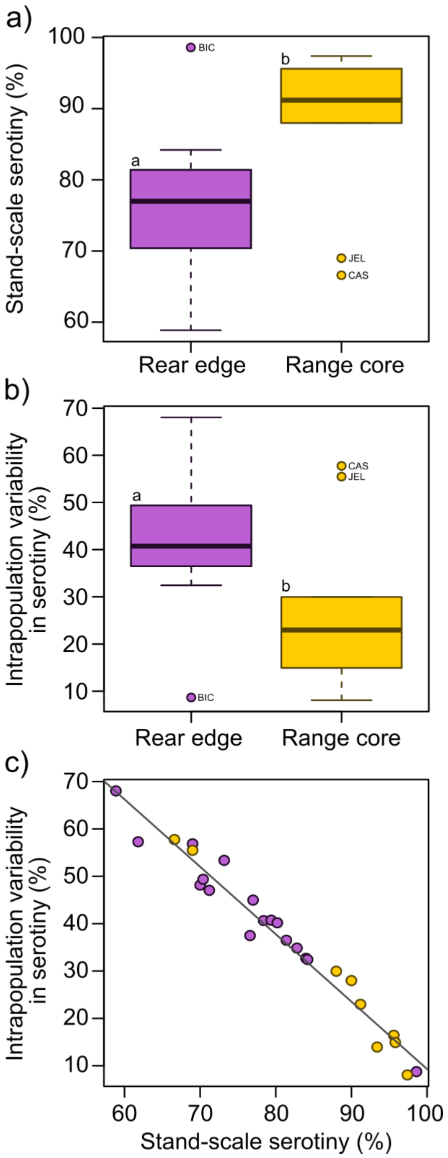

Figure 3. Intraspecific variation in serotiny among 26 jack pine (*Pinus banksiana*) stands including 17 rear-edge populations and 9 populations from the core of the range in eastern Québec. a) Comparison of stand-scale serotiny between rear-edge and core populations. b) Comparison of intrapopulation variability in serotiny between rear-edge and core populations. Boxplots indicate lower quartile, median, and upper quartile, and whisker length is 1.5 × 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.

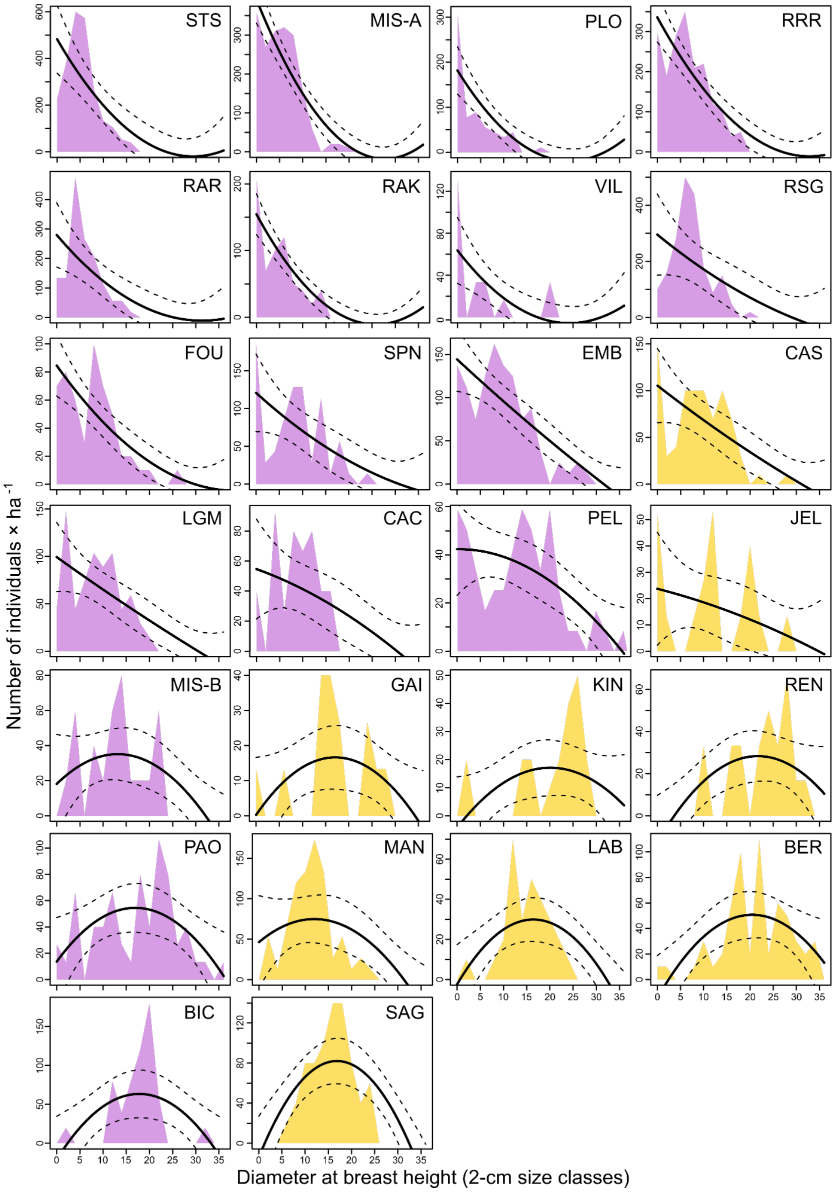

Figure 4. Empirical size structure and fitted quadratic model for 26 jack pine (*Pinus banksiana*) stands in eastern Québec. Colored polygons illustrate the actual number of individuals (per ha) in each 2-cm size class with rear-edge and range-core stands shown in purple and yellow, respectively. Solid 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.

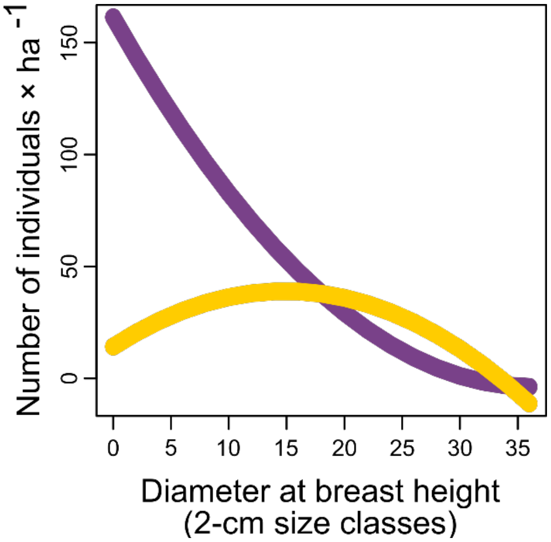

Figure 5. Composite quadratic models describing mean regional jack pine (*Pinus banksiana)* stand size structure at the rear edge (purple) and in the core of the range (yellow) in eastern Québec.

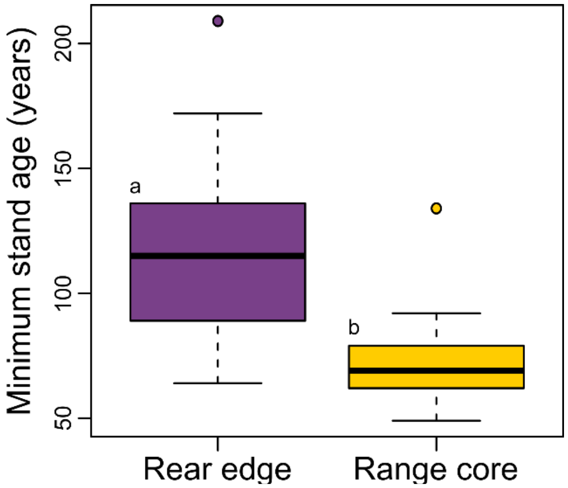

Figure 6. Comparison of minimum stand age between rear-edge and range-core jack pine (*Pinus banksiana*) forests in eastern Québec. Boxplots indicate lower quartile, median, and upper quartile, and whisker length is 1.5 × interquartile range. Different letters indicate statistically significant difference.

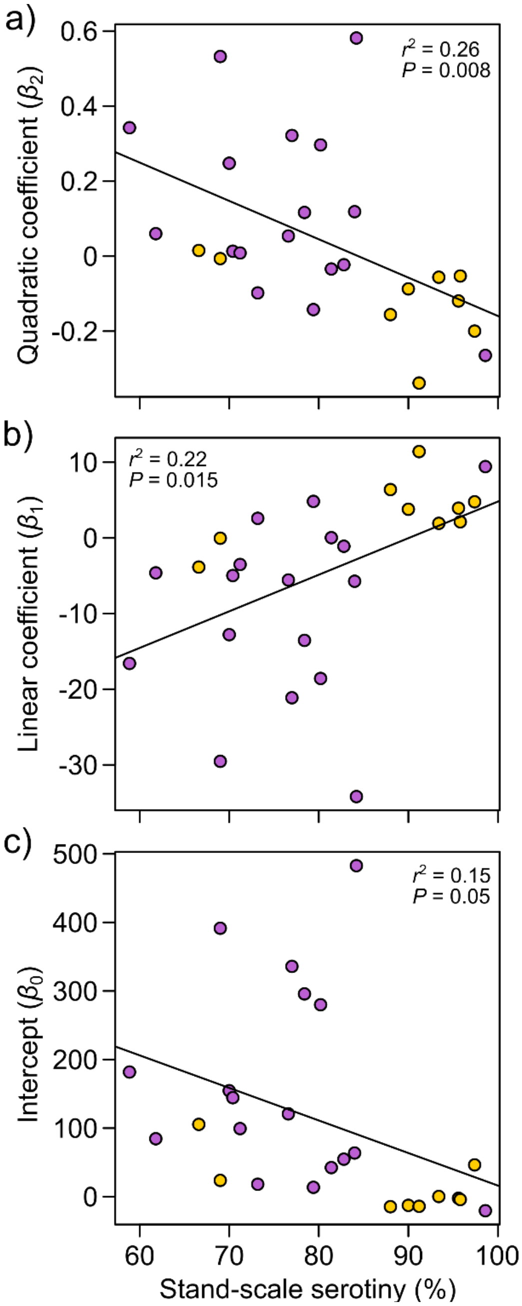

Figure 7. Parameters of the fitted quadratic model describing tree size structure – a) quadratic coefficients, b) linear coefficients, and c) intercepts – as a function of stand-scale serotiny in 26 jack pine (*Pinus banksiana*) stands in eastern Québec. Rear-edge and range-core populations are shown in purple and yellow, respectively.

1.3 SUPPLEMENTARY INFORMATION

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***	

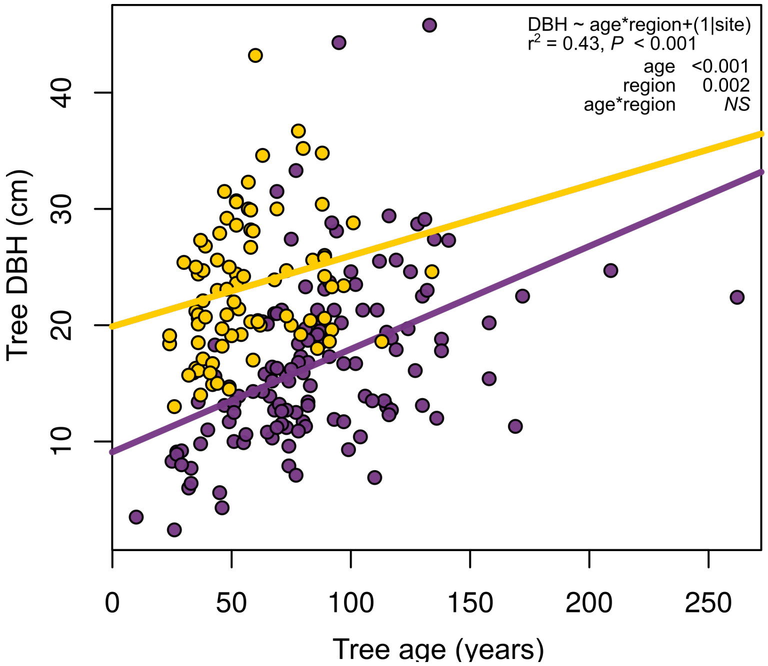

Figure S1. Relationship between tree age and tree diameter at breast height (DBH) in jack pine (*Pinus banksiana*) stands from eastern Québec. Rear-edge and range-core populations are shown in purple and yellow, respectively. The relationship is based on the 10 cored trees per study site used to estimate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

CHAPITRE 2

DÉCHIFFRER LA VARIABILITÉ INTRASPÉCIFIQUE D'UN TRAIT ADAPTATIF CLÉ À LA MARGE SUD D'UN CONIFÈRE NORD-AMÉRICAIN LARGEMENT RÉPANDU

2.1 RÉSUMÉ EN FRANÇAIS DU DEUXIÈME ARTICLE

Prémisse

Mieux comprendre les mécanismes favorisant la persistance à long terme des populations marginales devrait fournir des informations clés sur la résilience des espèces face aux changements climatiques. Le sérotinisme des cônes est un trait adaptatif chez le pin gris qui varie en fonction du régime de feu local. Comparativement aux populations au cœur de l'aire de répartition de l'espèce dans la forêt boréale sujette aux feux, le degré de sérotinisme faible et variable observé dans les populations de la marge sud suggère une adaptation locale à un régime de feux peu fréquents et imprévisibles. Nous avons évalué divers facteurs environnementaux et physiologiques susceptibles de moduler la variation intraspécifique du sérotinisme des cônes.

Méthodes

Nous avons expérimentalement soumis des cônes fermés à des températures croissantes et effectué des tests de germination des graines pour déterminer comment divers facteurs écologiques (âge des cônes, hauteur des branches, taille de l'arbre, âge de l'arbre) sont liés à la déhiscence des cônes et à la viabilité des graines chez des populations de pins gris provenant de sa marge sud et du centre de son aire de répartition dans l'est du Canada.

Résultats

Les cônes des populations à la marge sud déhiscent à une température d'ouverture plus basse, qui augmente avec l'âge du cône. Les cônes provenant du cœur de la répartition s'ouvrent à une température plus constante, mais plus élevée. Il faut entre 13 et 27 ans pour que les cônes des peuplements de la limite sud atteignent un niveau de sérotinisme comparable à celui des cônes des populations centrales. À la marge sud, la viabilité des graines est stable (51% des graines viables), alors qu'elle diminue de 40% en 20 ans (passant de 70% à 30% de graines viables) au centre de l'aire de répartition.

Conclusion
À la marge sud, nous inférons les mécanismes d'une stratégie de minimisation des risques par la diversification du phénotype, assurant à la fois un recrutement régulier pendant les intervalles sans feu en plus d'une régénération après feu. Cette capacité à faire face à un régime de feux peu fréquents et imprévisibles devrait accroître la résilience des populations de pins gris alors que les changements globaux modifient la dynamique des feux de la forêt boréale.

Mots-clés : stratégie de minimisation des risques, biome boréal, dynamique éco-évolutive, perturbation écologique, régime de feu, adaptation locale, populations marginales, *Pinus banksiana*, marge sud, sérotinisme

Cet article, intitulé « *Jack pine of all trades: deciphering intraspecific variability of a key adaptive trait at the rear edge of a widespread fire-embracer North American conifer* », sera soumis à la revue scientifique *American Journal of Botany*. En tant que première autrice, j'ai contribué à l'établissement des objectifs et hypothèses de travail, développé le protocole de recherche, exécuté la collecte de données, effectué les analyses statistiques et rédigé l'article. Mon directeur de recherche, Guillaume de Lafontaine, est le deuxième auteur de cet article et a développé l'idée originale du projet. Il a également participé à toutes les étapes menant à la rédaction de cet article, incluant l'élaboration des objectifs et hypothèses, les analyses statistiques et la révision de l'article. Les résultats préliminaires de cet article ont été présentés lors du colloque *International Research Network* sur les forêts froides le 2 novembre 2020 et lors du colloque du Centre d'étude de la forêt le 11 février 2021. Finalement, les résultats de cet article ont fait l'objet d'une présentation orale lors du 14^{e} colloque annuel du Centre d'étude de la Forêt le 11 mai 2021.

2.2 JACK PINE OF ALL TRADES: DECIPHERING INTRASPECIFIC VARIABILITY OF A KEY ADAPTIVE TRAIT AT THE REAR EDGE OF A WIDESPREAD FIRE-EMBRACER NORTH AMERICAN CONIFER

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ABSTRACT

Premise

Understanding mechanisms fostering long-term persistence of marginal populations should provide key insights about species resilience facing climate change. Cone serotiny is a key adaptive trait in jack pine, which shows phenotypic variation according to the fire regime. Compared to range-core populations within the fire-prone boreal forest, low and variable serotiny in rear-edge populations suggest local adaptation to uncommon and unpredictable wildfire regime. We assessed environmental/physiological factors that might modulate intraspecific variation in cone serotiny.

Methods

We experimentally submitted closed cones to incrementing temperatures followed by seed germination tests to investigate if and how various ecological factors (cone age, branch height, tree size, tree age) are related to cone dehiscence and seed viability in jack pines from rear-edge and range-core populations in eastern Canada.

Key results
Cones from rear-edge populations dehisce at a lower opening temperature, which increases with cone age. Cones from range-core stands open at a more constant, yet higher temperature. It takes between 13 and 27 years for cones from rear-edge stands to reach the level of serotiny achieved at the range core. At the rear edge, seed viability is steady (51%), whereas it decreases from 70% to 30% in 20 years at the range core.

Conclusion
At the rear edge, we inferred the mechanisms of a bet-hedging strategy ensuring steady recruitment during fire-free intervals and successful postfire regeneration. This capacity to cope with infrequent and unpredictable fire regime should increase the resilience of jack pine populations as global changes alter fire dynamics of the boreal forest.

Keywords: bet-hedging strategy, boreal biome, eco-evolutionary dynamics, fire disturbance, local adaptation, marginal populations, *Pinus banksiana*, rear edge, serotiny

Introduction

In the face of global change, natural populations can either migrate to newly suitable environments or adapt locally to their altered ecosystem in order to avoid extirpation (Jackson and Overpeck, 2000; Davis and Shaw, 2001; Aitken et al., 2008; de Lafontaine et al., 2018). Although migration (*i.e.*, range shift) was undoubtedly a major plant response during postglacial warming (Huntley and Webb, 1989), for many plant species the migration rate required to keep up with the of pace of modern-day global change velocity might be unattainable (Zhu et al., 2012; Corlett and Westcott, 2013). Thus, population collapses might be expected without local adaptations to the new environmental conditions (de Lafontaine et al., 2018). These responses are exacerbated in marginal populations, which are already at the limit of a species' climatic or environmental tolerance and often at the edge of their species distribution (Nadeau and Urban, 2019). The small size and spatial isolation of marginal populations reduce gene flow and promote genetic drift (Lesica and Allendorf, 1995; Vucetich and Waite, 2003), which should foster interpopulation genetic structure as well as local adaptation within populations in response to the high selection pressures caused by a stressful environment (Hampe and Petit, 2005; Eckert et al., 2008; Sexton et al., 2009; de Lafontaine et al., 2013, 2018). Marginal environmental conditions currently restricted to the warm limit of species distribution (*i.e.*, rear edge), may become increasingly widespread throughout species range under a warmer climate (Rehm et al., 2015). Hence, peripheral rear-edge populations are the first to encounter new conditions triggered by global warming and thus the most imminently threatened (Nadeau and Urban, 2019). Besides, they are reservoirs of unique genetic variation (de Lafontaine et al., 2013), which makes them overly instrumental for the long-term conservation of genetic diversity, phylogenetic history and evolutionary potential (Hampe and Petit, 2005). Understanding how the eco-evolutionary dynamics at the rear edge can uphold long-term persistence of peripheral rear-edge populations will provide key insights about species resilience facing climate change (Lesica and Allendorf, 1995; Hampe and Petit, 2005; Kawecki, 2008; Rehm et al., 2015).

Intraspecific trait variation reflects heritable genetic differences and phenotypic plasticity across varying environments (Moran et al., 2016). Local adaptation increases genetic divergence among populations over generational timescales as a result of natural selection to contrasted environments (Lenormand, 2002; Kawecki and Ebert, 2004). Plasticity allows individuals to rapidly adjust phenotypes according to changes in local environmental conditions, dampening adaptive evolution by buffering selective pressures. However, the extent of trait plasticity is ultimately under genetic control and heterogeneous environments might foster adaptive plasticity (Ghalambor et al., 2007; Crispo, 2008; Chevin and Lande, 2011; Chevin and Hoffmann, 2017). Hence, whether adaptive or plastic, intraspecific trait variation driving demographic trajectories is instrumental to understand population responses to rapid environmental alteration brought about by ongoing global changes (Moran et al., 2016; Kelly, 2019). This is intensified in marginal populations, where high demographic stochasticity and spatially-structured trait variation are expected (Valladares et al., 2014; Banitz, 2019).

The extent of intraspecific trait variation can change across ecological gradients in response to environment heterogeneity (Westerband et al., 2021). For instance, some fire-adapted species can exhibit variation in serotiny − a highly heritable fitness-related trait − according to contrasted disturbance regimes (Pausas et al., 2015; Lamont et al., 2020). Serotiny is the retention of mature seeds in closed cones or fruits for more than a year implying the buildup of a canopy seed bank through delayed seed dispersal (Enright et al., 1998). The opening of the cones/fruits is triggered by wildfires (pyriscence), drought periods (xeriscence) or both, depending on the species (Lamont, 1991; Nathan et al., 1999; Espelta et al., 2011). Out of 95 pine species (*Pinus* sp.) examined by Lamont et al. (1991), 22 are serotinous but only six are considered obligate pyriscent, meaning cone opening is strictly contingent on fire. Hence, most serotinous species have a dual life-history strategy, bearing pyriscent structures enabling postfire regeneration as well as non-serotinous cones/fruits that open at maturity, which allows continuous interfire recruitment (Lev-Yadun, 1995; Nathan et al., 1999; Whelan et al., 1998; Goubitz et al., 2004; Hernández-Serrano et al., 2013). The percentage of closed mature cones/fruits in individuals of many serotinous species (*i.e.*, apparent serotiny, *sensu* Lamont 2021) has been shown to decrease in populations where fire frequency is low (Givnish, 1981; Muir and Lotan, 1985; Gauthier et al., 1996; Schoennagel et al., 2003; Hernández-Serrano et al., 2013; Lamont et al., 2020). Such dual life-history strategy within individuals showing high but incomplete serotiny is often considered as bet-hedging in environments where fire interval is unpredictable and/or on average longer than the mean longevity of the species (Enright et al., 1998). Diversified bet-hedging is a reproduction strategy that optimizes the long-term individual fitness by sacrificing mean fitness to reduce fitness variance between years in unpredictable environments (Philippi and Seger, 1989; Olofsson et al., 2009; Childs et al., 2010). Individuals 'hedge their bets' by simultaneously expressing multiple phenotypes conferring fitness advantage under different environmental conditions (Simons, 2011). Accordingly, in fire-prone species, those individuals adept at producing both serotinous and non-serotinous cones/fruits should be advantaged in environments where the fire return interval is long and unpredictable (Goubitz et al., 2004).

Global change will inevitably affect fire regimes in complex and uncertain ways, increasing or decreasing fire frequency depending on the specific region (Moritz et al., 2012). Fire is one of the main drivers structuring the boreal forest, which is particularly affected by climate change. Indeed, climate in the boreal biome is warming approximately twice as fast as the global average (Bush and Lemmen, 2019; IPCC, 2021). Higher fire hazard is forecasted in the boreal forest due to warmer and drier climate (Wotton et al., 2010). However, this tendency is likely to be outweigh in the southern part of the boreal biome where a northward range shift and massive infilling of less flammable broadleaf temperate vegetation is expected under a warmer climate (Girardin et al., 2013; Walker et al., 2020; Huang et al., 2021). It is thus crucial to understand how rear-edge populations of fire-dependent boreal species can cope with unfavorable fire regimes.

Jack pine (*Pinus banksiana* Lamb.) is the North American boreal tree species best adapted to wildfires (Rowe and Scotter, 1973). Mature cones of this obligate pyriscent species generally remain closed until the resin layer on their outer surface is melted by high temperatures reached in wildfires (Cameron, 1953). Massive postfire seed release triggers a high recruitment rate and rapid establishment on a mineral substrate, rich in resources and without competition (Cayford et al., 1967; Lamont et al., 2020). Because it is shade-intolerant, jack pine is eventually replaced by more competitive species such as black spruce (*Picea mariana*) or balsam fir (*Abies balsamea*) as stands senesce in prolonged absence of fire (>220 years; Le Goff and Sirois, 2004). Serotiny has been extensively studied in Australia, South Africa and in Mediterranean pines, but factors driving its variability remain poorly investigated in jack pine (but see Gauthier et al., 1993a). Indeed, reduced serotiny was reported in some jack pine stands where the frequency of lethal wildfire is low and unpredictable (Gauthier et al., 1993b, 1996), a noticeable trend at the rear-edge of the species distribution (Radeloff et al., 2004). For instance, Pelletier et al. (in prep.) reported lower yet more variable serotiny within rear-edge jack pine populations from eastern Canada compared to range-core populations. Furthermore, these uneven-aged stands at the rear edge are in demographic equilibrium with steady regeneration whereas younger range-core stands are single cohorts lacking interfire recruitment. Pelletier et al. (in prep.) argued that, unlike range-core jack pine populations, rear-edge populations locally rely on a bet-hedging evolutionary strategy to ensure both steady recruitment during long fire-free intervals as well as eventual successful postfire regeneration. The variation in serotiny in rear-edge populations could thus represent an adaptive solution to the infrequent and unpredictable fire regime.

Nevertheless, other confounding factors potentially influencing dehiscence of serotinous cones/fruits have been reported in the literature. For instance, studies have shown serotiny to decrease with increasing cone age in other serotinous pine species (Tapias et al., 2001; Espelta et al., 2011; Martín-Sanz et al., 2017). The rationale is that older serotinous structures eventually open as their enclosure senesce and die (necriscence; Lamont, 1991), which could lead to the release of less viable seeds (Causley et al., 2016). This occurs when the maintenance costs of serotiny in older cones come in competition with younger cone cohorts, especially for water allocation (Martín-Sanz et al., 2017). A possible loss of serotiny in older jack pine cones has been reported from field observations (Gauthier et al., 1993a) but was never tested empirically. Cone height above the ground is another factor related to serotiny in lodgepole pine (*Pinus contorta*). Lower branches bear a higher percentage of opened cones compared to upper branches likely because radiative thermal energy transferred from the ground upward can accumulate heat within cones closer to the ground (Crossley, 1956). Field measurements suggest a limited positional effect in jack pine cones (Gauthier et al., 1993a), but lifelong exposition to higher radiative energy in cones closer to the ground could lower their opening temperatures compared to cones from upper branches. Tree age and size could also matter. In lodgepole pine, serotinous cones do not appear before trees reach 15-60 years, which contributes to a rapid stand densification after fire (Critchfield, 1980; Schoennagel et al., 2003). Fewer closed cones were also associated with younger trees in jack pine, but this was possibly related to the diameter at breast height (DBH) rather than age *per se* (Gauthier et al., 1993a). However, the opposite effect was reported for Aleppo pine (*Pinus halepensis*) for which serotiny decreases with increasing tree size (Goubitz et al., 2004; Martín-Sanz et al., 2016). This promotes the rapid build-up of a seed bank ensuring stand replacement in frequent fire regimes that induce immaturity risk (Keeley et al., 1999).

Although multiple factors potentially affect seed release in jack pine, we still largely ignore whether they actually contribute to modulate intraspecific variation in serotiny in contrasted fire regimes. To address this knowledge gap, we experimentally submitted closed cone to incrementing temperatures (*i.e.*, cumulative heat exposure; temperature × time) followed by seed germination tests to investigate if and how various ecological factors are related to cone dehiscence and seed viability in jack pine from rear-edge and range-core populations in eastern Canada. Assuming that the energy required for cone opening is ultimately related to serotiny, we expect that cones from rear-edge populations require less cumulative heat exposure than those from the core of the range. We then hypothesize that i) older cones open at lower temperature and bear less viable seeds than younger cones; ii) cones that were closer to the ground in the field require less energy than cones from upper branches in order to open; and iii) cones from younger and/or smaller trees open at lower cumulative heat exposure than those from older/larger trees. While we work under the null hypothesis that these responses are immutable in jack pine, our interest is actually to explore differences between range-core populations and rear-edge populations. Indeed, assessing determinants of cone dehiscence and their consequences on seed viability relative to intraspecific variation in serotiny should provide key insights on eco-evolutionary dynamics of marginal stands.

Methods

Study sites and field sampling

During the growing season of 2019, we sampled 24 jack pine stands from the core (n = 7) and the rear edge (n = 17) of the species distribution in eastern Québec, Canada (47−51°N; 68−70°W; Fig. 8). Range-core sites represent haphazard examples of typical boreal jack pine stands that were easily accessible by roads. These are located on well-drained sandy glacial deposits topped by a shallow organic horizon within the boreal forest, dominated by black spruce, balsam fir and paper birch (*Betula papyrifera*). We investigated the rear edge more comprehensively. In this area, most sites are located on rock outcrops within the northern temperate forest, mainly composed of sugar maple (*Acer saccharum*), yellow birch (*Betula alleghaniensis*) and balsam fir. These peripheral rear-edge stands are smaller, more isolated and occupy a lower share of the terrestrial landscape than those in the core of the range (Pelletier et al., in prep.). According to the Canadian fire regime zonation system (Erni et al., 2020), the rear edge has a very low fire activity with virtually no natural wildfire (*e.g.*, natural fire rotation period >1600 years in preindustrial forests of this area; Elzein et al., 2020) whereas range-core sites are located in fire units prone to recurrent lightning-ignited wildfires (Fig. 8). On average, serotiny is lower and more variable within rear-edge populations compared to those from the core of the range (Pelletier et al., in prep.).

At each site, 10 randomly-chosen mature jack pines were sampled. Three cone-bearing branches from different measured heights (lower, middle, and upper parts of the tree crown) were cut using an extendable tree pruner pole (Fiskars®, Espoo, Finland). If the upper parts of the crown were unreachable, we only collected the branch closest to the ground. All sampled branches (n = 492) were kept in opened paper bags at room temperature until further laboratory treatments. For each tree, DBH was recorded and a core was sampled using a Pressler increment borer as close to the ground as possible. Detailed methods used to estimate stand-scale serotiny are reported elsewhere (Pelletier et al., in prep.). Briefly, at each site, up to 100 mature jack pine individuals were assigned to one of six serotiny classes (based on the relative abundance of closed cones) and average class-value was reported as a percentage reflecting apparent stand-scale serotiny.

Laboratory analysis

At the laboratory, three fully closed cones of contrasted ages were sampled from each branch (n = 1381 cones). Specifically, for each sampled branch, the mature closed cone nearest to the branch tip (the youngest mature cone) and the one closest to the trunk (the oldest cone) as well as a third one roughly in the middle of the branch were collected. Cone age was determined by cutting the branch at the insertion point, sanding the surface until late and early wood rings were clearly visible, and counting growth rings under a stereomicroscope (Olympus SZ61, Tokyo, Japan). To estimate a minimal age of individual trees, core samples were dried, mounted, and sanded before tree rings were counted. For samples that failed to intersect the pith, minimal tree ages were adjusted by adding the estimated number of missing rings using a geometric pith locator (Applequist, 1958).

Cone opening experiment (heating experiment) was carried out according to a completely randomized design. Each cone was placed in a 100 mL glass beaker randomly positioned on a sheet pan in the middle height position of a forced convection laboratory oven (JeioTech ON-12GW, Seoul, South Korea) preheated to 48°C. After one hour, we removed the sheet pan from the oven while i) the oven was set to a higher temperature and ii) cone opening level was assessed. The opening level refers to the relative abundance of open scales on each individual cone (level 1: 1-25% opening, level 2: 26-50% opening, level 3: 51-75% opening and level 4: 76-100% opening; Fig. 9). The above cycle was repeated so that the oven temperature was iteratively increased by 3°C increment every hour, when cone opening level was recorded. Each cone was thus heated in the oven for a total run of six hours with one hour at 48°C, 51°C, 54°C, 57°C, 60°C, and 63°C, respectively. The cone opening experiment took 33 days to complete since the oven can accommodate up to 48 randomly assigned cones per six-hour run.

At the end of each daily run of the cone opening experiment, all cones were heated at 80°C overnight in order to fully open all scales on every cone. The seeds from these fully opened cones were then manually extracted. For each cone, the total number of seeds and the number of filled seeds (*i.e.*, containing an embryo) were recorded. The filled seeds of each cone were batch-weighed using an analytical balance (Sartorius Entris64-1S, Goettingen, Germany) and stored in small kraft envelopes until used for germination assay. Individual seed weight was estimated by dividing the total weight to the number of filled seeds recovered from each cone. For the germination assay, a maximum of 20 seeds per cone were uniformly distributed on a filter paper in a 9-cm petri dish for each cone. The filter papers were dampened with 3 mL of primary grade pure water and kept moist throughout the experiment. In total, 23,404 seeds were set to germinate in growth chambers (PHCbi MLR-352H-PA, Wood Dale IL, USA) at an optimal temperature of 20°C with a humidity rate of 75% and a luminous flux of 22,000 lux during 16 hours of daylight and 0 lux during 8 hours of night (16 h : 8 h photoperiod). Every day, germinated seeds (radicle > 2 mm) were counted and removed from the petri dishes. The experiment carried on until there were no new germinated seed on a given day (*i.e.*, 27 days).

Statistical analysis

The opening levels after each 1h-cycle in oven were used to generate four non-independent response variables for statistical analyses. For simplicity, the response variable of the heating experiment is expressed as the temperature at which cones reach a given opening level but keep in mind that each temperature increment entails that cones were previously exposed 1h to every lower-temperature iteration. Hence the response variable (cone opening temperature) actually reflects cumulative heat exposure (temperature × time) required to open the cone at the given level. All statistical analyses with cone opening temperature as the response variable were conducted individually for each opening level (levels 1-4). Because they are not independent, repeating these tests for each opening level merely reflect whether the relationship assayed between a given ecological factor and cone opening temperature is stable during the various stages of cone opening. A simple linear regression model was used to test the assumption that stand-scale serotiny (estimated from field observations) is actually related to cone opening temperature (assayed in laboratory heating experiment). Difference between rear-edge and range-core sites in terms of cone opening temperature or mean stand-scale serotiny was assessed using Welch two-sample *t*-test (Welch, 1938). We determined whether putative explanatory variables (cone age, branch height, tree age, and DBH) are related to cone opening temperature using a linear mixed model with the study sites as a random factor [Model formula = *Opening temperature ~ cone age + DBH + branch height + tree age + (1|site)*] with *lmer*() function in the R package *lmerTest* (Bates et al., 2015; Kuznetsova et al., 2017). We used a type-III analysis of variance (ANOVA) with Satterthwaite's method to provide inferences on the parameters of the linear mixed model (function *anova*() in R package *car*; Fox and Weisberg, 2019). We then analyzed explanatory variables with a significant *p*-value individually, separating our dataset between geographical regions (rear-edge and range-core). Simple linear regression models were computed to assess whether explanatory variables had a significant effect on cone opening temperature within each region. Because available data are relatively sparse for cones > 20 years, all statistical analyses involving cone age relied on a comprehensive subset including cones ≤ 20 years (n = 1353 cones).

For each cone, germination percentage (number of germinated seeds/total number of seeds assayed) and germination velocity ($\sum n_i/d_i$, where n_i is the number of seeds that germinated on day d_i; Maguire, 1962) were computed. Next, Welch two-sample *t*-tests were used to assess the differences in mean number of seeds per cone, percentage of filled seeds, seed weight, number of germinations, percentage of germinations, and germination velocity between rear-edge and range-core sites. Finally, simple linear regression model was fitted to test for an association between cone age and percentage of germination at the rear-edge and in the core of the range.

All statistical analyses were performed in R statistical software 4.1.1 (R Core Team, 2021). A significance level of $\alpha = 0.05$ was used for all statistical tests. Assumptions of normality and homogeneity of the residuals were assessed prior to all analysis.

Results

Stand-scale serotiny estimated in the field is positively associated with cone opening temperature in the laboratory oven for each level of cone opening. Cones sampled in stands with a higher degree of serotiny needed more cumulative heat in order to dehisce compared to those from less serotinous stands (Fig. 10a; *p*-values < 0.001 for levels 1, 2, 3, and 0.016 for level 4). In the field, rear-edge stands are significantly less serotinous than range-core stands (74.9% vs 93.1%, *p*-value < 0.001; see also Pelletier et al., in prep.). Correspondingly, mean opening temperature was significantly lower for cones collected in rear-edge stands than for those from the core of the range at all opening levels (Table 3; Fig. 10b). The linear mixed model suggested that cone age and DBH of parental tree had significant effects on cone opening temperature, while branch height and tree age did not (Table 4). Separate analyses of the relationship between cone age and opening temperature in each region (rear edge vs range core) revealed that cone opening temperature was positively associated with cone age at the rear edge (Fig. 11a; *p*-values < 0.001 for levels 1, 2, 3, and 0.02 for level 4), but there was no significant relation in the core of the range (Fig. 11b; *p*-values between 0.30 and 0.88). In other words, older cones require greater cumulative heat in order to dehisce compared to younger cones, but only at the rear edge. For each cone opening level, the crossing point between intersecting linear regression models of the rear edge and the range core provides an estimate of the age at which cones from rear-edge stands should reach an opening temperature similar to those from the core of the range. We found that this should occur when cones from rear-edge stands reach 13 to 27 years old, depending on the opening level considered (estimated age at which rear-edge cones behave as range-core cones is 27.2, 25.6, 13.1, and 15.7 years for opening levels 1, 2, 3, and 4, respectively; Fig. S1). Cone opening temperature was positively associated with DBH both at the rear edge (Fig. 12a; *p*-values = 0.19, 0.002, < 0.001, and 0.003 for opening levels 1 to 4, respectively) and at the core (Fig. 12b; *p*-values = 0.03, 0.03, 0.27, and 0.092 for levels 1 to 4, respectively) for most, but not all, opening levels. Consistent with mixed models, no univariate relationship was found between branch height or tree age and cone opening temperature (Fig. S2; *p*-values > 0.05 for all opening levels).

Results from seed output and germination assay are reported in Table 5. The mean number of seeds per cone and the mean percentage of filled seeds per cone were significantly higher at the rear edge compared to the core of the range. However, the mean weight per seed was greater at the range core. Considering the mean number of seeds per cone × mean percentage of filled seeds per cone × mean weight per filled seed, jack pines at the rear edge invest *ca*. 35% more in seed output per cone than trees at the range core (0.031 g vs 0.023 g). The higher individual seed mass does not translate into increased germination potential at the core of the range. Indeed, the number of germinated seeds, germination percentage, and germination velocity were similar between the two regions. Germination percentage did not vary with cone age at the rear edge (Fig. 13a; *p*-value = 0.75), but there was a significant negative relationship in range core stands (Fig. 13b; $t_{(190)} = 3.93$, *p*-value < 0.001). Hence, seed viability declines with increasing age since maturation but only in the core of the species range, not at the rear edge.

Discussion

This study sets out to investigate various ecophysiological factors potentially driving seed release and viability in jack pine from the rear edge and the core of species distribution. By doing so, we assessed whether and how these factors might contribute to the variable level of cone serotiny observed in jack pine stands from regions marked by contrasted fire activity (Pelletier et al., in prep.). The study relies on the assumption that the energy required for cone opening in laboratory heating experiments represents a good proxy of cone serotiny observed in the field. Indeed, our results show that the cumulative heat exposure necessary to open cones (*i.e.*, estimated by the response variable 'cone opening temperature') is positively associated with stand-scale serotiny. Closed cones from populations with higher level of serotiny thus require more cumulative heat to open compared to closed cones sampled in stands where serotiny is low/variable. This indicates that our cone heating experiment testing how ecophysiological factors relate to the thermal energy required to open cones can be scaled up to provide key insights about the intraspecific variability in serotiny observed in the field.

As expected, we found a significant difference in cone opening temperature between the two study regions (rear edge vs range core). Closed cones from rear-edge jack pine sites in the temperate forest, where wildfires are infrequent and highly unpredictable, require less cumulative heat to open than those from range-core sites in the fire-prone boreal forest. This result reflects the difference in stand-scale serotiny observed in nature, whereby serotiny at the rear-edge is lower and more variable compared to range-core populations (Pelletier et al., in prep.; this study) and lends further support to the idea that marginal rear-edge populations are locally adapted to the infrequent/unpredictable wildfire regime. Such adaptive response is in fact possible because serotiny is a highly heritable trait in many pine species (Perry and Lotan, 1979; Wymore et al., 2011; Ledig et al., 2013; Hernández-Serrano et al., 2014; Castellanos et al., 2015) including jack pine (Rudolf et al., 1959; Teich, 1970; Pike, 2011). Furthermore, cone serotiny in pine species shows phenotypic variation within and/or among natural populations according to fire regime (Givnish, 1981; Gauthier et al., 1993b, 1996; Schoennagel et al., 2003; Radeloff et al., 2004; Hernández-Serrano et al., 2013; Romero and Ganteaume, 2020; Pelletier et al., in prep.). Finally, genome-wide association studies exploring the genetic architecture underlying serotiny in pines have uncovered many putative adaptive genes across the genome, which suggest a complex genetic basis (Parchman et al., 2012; Budde et al., 2014; Feduck et al., 2015). Taken together, these findings have rightfully led many authors to argue that variation in serotiny represents an evolutionary response to the natural selection pressure exerted by fire regimes (Enright et al., 1998; Pausas, 2015; Lamont et al., 1991, 2020). However, this conclusion is likely to be toned down if cone opening is in part driven by multiple environmental factors unrelated to the fire regime such as age/size/position (Lamont et al., 2020).

For instance, we hypothesized that cones located closer to the ground in the field would require less energy to dehisce than cones from higher up in the canopy. The rationale behind this positional hypothesis was that a long-lasting exposition to higher radiative heat from the ground eventually reduces resin bond strength in cones from lower branches making them more prone to open at lower temperature. However, results from our heating experiment indicate that branch height is not related to the opening temperature. This contrasts with field observations in lodgepole pine where lower branches bear a greater proportion of opened cones compared to upper branches (Crossley, 1956). This pattern could reflect a more direct positional effect whereby radiative heat reaches opening temperatures *in situ* rather than the lingering effect of a lifelong exposition to radiative heat as tested here. Still, we did not observe a disproportionate number of opened cones in the lower branches of jack pines on our sampled sites (pers. obs.). Although we did not formally test the positional hypothesis in the field, we had no problem finding closed cones from very low branches (*e.g.*, 0 to 1.5 m) to include in our experiment. Gauthier et al. (1993a) found that the proportion of serotinous cones was slightly reduced on branches below 2.6 m, but only for trees with a DBH ≥ 10 cm. These equivocal results also tend to dismiss the existence of a direct positional effect caused by ground-radiated heat in jack pine because the relationship collapse in smaller individuals.

Our results support the contention that tree size, but not tree age, modulates serotiny. Indeed, opening temperature of the cones from both regions (rear edge/range core) was positively related to the DBH, but not the age of jack pine individuals. Thus, in agreement with our hypothesis, cones from smaller trees require less cumulative heat exposure to dehisce, but contrary to our hypothesis, this relationship is independent of tree age. Gauthier et al. (1993a) reported a tendency for smaller/younger jack pine trees (DBH < 7 cm; tree age < 32 years) to bear fewer serotinous cones relative to larger/older individuals. Such delayed serotiny might contribute to a rapid postfire stand densification, thanks to continuous seedling establishment during the first few decades after fire (Critchfield, 1985; Lamont et al., 1991). Our results partly agree with this hypothesis, although we did not find an effect of tree age. We thus advocate for an effect of low resource availability rather than tree juvenility to explain cone opening at lower temperature in small individuals. Redmond et al. (2019) found no trade-off between reproduction and vegetative growth (*i.e.*, increased cone production in years of high vegetative growth) for the pinyon pine (*Pinus edulis*). Despland and Houle (1997) reached a similar conclusion in jack pine. Thus, tree size should be roughly proportional to the amount of resources available for cone production. Larger trees, regardless of their age, might afford to allocate more resources to the production of serotinous cones than smaller trees that fail to develop full serotiny. The opposite pattern was found in Aleppo pine, for which there is a trade-off between vegetative growth and cone production

(Climent et al., 2008) and where serotiny decreases with tree height (Goubitz et al., 2004; Martín-Sanz et al., 2016). This might reflect an adaptation of Mediterranean pines to a recurrent, low-severity fire regime, which induce the risk of being burned before accumulating enough seeds in the canopy seed bank for postfire recruitment (Lamont et al., 1991; Keeley et al., 1999). By contrast, in the boreal forest, the likelihood of severe, stand-replacing fire increases as fuel accumulates in dense stands with large trees (Terrier et al., 2017; Thompson et al., 2017). It would thus seem advantageous for jack pine to produce serotinous cones that require gradually more thermal energy to dehisce (*i.e.*, higher melting point of the resinous compound or thicker resin layer) as trees become larger (Crossley, 1956; Lamont et al., 1991).

Based on previous studies on other pine species, we expected serotiny to decrease with cone age due to the maintenance costs of older, senescent cones (Tapias et al., 2001; Espelta et al., 2011; Martín-Sanz et al., 2017). We found that dehiscence is indeed related to cone age but, contrary to our hypothesis, opening temperature increased with cone age, meaning serotiny should increase with time since cone maturity. However, and quite interestingly, this relationship differs between regions. The cone age effect was found only at the rear edge, not in range-core populations where serotiny should not vary with cone age. Our results differ from those of Gauthier et al. (1993a) who compared jack pine cones older than 4 years old with younger cones in a field survey. They reported a lower proportion of closed cones ≥ 4 years, indicating that older cones tend to open in the field. However, more than half of the stands included in their study were located on islands submitted to recurrent non-lethal surface fires. Because each non-lethal fire event triggers cone opening while keeping individual trees alive, it is likely that their results reflect the fact that older cones in these atypical island stands had more opportunities to open compared to younger cone cohorts, instead of an actual physiological effect of cone aging. Our laboratory assay indicates that cones at the rear-edge require increasing amount of cumulative heat in order to break up their resin bound as they age. Cones from range-core sites, on the other hand, reach a level of serotiny at maturity that then remains constant. We estimate that it takes between 13 and 27 years for cones from rear-edge stands to reach this same level of serotiny. It is still unclear whether this is due to the resinous compound becoming thicker with time or because it reaches a higher melting point. Regardless, this result suggests that cones in rear-edge populations become more serotinous as they age, which should allow for continuous seed dispersal opportunities to arise between fire events. Indeed, the opening of young cones at lower temperature increases the odds of seed dispersal without fire during many years after cone maturation. After 13 to 27 years, the cones that remained closed eventually reach a level of serotiny comparable to those of jack pines from the boreal forest. These highly serotinous cones then incorporate the aerial seed bank to insure successful regeneration over the long term in case of wildfire (Lamont et al., 1991). This mechanism is not relevant in the boreal forest, where crown fires are likely to occur during the average lifespan of jack pines. As such, it contributes to explain the lower yet more variable degree of serotiny found within rear-edge jack pine populations compared to range-core populations (Pelletier et al., in prep.). However, it does not support the maintenance cost hypothesis invoked in Mediterranean pines, which states that older cones open by senescence as a result of intra-individual competition for water allocation with younger cone cohorts (Tapias et al., 2001; Espelta et al., 2011; Martín-Sanz et al., 2017). Unlike jack pine, these pine species are moderately serotinous and prone to open their cones without fire from desiccation during drought (Nathan et al., 1999). It is likely that the effect of cone age on serotiny might starkly differ on a physiological level in such species that are not obligate pyriscent.

Under the maintenance cost hypothesis, we expected that seed viability would decrease with cone age. Consistent with the cone opening experiment, our germination assay does not support the maintenance cost hypothesis. Indeed, germination percentages and germination velocity were similar between the rear edge and the range core. This rules out the possibility that lower stand-scale serotiny at the rear edge reflects cone opening by senescence, releasing less viable seeds (*i.e.*, necriscence; Lamont, 1991). Quite the opposite, cones from rear-edge stands hold more seeds, include less empty seeds, and disperse lighter seeds compared to cones from the boreal forest. All things considered, jack pines at the rear edge invest *ca*. 35% more in viable seed output per cone than trees in the range core. Cones releasing a greater number of viable, albeit lighter seeds should translate into higher dispersal capacity, which increases the odds of encountering suitable microhabitats for recruitment (Howe and Smallwood, 1982). This might be advantageous at the rear edge when seeds are released without fire because suitable microsites are scattered within mature stands, but not so much in the boreal forest where large wildfires expose extensive tracts of mineral seedbed, rich in resources and devoid of competition (Cayford et al., 1967; Lamont et al., 2020). A few studies have investigated seed viability over time in jack pine and reached conflicting conclusions. For instance, some authors have reported a decrease in seed viability associated with cone age in jack pine (Roe, 1963; Popovich et al., 1970; Jeffers, 1985) whereas others did not (Despland and Houle, 1997). Our results help reconcile these contradictory findings by pointing out that the relationship between seed viability and cone age is variable. On the one hand, percent germination does not vary according to cone age at the rear edge. In this area, where a fraction of the seed output is readily dispersed due to lower serotiny in young cone cohorts, cones gradually become fully serotinous while maintaining steady level of seed viability (*i.e.*, 51% germination, Fig. 13a, Table 5), which contributes to consolidate long-term regeneration capacity in case of fire. On the other hand, germination percentage decreases with cone age in the core of the range. In this fire-prone area, cones are fully serotinous from the outset and seed viability reaches its highest level at cone maturation (intercept of the linear regression model indicates 70% germination; Fig. 13b). Because the latest mature cone cohort immediately integrates the aerial seed bank, it might be advantageous for jack pine in fire-prone areas to continuously maximize seed viability of the latest cone cohort in case of wildfire, at the cost of gradually reducing seed viability in older cones, while still maintaining a low proportion of viable seeds (down to 30% germination after 20 years, Fig. 13b; see also Roe, 1963 for similar results). In fire-prone areas, a higher amount of empty seeds and the decrease in seed viability over time could represent a strategy to reduce seed predation (Perea et al., 2013). Seed foragers benefit from massive postfire seed release events because it increases their energy intake while reducing effort and time costs, incurring a higher cost of reproduction for plants (Crawley, 2000). Deceptive seeds (empty or dead) might contribute to overall jack pine fitness in fire-prone areas by increasing the proportion of viable seeds that escape post-dispersal predation.

At the rear edge of jack pine distribution, where fire occurrence is uncommon and uncertain, cones become increasingly serotinous without losing seed viability as they age. Individuals in these marginal populations can thus rely on a reproductive strategy implying continuous regeneration throughout their lives (iteroparity) instead of a single massive reproduction event (semelparity) as is generally the case for jack pine (Enright et al., 1998; Nevoux et al., 2010). This would imply a diversified bet-hedging strategy whereby individuals can optimize fitness in stochastic environments by sacrificing mean fitness to reduce temporal variance in fitness (Simons and Johnston, 1997; Olofsson et al., 2009; Childs, 2010; Simons, 2011). In the low and unpredictable fire environment of the rear edge, young cones can open without fire after reaching maturity, insuring a steady release of seeds with high dispersal capacity for interfire recruitment. While seed viability is not different on average between rear-edge and range-core cones, it is lower in younger cones from the rear edge (*ca*. 50% germination) than in younger cones from the core (up to 70% germination). Eventually, older rear-edge cones that have remained closed become as serotinous as cones from fire-prone areas, at which point they become part of the long-term aerial bank. In the unlikely event of a wildfire, these older cones will release seeds that retained their full viability (*ca*. 50% germination), which is higher than in old cones from the core (30% germination at 20 years). Jack pine individuals from rear-edge populations thus warrant at least some postfire regeneration, albeit with a lower average fitness compared to their conspecifics from the core of the range that end up with a larger aerial seed bank. Weak serotiny has previously been discussed as a bet-hedging strategy in other fire-prone species, allowing for site exploration and recruitment both interfire and postfire (Enright et al., 1998; Whelan et al., 1998; Nathan et al., 1999; Cramer and Midgley, 2009). This adaptation was invoked where interfire recruitment is possible and fire intervals are long and variable (Tonnabel et al., 2012), such as in rear-edge jack pine stands (Pelletier et al., in prep.).

Intraspecific variation in serotiny is often viewed as an adaptive solution to the infrequent and unpredictable fire regime (Lamont et al. 1991; Pausas, 2015; Lamont et al. 2020). However, confounding factors affecting dehiscence of serotinous structures might potentially obfuscate the evolutionary importance of this variation (Martín-Sanz et al., 2016). In this study, we elucidate some physiological and environmental factors modulating intraspecific variation in serotiny in jack pine from contrasted fire regimes. We inferred a hypothetical mechanism driving the bet-hedging strategy seemingly observed in marginal jack pine stands at the rear edge of the species distribution (Tonnabel et al., 2012; Pelletier et al., in prep.). The genetic basis of this dual life-history strategy remains to be investigated but our findings suggest rapid evolutionary adaptation is possible in peripheral populations of a widespread boreal conifer as a consequence of local environmental conditions that contrast with those generally found in the boreal forest. Understanding the eco-evolutionary dynamics at the edge of species distribution is fundamental to accurately assess the resilience of natural ecosystems in the face of climate change and to design efficient conservation strategies (Alberto et al., 2013; Rehm et al., 2015; Nadeau and Urban, 2019). This study adds to a growing body of literature emphasizing the need to take into account the possibility of local adaptation and intraspecific trait variability for populations eco-evolutionary responses to global change (Dawson et al., 2011; Violle et al., 2012; Franks et al., 2014; Valladares et al., 2014; Catullo et al., 2015; Des Roches et al., 2018; de Lafontaine et al., 2018; Snell-Rood et al., 2018; Benito Garzón et al., 2019).

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Table 3. Comparison of the mean opening temperature (T; °C) necessary to reach the four opening levels between cones collected in rear-edge and range-core sites along with *p*-values, *t*-values and degrees of freedom (df) for each *t*-test.

Cone opening level	$T_{\text{rear-edge}}$	$T_{\text{range-core}}$	*P*	$t_{(\text{df})}$
1	56.4	57.7	**< 0.001**	$4.67_{(261)}$
2	58.0	59.4	**< 0.001**	$5.03_{(252)}$
3	59.2	60.0	**0.001**	$3.53_{(200)}$
4	60.7	61.2	**0.047**	$2.00_{(131)}$

Table 4. ANOVA of the linear mixed model for each opening level with their respective sum of squares (SS), denominator degrees of freedom (DENdf), *F* and *p*-values and for each variable. The site was included as a random factor. Significant *p*-values are in boldface and marginally significant ones (≤ 0.1) are italicized.

Cone opening level	Fixed effect	SS	DENdf	*F*	*P*
1	Cone age***	239.7	1133	21.03	**< 0.001**
	DBH .	31.5	277	2.76	*0.098*
	Branch height	3.4	69	0.29	0.589
	Tree age	10.7	275	0.94	0.333
2	Cone age***	232.9	1112	20.94	**< 0.001**
	DBH**	91.8	283	8.25	**0.004**
	Branch height	3.1	67	0.27	0.602
	Tree age	1.6	269	0.14	0.706
3	Cone age***	170.7	998	16.78	**< 0.001**
	DBH**	107.9	402	10.60	**0.001**
	Branch height	0.26	103	0.03	0.873
	Tree age	13.4	393	1.32	0.251
4	Cone age .	19.5	692	2.66	*0.103*
	DBH*	41.5	318	5.67	**0.018**
	Branch height	0.02	55	0.003	0.959
	Tree age	5.6	181	0.76	0.384

Table 5. Comparison of the mean number of seeds per cone, mean percentage of filled seed per cone, mean weight per seed (g), number of germinated seeds, germination percentage and germination velocity between rear-edge and range-core sites, along with *p*-values, *t*-values and degrees of freedom (df) for each *t*-test.

Variable	Rear edge	Range core	*P*	$t_{(\mathrm{df})}$
Mean *n* of seeds/cone***	23.56	18.62	**< 0.001**	$5.10_{(286)}$
Mean % of filled seeds/cone***	55.10	44.94	**< 0.001**	$6.10_{(267)}$
Mean weight/seed***	0.0024	0.0028	**< 0.001**	$5.17_{(317)}$
n germinated seeds	8.45	8.33	0.806	$0.25_{(239)}$
Germination %	50.77	52.96	0.370	$0.70_{(243)}$
Germination velocity	1.13	1.14	0.845	$0.20_{(238)}$

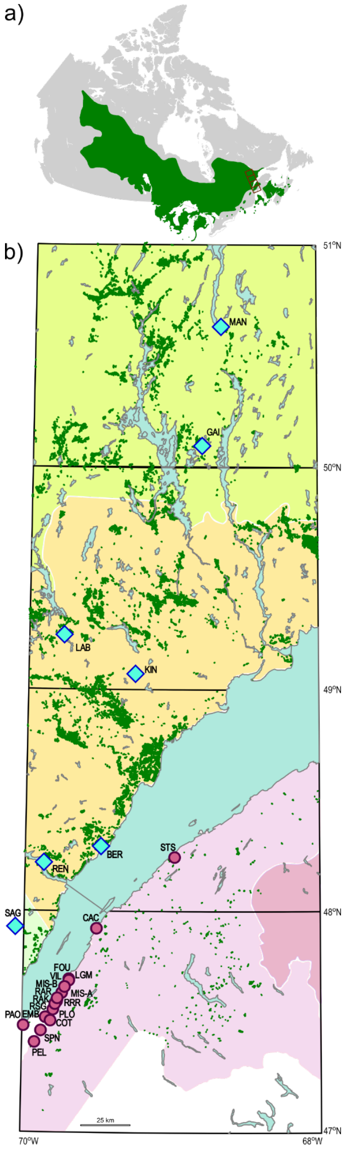

Figure 8. Study sites and biogeographic setting of jack pine (*Pinus banksiana*). a) Transcontinental range of jack pine and sampling area in eastern Québec. b) Rear-edge and range-core sites are represented by purple dots and blue diamonds, respectively. Green polygons indicate jack pine stands >4 ha according to Québec's ecoforest data map sheets 21N, 22C, 22F and 22K from south to north (MFFP, 2020). Background colors represent different fire regime units (FRUs; Erni et al., 2020), where purple is FRU 4 (0.03 fire·Mha^{-1}·yr^{-1}), yellow is FRU 11 (0.33 fire·Mha^{-1}·yr^{-1}), and light green is FRU 10 (0.64 fire·Mha^{-1}·yr^{-1}).

Figure 9. Levels of jack pine (*Pinus banksiana*) cone opening during the heating experiment: 1 = 1-25% of the scales are open, 2 = 26-50% of the scales are open, 3 = 51-75% of the scales are open, and 4 = 76-100% of the scales are open.

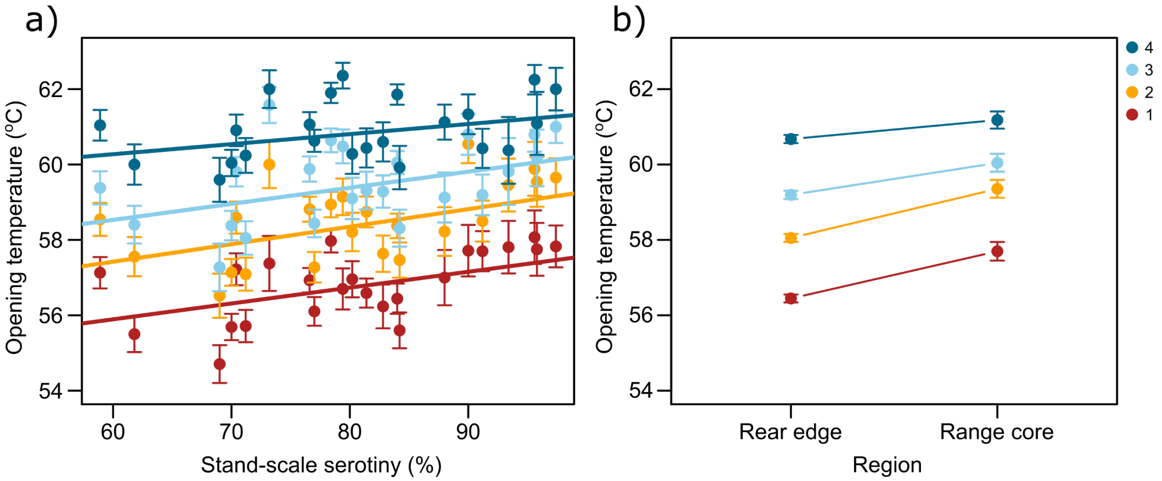

Figure 10. Cone opening temperature at the four opening levels as a function of stand-scale serotiny (a) and comparison of mean opening temperature at the four opening levels between rear-edge and range-core jack pine (*Pinus banksiana*) stands (b). Solid lines indicate significant statistical tests (linear regressions or *t*-tests), means ± SE are shown. Cone opening levels 1, 2, 3, and 4 are shown in red, yellow, light blue, and dark blue, respectively.

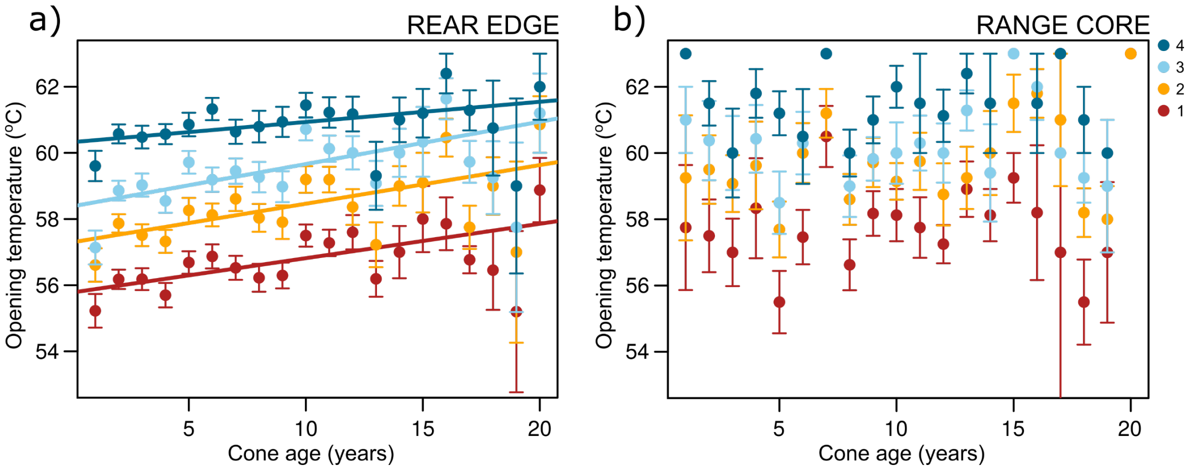

Figure 11. Cone opening temperature at the four opening levels as a function of cone age at the rear edge (a) and the core (b) of jack pine (*Pinus banksiana*) distribution. Solid lines indicate significant linear regression models at the rear edge, no significant linear regression model was found in the core of the range, means ± SE are shown. Cone opening levels 1, 2, 3, and 4 are shown in red, yellow, light blue, and dark blue, respectively.

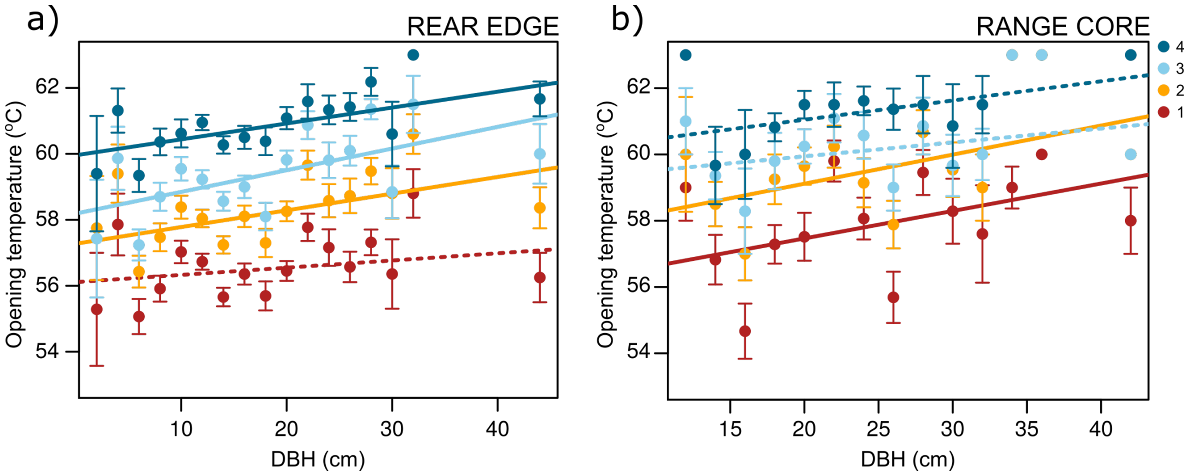

Figure 12. Cone opening temperature at the four opening levels as a function of diameter at breast height (DBH) at the rear edge (a) and the core (b) of jack pine (*Pinus banksiana*) distribution. Solid lines are significant linear regression models, broken lines are not. Means ± SE of 2-cm DBH classes are shown instead of a scatterplot of raw data to simplify visualization. Cone opening levels 1, 2, 3, and 4 are shown in red, yellow, light blue, and dark blue, respectively.

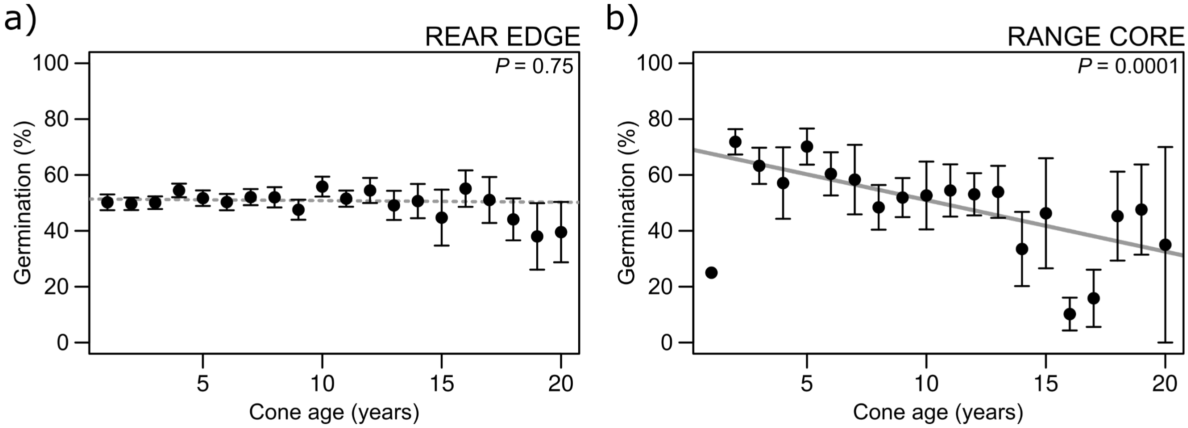

Figure 13. Germination percentage as a function of cone age at the rear edge (a) and the core (b) of jack pine (*Pinus banksiana*) distribution. The linear regression model is significant in the range core (solid grey line) but not at the rear edge (broken grey line), means ± SE are shown.

2.3 SUPPLEMENTARY INFORMATION

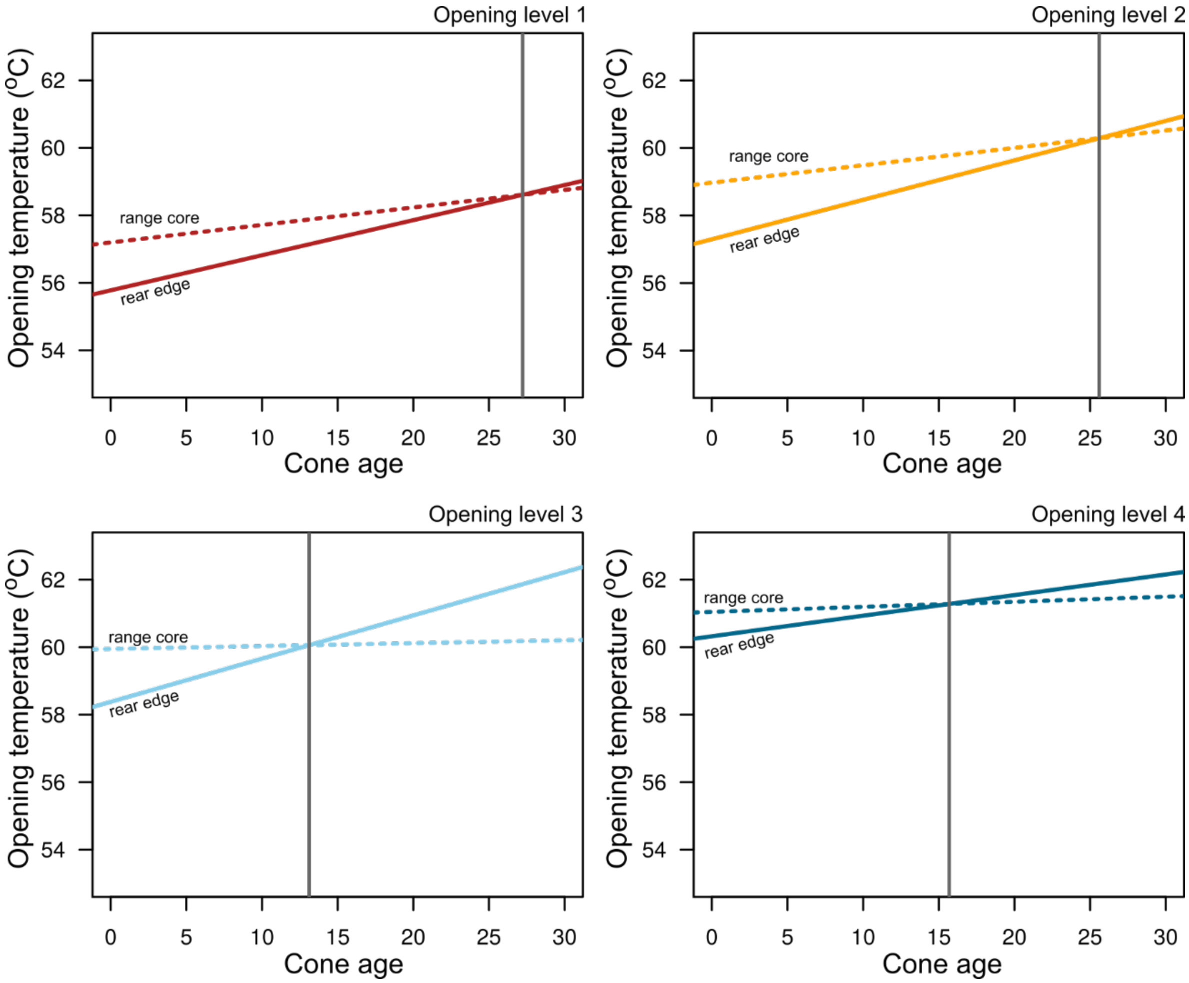

Figure S2. For each cone opening level, the crossing point between intersecting regression lines of the rear edge (solid line) and the range core (broken line) models provides an estimate of the age at which cones from rear-edge jack pine (*Pinus banksiana*) stands reach an opening temperature similar to those from the core of the range.

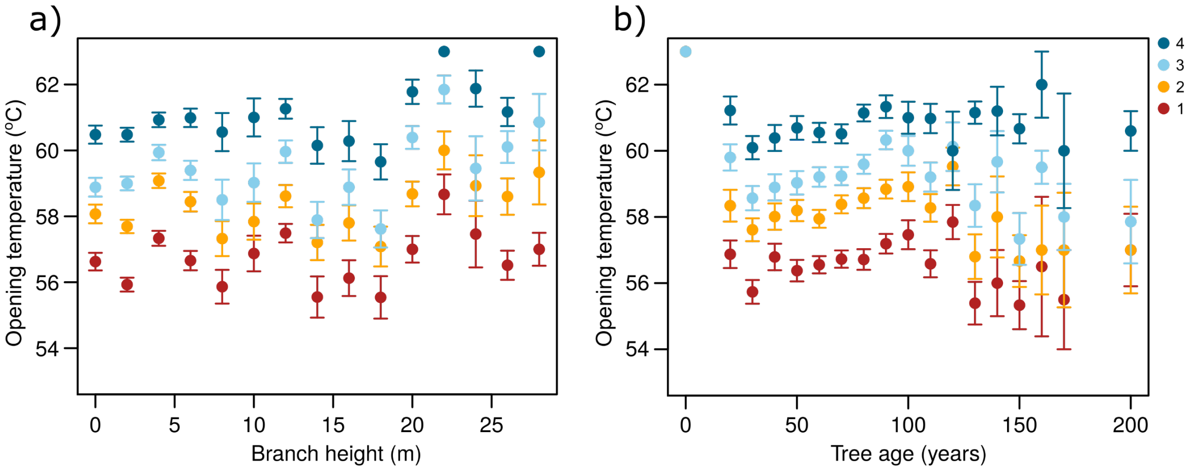

Figure S3. Cone opening temperature at the four opening levels as a function of branch height (a) and tree age (b) in jack pine (*Pinus banksiana*). No significant linear regression model was found. Means ± SE of 2-cm branch height classes or 10-years tree age classes are shown instead of scatterplots of raw data to simplify visualization. Cone opening levels 1, 2, 3, and 4 are shown in red, yellow, light blue, and dark blue, respectively.

CONCLUSION GÉNÉRALE

Cette étude s'inscrit dans le cadre de travaux de recherche visant à déterminer les réponses des populations d'espèces végétales face aux altérations environnementales causées par les changements globaux. Ces réponses pourraient s'avérer indispensables pour la résilience de certaines espèces, notamment en permettant d'éviter l'extirpation de leurs populations marginales à la limite de leur enveloppe environnementale et donc en limitant la perte d'une partie importante de leur patrimoine génétique. Plus spécifiquement, cette étude visait i) à déterminer si la variabilité intraspécifique du sérotinisme permet la persistance des populations marginales de pin gris à la limite sud de l'aire de répartition de l'espèce malgré le régime de feu peu propice à l'espèce, en plus ii) d'approfondir nos connaissances sur les facteurs écophysiologiques affectant la variabilité du sérotinisme. Les peuplements étudiés sont répartis à travers deux régions soumises à des régimes de feux contrastés. Les feux de forêt naturels sont rares et ainsi imprévisibles à la marge sud, alors que la fréquence des feux létaux est élevée et plus régulière dans les peuplements boréaux au cœur de l'aire de répartition de l'espèce. Cette section du mémoire présente d'abord les principaux résultats et la portée de l'étude. Par la suite, les limites de l'étude et les perspectives de recherche futures sont exposées.

PRINCIPAUX RÉSULTATS ET PORTÉE DE L'ÉTUDE

Les résultats du chapitre 1 indiquent un degré de sérotinisme réduit et plus variable dans les populations à la marge sud de l'aire de répartition du pin gris, là où les feux sont rares et par le fait même, peu prédictibles. Quoique la diminution du sérotinisme a déjà été observée chez le pin gris dans des régions marquées par des régimes de feux peu fréquents ou peu sévères (Gauthier, Bergeron et Simon, 1996; Radeloff *et al.* 2004), la variation intra-populationnelle de ce trait demeure peu abordée (Pausas, 2015; Romero et Ganteaume, 2020). Pourtant, une plus grande variabilité phénotypique intra-populationnelle de divers traits, due au stress environnemental en marge de l'aire de répartition, a été rapportée chez plusieurs espèces (Volis *et al*., 1998; Valladares *et al.*, 2014; Lázaro-Nogal *et al*., 2015). Nos résultats démontrent que la grande variabilité du sérotinisme, un trait écophysiologique hautement héritable chez les pins (Teich, 1970; Perry et Lotan, 1979; Hernández-Serrano *et al*., 2014; Castellanos *et al*., 2015), permet la libération de graines et l'établissement de plantules de façon continue dans les peuplements marginaux. Cet effet sur la trajectoire démographique est visible dans les modèles quadratiques décrivant la structure de tailles à chacun des sites. En effet, nos résultats permettent de proposer un seuil de sérotinisme sous lequel la persistance de peuplements de pin gris est possible malgré l'absence de feu. Lorsque le sérotinisme diminue sous un seuil de 85% dans les peuplements, on observe un déplacement d'une structure de taille unimodale, indiquant un peuplement vieillissant formé d'une cohorte équienne provenant du dernier feu, vers une structure de taille en « J-inversé », témoignant plutôt d'un peuplement inéquienne, à l'équilibre, avec une régénération continue. Les sites marginaux étant généralement plus vieux que les sites au centre de l'aire de répartition, cette différence indique un recrutement stable au sein de peuplements périphériques matures établis depuis plus longtemps que les peuplements boréaux. L'abondance de plantules présentes dans les peuplements marginaux est inversement corrélée avec le degré de sérotinisme et atteint zéro lorsque le degré de sérotinisme est à son maximum au cœur de l'aire de répartition. Ces résultats suggèrent que la variabilité intraspécifique du sérotinisme pourrait refléter l'adaptation locale à une occurrence de feux rare et incertaine dans les populations marginales, permettant leur maintien à long terme en dehors de l'aire de répartition continue de l'espèce. Un sérotinisme plus faible et plus variable à la marge sud devrait ainsi augmenter la résilience et la résistance des populations de pins gris face aux futures perturbations du régime de feux local causé par les changements globaux (Young *et al.*, 2017; Hart *et al.*, 2018).

Le chapitre 2 a permis d'explorer le rôle potentiel de divers facteurs physiologiques et environnementaux sur la variation intraspécifique du sérotinisme. S'ils sont indépendants du régime de feux, de tels facteurs confondants pourraient réduire l'importance évolutive de la variation de ce trait. Cette étude a permis de déterminer l'effet de l'âge des cônes (ouverture par sénescence), la hauteur des branches portant les cônes (ouverture grâce à la radiation thermique du sol), l'âge et la taille des individus (ouverture due à l'immaturité) sur la température d'ouverture des cônes. Les cônes échantillonnés dans des sites marginaux et boréaux ont été chauffés à l'étuve en augmentant graduellement la température, ce qui a permis de comparer l'énergie thermique accumulée nécessaire à leur ouverture (*température d'ouverture*) selon leur provenance et en fonction des divers facteurs écophysiologiques considérés. Nos résultats indiquent que la température d'ouverture des cônes sérotineux au laboratoire est effectivement associée au degré de sérotinisme estimé sur le terrain, dans les peuplements de provenance. En effet, les cônes provenant de sites où le degré de sérotinisime est plus élevé requièrent une plus grande exposition à la chaleur pour déclencher leur ouverture à l'étuve. L'impact des facteurs évalués sur la température d'ouverture en laboratoire reflète donc adéquatement le potentiel d'ouverture des cônes sur le terrain.

Les résultats du chapitre 2 indiquent une stratégie de reproduction différente entre les sites marginaux et les sites au centre de l'aire de répartition de l'espèce. De façon générale, les cônes à la marge sud s'ouvrent à des températures inférieures et contiennent plus de graines pleines, quoique moins lourdes, que les cônes au centre de l'aire de répartition. Ce type de production de graines dans les populations de la marge sud pourrait favoriser la recherche de microsites favorables à travers les peuplements matures inéquiennes décrits au chapitre 1. La température d'ouverture augmente avec l'âge des cônes dans les populations marginales, alors que la viabilité de leurs graines reste constante. Une viabilité stable avec l’âge des cônes a également été rapportée par l’étude de Despland et Houle (1997) portant sur l’allocation de ressources chez des populations marginales de pin gris au nord de son aire de répartition. Ces résultats suggèrent que le degré de sérotinisme moindre observé à la marge sud n’est pas dû à l’ouverture des plus vieux cônes par sénescence, tel qu’il a été proposé chez le pin d’Alep (Tapias *et al.*, 2001; Espelta *et al.*, 2011; Martín-Sanz *et al.,* 2017). Cette stratégie leur permet plutôt de porter à la fois des cônes pouvant potentiellement s’ouvrir plus facilement sans feu (les cônes plus jeunes), en plus de contribuer à l’établissement d’une banque aérienne de graines viables en cas de feux (les cônes plus âgés). Nos résultats indiquent que la température d’ouverture des cônes des populations marginales atteint éventuellement celle des cônes au centre de la forêt boréale entre 13 et 27 ans après la maturité du cône. En forêt boréale, les individus portent des cônes qui s’ouvrent à une température plus élevée et constante, dispersant moins de graines plus lourdes, qui perdent leur viabilité avec l’âge. En effet, le pourcentage de germination des graines des cônes au centre de l’aire de répartition est négativement associé avec leur âge, un résultat qui corrobore ceux de Gauthier, Bergeron et Simon (1993). Les feux létaux étant fréquents en forêt boréale, le renouvellement du peuplement après feu peut être assuré par les dernières cohortes de cônes très sérotineux. Nos résultats suggèrent une plus grande allocation d’énergie vers le caractère sérotineux des cônes plutôt que vers la viabilité à long terme de leurs graines.

Outre l’effet de l’âge sur la température d’ouverture, les résultats de l’étude indiquent que le DHP de l’arbre est positivement relié à la température d’ouverture des cônes du pin gris et ce, sur l’ensemble des sites étudiés. Cette observation est en accord avec les résultats de l’étude de Gauthier, Bergeron et Simon (1993) qui indiquent que le délai d’apparition du sérotinisme chez le pin gris permet la densification du peuplement après un feu. Puisque l’âge des arbres ne semble pas avoir d’effet sur la température d’ouverture des cônes, nos résultats suggèrent que ce délai n’est pas lié à la juvénilité des individus tel que proposé par Gauthier, Bergeron et Simon (1993), mais plutôt à la disponibilité en ressources. Néanmoins, la production de cônes pouvant s’ouvrir sans feu chez les individus de petits DHP ne varie pas entre la marge et le cœur de l'aire de répartition. Cela semble donc refléter une stratégie générale à l'espèce qui permet la densification du peuplement dans les années suivant un feu. Les plantules ayant plus de difficulté à s'établir lorsqu'elles entrent en compétition avec des arbres matures, l'ouverture des cônes à une température plus élevée et l'accumulation d'une banque de graines deviennent donc avantageux dans un peuplement dense plus propice aux feux (Crossley, 1956; Lamont *et al.*, 1991). Finalement, les résultats du chapitre 2 ont permis d'élucider le rôle de la position des cônes dans l'arbre sur leur température d'ouverture. Les sites marginaux étant localisés majoritairement sur des affleurements rocheux, le degré de sérotinisme réduit dans la région aurait pu s'expliquer par une accumulation d'énergie thermique accrue due à la chaleur émise par le sol. Or, la hauteur des cônes dans l'arbre n'a aucun effet sur leur température d'ouverture en laboratoire. Il ne semble donc pas y avoir d'accumulation d'énergie thermique dans les cônes de façon à permettre leur ouverture après une plus courte exposition à la chaleur selon leur accumulation d'énergie thermique en milieu naturel.

Les résultats des deux chapitres du mémoire ont permis d'identifier certains facteurs affectant l'ouverture des cônes de pin gris et donc potentiellement responsables de la variabilité du sérotinisme qui permet la persistance locale des peuplements à la marge sud de sa répartition. Ces résultats suggèrent une stratégie de minimisation des risques (*bet-hedging*) par la diversification de la capacité d'ouverture des cônes à la marge sud, là où l'occurrence de feux de forêt est peu fréquente et incertaine. En portant à la fois des cônes jeunes pouvant s'ouvrir plus facilement sans feu et des cônes âgés complètement sérotineux qui permettent l'accumulation d'une banque aérienne de graines viables, les pins gris à la marge sud assurent leur régénération avec ou sans feu et ainsi leur persistance locale peu importe le scénario. Une stratégie de minimisation des risques permettant le recrutement avec et sans feu a également été proposée chez d'autres espèces de pins présentant un degré de sérotinisme variable (Enright *et al.,* 1998; Whelan *et al.*, 1998; Nathan *et al.*, 1999; Cramer et Midgley, 2009). Bien que des études évaluant plus directement l'effet de la variabilité du sérotinisme sur la valeur adaptative (*fitness*) des individus soient requises afin de tester rigoureusement l'hypothèse de la stratégie de minimisation des risques à la marge sud, la présente étude indique que la variabilité du sérotinisme des cônes permet le maintien des populations malgré un régime de feux sous-optimal dans la région. Toutefois, la possibilité de régénération des peuplements de pin gris à la limite sud semble dépendre non seulement du sérotinisme réduit, mais également de la disponibilité de microsites favorables. En effet, peu de régénération a été observée sur les sites à faible degré de sérotinisime situés sur des sols mésiques où d'autres espèces entrent en compétition avec le pin gris (Gauthier, Gagnon et Bergeron, 1993). Le recrutement de plantules suivant l'ouverture des cônes sans feu semble donc être possible lorsque les sites ne permettent pas la croissance d'espèces compétitrices, tels que sur les affleurements rocheux. Ainsi, le maintien des populations marginales demeure incertain malgré leur adaptation aux régimes de feux locaux, due à l'utilisation anthropique du territoire et la perte des sites propices à leur régénération.

L'approfondissement de nos connaissances sur un trait affectant directement la reproduction du pin gris devrait guider les efforts de conservation de l'espèce dans le futur. Les semences provenant de sites caractérisés par un degré de sérotinisme faible et variable devraient être conservées afin de promouvoir la diversité génétique intraspécifique. Ainsi, en présumant que la variabilité du sérotinisme a une forte base génétique chez le pin gris (Teich, 1970; Perry et Lotan, 1979; Hernández-Serrano *et al.*, 2014; Castellanos *et al.*, 2015), cette diversité génétique devrait permettre le maintien des peuplements dans un régime de feux peu fréquents et assurer une meilleure résilience de l'espèce face aux changements globaux. Plus généralement, les résultats de cette étude suggèrent que les adaptations locales dans les populations formant la marge chaude des aires de répartition pourraient contribuer au maintien des espèces face à un environnement en changement. La vitesse de migration de plusieurs espèces n'étant pas assez élevée pour suivre la vélocité des changements climatiques, la persistance des populations aux limites des aires de répartition contribuera à éviter leur remplacement par des espèces migrant vers le nord et permettra la conservation de leur patrimoine génétique. Le grand potentiel adaptatif des populations marginales, en plus de la menace du réchauffement dans ces populations déjà situées à leur limite climatique, devrait leur conférer une importance particulière en termes de conservation afin de promouvoir la résilience des espèces (Lesica et Allendorf, 1995; Hampe et Petit, 2005; Rehm *et al.*, 2015; Snell-Rood *et al.*, 2018). Par exemple, les traits distinctifs observés au sein de ces peuplements peuvent s'avérer utiles dans un contexte de migration assistée. Cette méthode de conservation consiste à semer des individus de provenance particulière à travers ou en dehors de l'aire de répartition d'une espèce afin de promouvoir sa diversité génétique et sa dispersion en dépit des changements climatiques (Winder, Nelson et Beardmore, 2011).

LIMITES DE L'ÉTUDE ET PERSPECTIVES DE RECHERCHE FUTURES

Ce mémoire est une contribution importante pour l'avancement des connaissances concernant la variabilité du sérotinisme chez le pin gris. En effet, outre l'étude de Gauthier, Bergeron et Simon (1993), aucune autre étude ne s'était préalablement attardée aux facteurs physiologiques et environnementaux reliés aux variations du degré de sérotinisme chez cette espèce. D'ailleurs, aucune étude n'avait étudié les cônes du pin gris en laboratoire, ce qui permet de mieux distinguer l'effet de chacun des facteurs. Cette étude a permis d'identifier le degré de sérotinisme permettant la persistance des populations de pins gris en l'absence de feu. De plus, elle a démontré que les populations situées à la marge sud de l'aire de répartition de l'espèce sont stables et peuvent se régénérer sans feu, indiquant que leur extirpation due aux conditions environnementales locales non favorables à cette espèce n'est pas imminente.

En dépit de ces points forts, cette étude comporte quelques limites importantes à souligner. D'abord, l'impact de facteurs pouvant affecter l'ouverture des cônes a été étudié en laboratoire sur des cônes fermés récoltés sur le terrain. Bien qu'il aurait été intéressant de s'assurer que les mêmes facteurs aient un impact sur les cônes ouverts préalablement à cette étude, ceux-ci n’ont pas pu être pris en considération. Or, à plus long terme, un suivi de l’ouverture des cônes *in situ* sur plusieurs années permettrait d’avoir un portait du degré de sérotinisme plus global et de sa variation dans le temps, ainsi qu’une meilleure compréhension des éléments déclenchant l’ouverture des cônes. Ensuite, l’impact du type de sol sur la variabilité du degré de sérotinisme n’a pas pu être pris en compte. Bien que les sites au cœur de l’aire de répartition de l’espèce se retrouvent généralement sur des sols sableux, qui sont pauvres en nutriments et secs comme le sont les sols rocheux des sites à la marge sud, il n’est pas impossible que cette différence au niveau des caractéristiques du sol affecte la production de cônes et leur couche de résine protectrice. Cependant, il est difficile d’éliminer l’effet de cette variable, puisqu’une grande majorité des peuplements à la limite sud se retrouvent sur des affleurements rocheux, alors que la majorité des peuplements en forêt boréale se retrouvent en sol sableux. Le rôle de l’environnement sur la variabilité du sérotinisme devrait donc être évalué dans le futur en étudiant le phénotype des pins gris provenant de divers sites plantés ensemble en jardins communs.

En outre, des études associant la variabilité des phénotypes aux génotypes des populations demeurent nécessaires afin d’étudier l’adaptation locale proposée par cette étude. Les efforts de recherche futurs devraient porter sur l’identification de régions génomiques soumises à une pression de sélection liée au régime de feux qui pourraient être responsables de la variabilité du sérotinisme. Si la variabilité du sérotinisme est effectivement spécifique à l’environnement local, les régions génomiques identifiées seraient associées à un degré de sérotinisme faible et/ou plus variable et à un cycle de feu plus long. Finalement, des tests de jardins communs permettraient de déterminer le poids de la génétique et de la plasticité phénotypique sur la variabilité du sérotinisme chez le pin gris. Si la variabilité de ce trait est simplement due aux variations du génome et non à la plasticité phénotypique, on devrait observer des cônes plus faiblement sérotineux chez les individus provenant de la marge sud que chez les individus provenant du biome boréal, et ce, peu importe l’emplacement géographique du jardin commun.

Qu’elle soit de nature plastique ou adaptative, ce mémoire met de l’avant l’importance de conserver la variabilité phénotypique intraspécifique présente au sein des populations périphériques situées à la marche chaude de leur aire de répartition. Ces populations sont les plus directement menacées par une utilisation anthropique croissante du territoire, en plus des conditions environnementales locales à la limite de leur enveloppe de tolérance bioclimatique. Or, l’ensemble de ce mémoire souligne l’importance de leur variabilité intraspécifique locale pour la résilience des espèces largement distribuées face aux changements globaux.

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